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ADULT AND JUVENILE FLASHES IN THE TERRESTRIAL SNAIL *DYAKIA STRIATA*

Jonathan Copeland[1] & Maryellen Maneri Daston[2]

ABSTRACT

Photomultiplier recordings were used to categorize the flash types produced by caged adults and juveniles of the terrestrial bioluminescent snail *Dyakia striata*. Simple and modulated flashes were produced by both adult and juvenile snails. Flash duration and interflash interval were measured in both adults and juveniles. Adult flashes were less bright than juvenile flashes, and adult flashes were usually simple (non-modulated) flashes. Interflash intervals were usually longer for adult snails than juveniles. These findings are interpreted in terms of the neural control of this unusual effector organ.

Key words: bioluminescence, *Dyakia*, behavior.

INTRODUCTION

Dyakia striata (Ariophantidae), found in Singapore and Malaysia (Parmentier & Barnes, 1975) is the only terrestrial snail known to be luminescent. It produces light from a luminescent organ, called the organ of Haneda (reviewed in Haneda, 1981), located within the head-foot. Discrete flashes of light, sometimes single-peaked and sometimes multiple-peaked, are produced (Haneda, 1981; Parmentier & Barnes, 1975). Occasionally, glows occur (Haneda, 1981).

Luminescence was once thought to occur only in juvenile snails and then disappear (Haneda, 1981; Martoja & Bassot, 1970; Parmentier & Barnes, 1975). However, more recent studies have shown that it can sometimes persist to adulthood (Copeland & Maneri, 1984; Counsilman et al., 1987; Copeland & Daston, 1989).

Because previous workers had studied juvenile luminescence only (Haneda, 1981; Parmentier & Barnes, 1975), here, the flashes of adult and juvenile snails are compared. Differences in bioluminescence between young and adults have been found in other bioluminescent systems, and these differences have often been instructive in terms of neural and biochemical control (Herring, 1978).

MATERIALS AND METHODS

Snail flashes were recorded using a tripod-mounted photomultiplier tube (RCA 6655-A) that modulated the carrier frequency of a voltage controlled oscillator (A. R. Vetter, Inc.). In this way, the snail flashes, which were relatively slow, were sensed by the photomultiplier and this signal then modulated the high frequency oscillator. The high frequency oscillator signal increased and decreased in parallel with changes in the light intensity. This high frequency signal was stored on a portable A.C. tape recorder (SONY 3600). Later, the tape recorded signals were played back through a demodulator unit and then into a chart recorder (Grass Model 79B). The second tape recorder channel was used to record voice commentary simultaneously from the observer.

Flashes were recorded from snails placed either in a 10 gallon glass aquarium (adults) or a 50 mm diameter beaker (juveniles). Flashes from adult snails were recorded using a tripod-mounted photomultiplier which could be repositioned by the observer who simultaneously noted the occurrence and type (simple, modulated) of the flash. Adult snails moved considerably less than juvenile snails (Copeland & Daston, 1989). Flashes from juvenile snails were recorded with no observer present. These snails were placed in a beaker that faced the photocell. Because the juvenile snails moved a good deal, aluminum foil was wrapped around most of the beaker to ensure that flashes would be reflected toward the photomultiplier tube regardless of the orientation of the snail.

A snail would usually retract into the shell completely when picked up and transferred to

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the aquarium or beaker. Therefore, the first ten minutes of data from each one-hour recording session were ignored to allow time for the snail to recover from this disturbance. Most measurements with the photomultiplier were made in complete darkness. However, several observations of the movements of the snail's body while it flashed were made which used dim red illumination to silhouette the snail's body. Copeland (1988) showed that there was no response to red light when neural recordings were made from the optic nerve of *D. striata.*

All measurements were made from the chart recorder traces. Flash duration (from baseline to baseline) was measured, as was interflash interval (interval from the beginning of one flash to the beginning of the subsequent flash). Also, the number of peaks in each flash were counted. A peak was considered to have occurred when the flash decreased rapidly in amplitude (but not completely) to baseline.

Adult snails were collected in Singapore and tested at 27–29°C. Juvenile snails were raised from eggs hatched in the lab. They were kept in 5 cm × 30 cm plastic cages with sterilized potting soil on the bottom. Cages were misted daily. Juvenile snails were fed meat and vegetable Gerber's baby food (Mason & Copeland, 1988) which was changed every other day. A 12:12 light:dark cycle and 28°C were maintained. Juvenile recordings were made at 28°C.

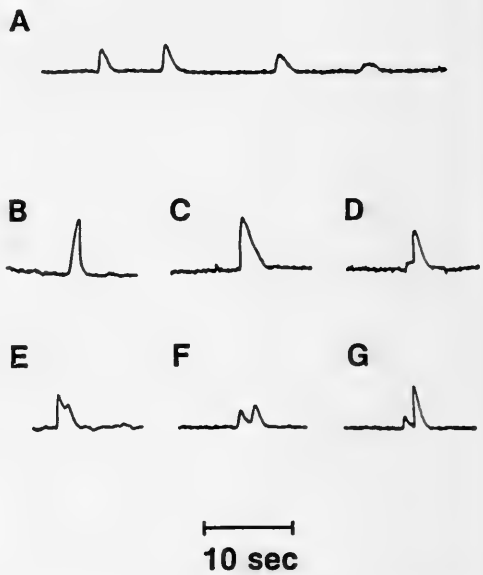

FIG. 1. Flashes recorded from freely moving adult snails with a tripod-mounted photomultiplier tube. The records read from left to right, with time in the x-axis and flash intensity in the y-axis. Simple and modulated flashes are shown. A–C, simple flashes; D–G, modulated flashes; A (first three) and C, asymmetrical flashes (quenched slowly); A (fourth flash) appeared as dim weak glow (not a flash).

RESULTS

Flash Types and Patterns

Adult Flash Types: The type of luminescence spontaneously produced by adult *D. striata* ranges from a discrete bright flash (Fig. 1A, first three flashes) to a very weak low intensity glow-like flash (Fig. 1A, 4th flash). Time from baseline until flash peak was variable but less than one second.

The flashes of seven adult snails were viewed. They flashed continuously (no interflash interval greater then 60 sec) for 19–45 minutes within the total one hour recording period (first 10 minutes ignored). These flashes, when viewed directly or monitored indirectly *via* the photomultiplier, were categorized as simple flashes (with a single peak), which were symmetrical (Fig. 1B, symmetrical rise and fall of flash) or asymmetrical (Fig. 1C), and modulated flashes (with more than one peak). In modulated flashes, an intensity modulation produced a pulsation of light (Fig. 1D–G). Sometimes, the pulsation could be resolved into two discrete flashes (Fig. 1G). Flashes with three or four peaks occurred, but these were rare (< 1%) in adult snails.

Both simple and modulated flashes in adult *D. striata* last from 0.5 to 6 seconds (Fig. 2A), although there was a tendency for simple flashes to be shorter than modulated flashes. This difference in flash duration was significant in snails 2 and 3 but not snail 1 in Figure 2A (t-test, $p < 0.05$).

All adult snails showed both simple and modulated flashes, although the ratio of simple:modulated flashes varied from about 1:1 to 2:1 in the seven snails viewed.

Usually, several flashes of one kind would be followed by several flashes of the other kind, but the two types of flashes (simple or modulated) could be interspersed. No obvious correlation was seen between snail behavior and flash type.

The interflash interval for the animals illus-

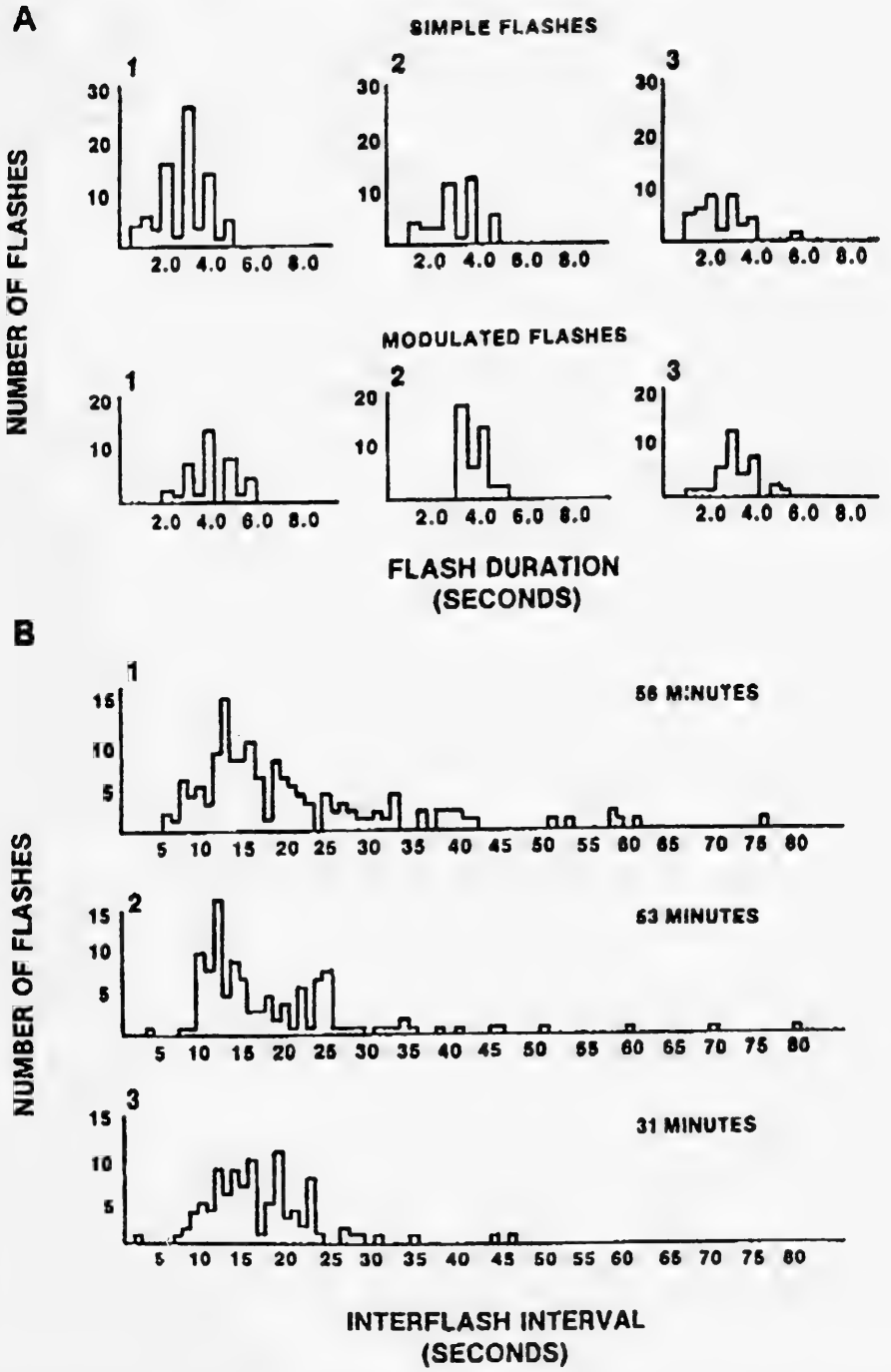

FIG. 2. Flash duration for simple (top row) and modulated (bottom row) flashes produced by three different adult snails (animals #1–3) over sample periods of 56 (left column, top), 53 (middle column, top), and 31 (right column, top) minutes respectively. B. Interflash intervals from the same snails during the same one hour test sessions as in A. All data measured from photomultiplier records.

trated in Figure 2A is shown in Figure 2B. The interflash interval for these individuals varied between 2–80 seconds, with a mean interflash interval of 18.0 ± 1.2 S.D. sec.

The adult flash was yellow-green in color and weak in intensity. Indeed, some dark adaptation was necessary before an observer could easily see the flash. (When compared by eye to the flash of the firefly *Pteroptyx mallacae,* the flash of *D. striata* was considerably weaker in intensity.) However, during the most intense flashes, the entire anterior part of the snail was illuminated.

Because any movement of the head-foot, which contains the luminescent organ of *D. striata,* could create the illusion of multiple peaks when the luminescent organ was viewed by a stationary photomultiplier, on several occasions a flashing adult *D. striata* was viewed using weak red backlighting to produce a silhouette. When modulated flashes occurred, the head-foot was continuously extended against the substrate. Thus, the modulated flashes could not have occurred because a continuously glowing luminescent organ was moved in and out of the shell like a shutter, something that has been found with other luminescent organs in other animals (Herring, 1978).

Juvenile Flash Types: Juvenile flash types in *D. striata* were similar to adult flash types: simple and modulated flashes occurred, as did glows. As in the adult, the color of the flash was yellow-green, but the flash was considerably brighter to the eye. Little dark adaptation was necessary to view juvenile snail flashes, and many of the flashes appeared to the eye to contain pulsations. In fact, the juvenile flash could be so bright and had such a range of intensities when compared to the adult flash that it was difficult to obtain complete records from all the juvenile snails tested (N = 10) because many of the flashes from some snails saturated the photomultiplier tube, thus preventing multiple flashes from being recorded.

The results from two juvenile snails whose flashes were within the range of the photomultiplier for the entire test period are shown in Figure 3. They flashed continuously (no interflash interval greater than 60 seconds) for 18 to 30 minutes. Simple flashes lasted 0.5–2.5 seconds and modulated flashes lasted 0.5–5.5 seconds (Fig. 3). The difference between simple and modulated flashes was significant (t-test, $p < 0.02$). The ratio of simple: modulated flashes was less than 1:2 for one snail and 1:7 for the other snail. Many modulated flashes had three peaks or more (12–41%).

The interflash interval from the two juvenile snails shown in Figure 3B varied between 2 and 50 seconds. Mean interflash interval (N = 2) was 9.8 ± 0.5 S.D. sec.

DISCUSSION

Adult *D. striata* produce weak intensity flashes that are usually simple flashes. The average interflash interval is about 18 seconds (Fig. 2). Adult simple flashes are usually shorter in duration than adult modulated flashes (Fig. 2). Juvenile flashes are much brighter to the eye and many appear to twinkle with multiple peaks. Most juvenile flashes are modulated flashes and have an average interflash interval of about 10 seconds (Fig. 3). Juvenile simple flashes are also shorter in duration than juvenile modulated flashes.

These findings extend the observations of Haneda (1981) and Parmentier & Barnes (1975), who noted the presence of simple flashes and flashes with multiple peaks (modulated flashes) in juvenile *D. striata* but did not quantify these flashes and did not compare the flashes of juveniles and adults.

Because it is now known that adult flashes occur in *D. striata* and that adult and juvenile flashes differ, it might be instructive to look at flash similarities and differences from the perspective of neural and biochemical control of flashing.

Virtually nothing is known about the neural control of bioluminescence in *D. striata.* No reflex-evoked luminescence (flashes, glows, scintillations) occur in response to tactile stimulation (Parmentier & Barnes, 1975) as it does in many bioluminescent organisms (Herring, 1978), but flashing can occur as fast as 0.5 Hz (Parmentier & Barnes, 1975). However, photic stimuli, either from a flashing conspecific snail or an electric torch, can change the flash rate of a flashing snail (Copeland & Daston, 1989). Additionally, ultrastructural evidence exists for the presence of nerve endings in the luminescence organ (Maneri, 1985). These facts, plus the rapid rise time of the flash, suggest that flashing in *D. striata* is under nervous control.

Even less is known about biochemical control of bioluminescence in *D. striata.* Haneda (1963), using dried and crushed bodies of

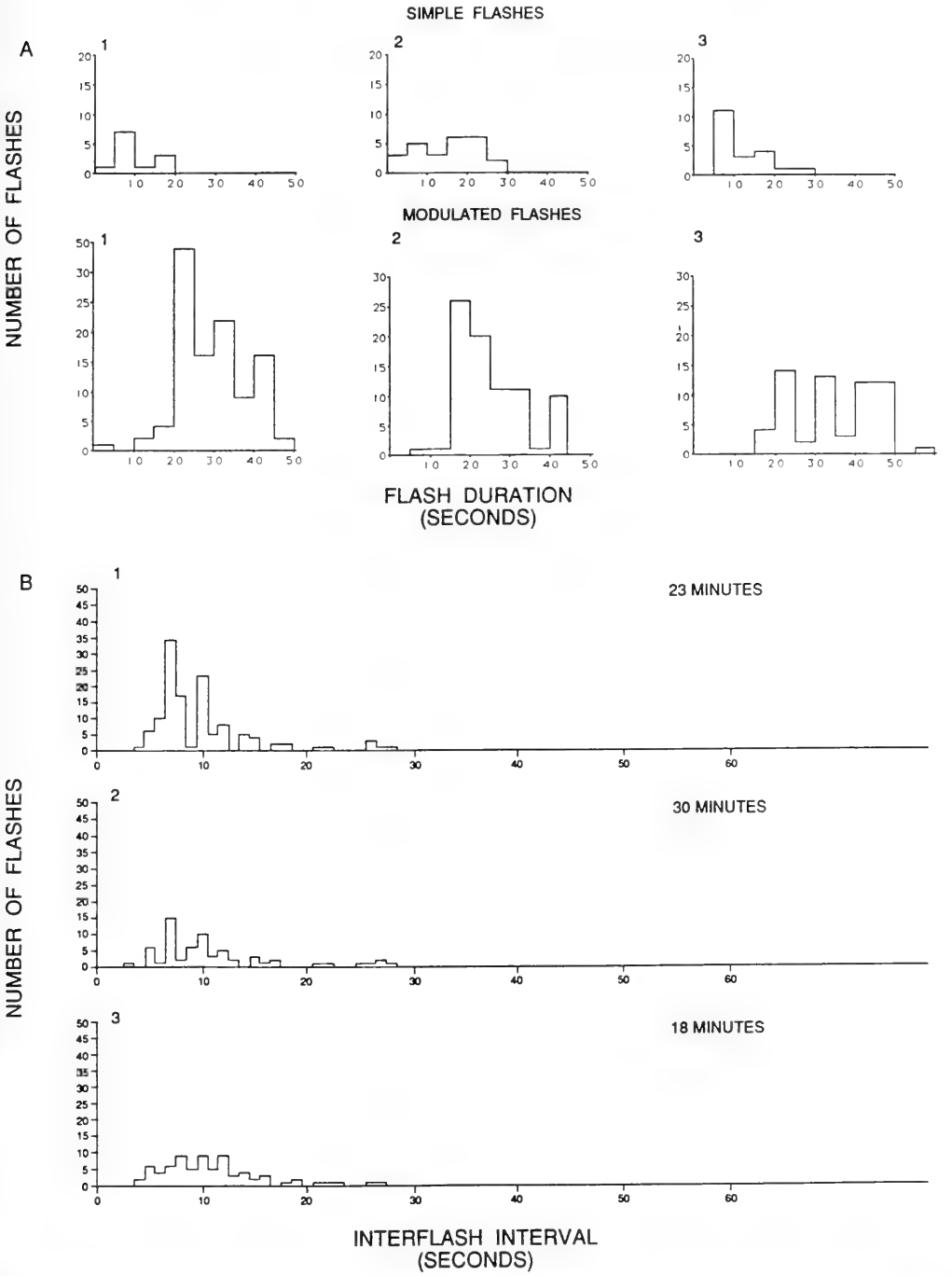

FIG. 3. Flash duration for simple (top row) and modulated (bottom row) flashes produced by two different juvenile snails (animals #4–5) over sample periods of 23 (left column, top), 30 (middle column, top), and 18 (right column, top) minutes respectively. Data in A2 and A3 are from the same snail. B. Interflash interval from the same snails during the same one hour test sessions as in A. All data measured from photomultiplier records.

snails, could not find evidence of a luciferin-luciferase reaction with hot or cold water extracts. He did, however, find microscopic evidence for granules in the cells of the luminescent organ which emitted a golden autofluorescence when viewed with a fluorescence microscope. Isobe et al. (1988) extracted a green fluorescent substance from *D. striata* (presumed to be the luminescent substance) that is probably different from the luminescent substance in fireflies.

Previous work in other bioluminescent systems, such as fireflies, have used the observations of flashes and their kinetics to suggest physiological and biochemical control mechanisms. For example, natural luminescence, such as continuous glow, intermittent glow, pulsation, and flash in fireflies (Buck, 1948), and experimentally induced luminescence in fireflies, such as pseudoflash, hypoxic glow, and scintillation (Buck, 1948; Harvey, 1951; Carlson, 1968) have all been used to support both the oxygen-control hypothesis of flash (Buck, 1948) and the nervous-system-control hypothesis (McElroy, 1947, 1951; Carlson, 1961).

The initiation of a flash in fireflies involves more than the chemical addition of the luminescent reactants. *In vitro,* it takes 60 msec for light production to occur if oxygen is added to a mixture of enzyme and substrate that has already formed an enzyme-substrate complex (DeLuca & McElroy, 1974). The same reaction takes several hundred milliseconds to develop if just enzyme and substrate are added in the presence of oxygen (DeLuca & McElroy, 1974). In adult fireflies, where a tracheal end organ is in the pathway between nervous system and photocyte (Smith, 1963), light production usually takes less than 100 msec to occur from the time the action potentials leave the 6th and 7th abdominal ganglia (Case & Buck, 1963). In larval fireflies, where the nervous system ends directly on the photocytes, light production can take up to a second to occur from the time the action potentials leave the 8th abdominal ganglion. In firefly larvae, the light production is a slow glow, not a rapid flash (Carlson, 1968).

The number of peaks and the intensity of the flash in juveniles suggest that a difference may exist in adult and juvenile luminescent organ peripheral neural control and biochemistry, a possibility reinforced by the ultrastructural findings of Maneri (1985), where differences between adults and juveniles in the size and density of photocyte granules were seen. Perhaps the larger, more electron-dense photocyte secretory droplets of juvenile snails contain more concentrated luciferin, or perhaps the photocytes are activated more often or more vigorously by the nervous system in juveniles.

In addition to peripheral changes, central changes may also occur. For example, the decrease in interflash interval in juveniles is paralleled by an increased locomotion in the juveniles (Copeland & Daston, 1989). Additionally, because simple flashes are usually of shorter duration than modulated flashes, the latter might be modulated because they are showing facilitation or summation. Summation, at least in skeletal and some smooth muscle, is due to both central nervous system activation at a rapid rate and peripheral effector inability to respond 1:1 to each central nervous system stimulus (Eckert et al., 1990).

Whether these differences reflect maturation or some other process, such as senescence (Martoja & Bassot, 1970), is not clear. Additionally, the actual locus of the changes, be they central, peripheral, or both, is also not known.

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THE LUMINESCENT ORGAN AND SEXUAL MATURITY IN *DYAKIA STRIATA*

Maryellen Maneri Daston[1] & Jonathan Copeland[2]

ABSTRACT

Dyakia striata, a snail found in Singapore and Malaysia, is the only terrestrial mollusc known to be luminescent. It produces flashes of light by means of a discrete luminescent organ in the head-foot. Previous studies of *D. striata* emphasized juvenile snail luminescence and its loss with sexual maturity. We, however, subsequently discovered that luminescence persisted in large snails that were probably adults. Here, the gross and ultrastructural anatomy of the reproductive system and the luminescent organ were compared between three snail categories: small snails with a luminescent organ, large snails with a normal luminescent organ, and large snails incapable of luminescence. We found that loss of luminescence did not coincide with sexual maturity. Mature gametes were found in the ovotestis of large snails capable of light production. Thus, some large *D. striata* were adults, possessed a structurally normal luminescent organ, and could flash. Because there is no good external marker for sexual maturity in *D. striata,* this leaves open the possibility that the flash is involved in reproductive behavior.

A comparison of the *D. striata* light organ with the light organs of two other mollusks suggests that the luminescence in *D striatia* is intraglandular and not intracellular.

Key words: *Dyakia,* luminescence, behaviour.

INTRODUCTION

Dyakia striata (Ariophantidae), found in Singapore and Malaysia (Parmentier & Barnes, 1975), is the only terrestrial gastropod known to be luminescent. It produces flashes of light similar to those of a firefly by means of a discrete luminescent organ (Haneda, 1981; Copeland & Daston, 1989).

The luminescent organ of *D. striata,* called the organ of Haneda (Martoja & Bassot, 1970), is a complex, histologically discrete lantern in which light production is thought to be intracellular (Haneda, 1963, 1981; Bassot & Martoja, 1968; Martoja & Bassot, 1970). The organ of Haneda, located within the pedal gland complex in the anterior head-foot (Parmentier & Barnes, 1975: fig. 1) is modified glandular tissue. It lies between the intermediate gland and the basal gland and consists of an epithelial integument, connective tissue, and photocytes (Martoja & Bassot, 1970).

That luminescence in *D. striata* occurs only in juvenile snails was first noted by Haneda and confirmed by others (reviewed by Haneda, 1981). At the onset of sexual maturity, the entire luminescent organ was thought to be reabsorbed by phagocytes and replaced by an absorption cyst (Bassot & Martoja, 1968; Martoja & Bassot, 1970). The disappearance of the luminescent organ was supposed to coincide with the first maturation division of the gametes (Martoja & Bassot, 1970). However, our field collections produced large-sized, apparently non-juvenile snails that were luminescent (Copeland & Maneri, 1984; Copeland & Daston, 1989).

The purpose of this study is to determine if large luminescent *D. striata* were sexually mature and to investigate differences between luminescent and non-luminescent large snails. Thus, we looked at the gross reproductive anatomy and the ultrastructure of the ovotestis and the ultrastructure of the organ of Haneda in small and large *D. striata,* and related this to light production. The gross reproductive anatomy has not been described for *D. striata,* nor has the ultrastructure of the luminescent organ or any part of the gonad.

MATERIALS AND METHODS

Snails were collected in public parks in Singapore over a six-week period. The gross anatomy dissections were done in the field using freshly collected snails. Living snails were fixed and then prepared for electron microscopy. *Dyakia striata* is difficult to maintain

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in laboratory culture. It is thin shelled and, thus, difficult to ship from Singapore to the United States, so the sample size in all categories is small.

The luminescent organ was viewed in the intact snail using a non-invasive ultraviolet light technique (Copeland & Maneri, 1984; Copeland & Daston, 1989). This allowed large snails to be classified as with or without a "visible" luminescent organ.

Because Copeland & Maneri (1984) and Counsilman et al. (1987) observed that *all* snails capable of light production show fluorescence when stimulated with an ultraviolet light, and because the luminescence of snails in captivity was often very infrequent (Maneri, 1985; Counsilman et al., 1987), we assumed that snails with a "visible" luminescent organ (bright yellow-green dot near the mouth on the ventral surface of the head-foot in response to stimulation with ultraviolet light) could flash and that all snails with a "non-visible" luminescent organ (no fluoresence in response to ultraviolet light stimulation but a luminescent organ was subsequently found by dissection) could no longer flash. Some of the large snails and all of the small snails were directly observed to produce flashes.

Two large snails (23.0 mm and 22.0 mm shell diameter) with "visible" luminescent organs, two large snails (23.0 mm shell diameter) with "non-visible" luminescent organs, and two small snails (4.5 mm and 5.0 mm shell diameter) were selected for ultrastructural studies.

The snails were anesthetized (ten min in a freezer) and then dissected in a chilled molluscan saline (Copeland & Gelperin, 1983). The ovotestis and organ of Haneda of large snails were removed and immediately placed in fixative. The ovotestis of the small snails could not be isolated due to its undeveloped and fragile state and, thus, no small snail ovotestes were included. To ensure uniform fixative penetration, the mature ovotestis was first cut into small pieces. The organ of Haneda was small enough (about 1 mm × 0.5 mm) to be fixed whole. The tissues were fixed in 2% glutaraldehyde in 0.1 M cacodylate buffer, then post fixed in osmium tetroxide in the same buffer (Eaken & Brandenburger, 1975). The tissues were then dehydrated in an ethanol series and embedded in Spurr's low viscosity embedding medium. Thin sections were cut using a glass knife on a Porter-Blum MT-II Ultramicrotome and then placed on a 300-gauge copper grid. The specimens were viewed using a Hitachi HU-11B-2 electron microscope.

The gross anatomy of the reproductive system was examined in freshly caught animals. Eleven small snails, the most abundant *D. striata* found, were dissected. Nine large snails with a "visible" luminescent organ were dissected, as were three large snails with a "non-visible" luminescent organ. These latter were the most difficult to find in a collection. The reproductive organs were isolated in molluscan saline and sketched while viewed through a 30× dissecting microscope.

RESULTS

Gross Anatomy

The small snails (shell diameter 13–16 mm; N = 4) had small, poorly developed reproductive systems when compared to the large snails (shell diameter = 20 mm, N = 9). Typical small snail and large snail reproductive systems are shown in Figure 1A and in Figure 1B, C, respectively. The small snail reproductive system was relatively small and undeveloped compared to that of the large snails.

A comparison between a large snail with a "visible" luminescent organ and a large snail with a "non-visible" luminescent organ is shown in Figure 1B, C. The snail with a "visible" luminescent organ had an expanded dart gland (lobes were separated and expanded), a swollen dart gland duct, and a dart in the dart sac (Fig. 1B). These features were also seen in four other large snails that had a luminescent organ. The snail with a "non-visible" luminescent organ had a more compact dart gland (the lobes were tightly folded together), a narrower dart gland duct, and no dart in the dart sac (Fig. 1C). These features were also found in two additional snails with a "non-visible" luminescent organ. The spermoviduct of the snail with the "visible" luminescent organ was swollen in comparison to the snail with no luminescent organ. Both animals had a reddish spermatheca.

Microscopic Anatomy

Ovotestis: The ovotestis of all of the large snails (N = 2 with "visible" luminescent organ and N = 2 with "non-visible" luminescent organ) contained mature spermatozoa. Mature sperm were identified by the appearance of the axoneme of the flagellum in cross sec-

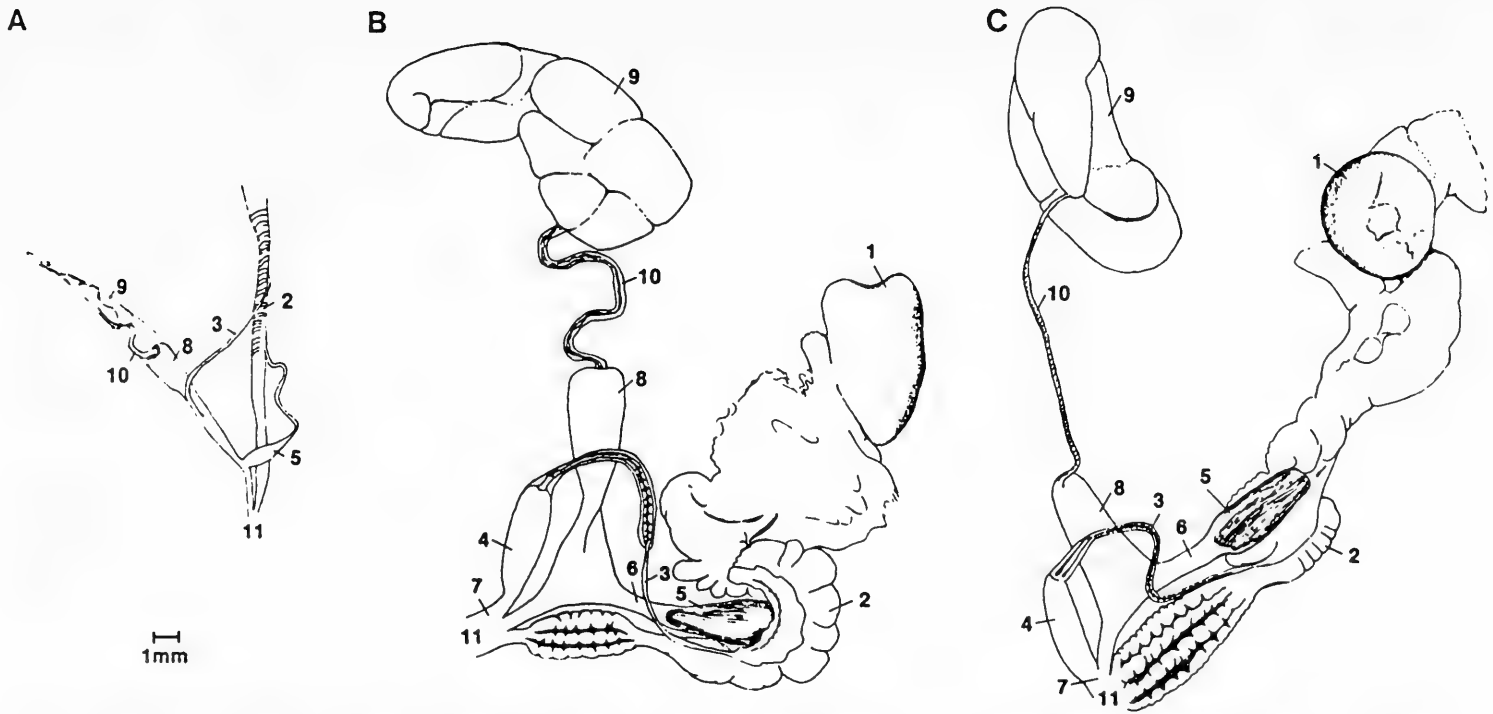

FIG. 1. Reproductive system of juvenile and mature *D. striata*. A. Small snail (shell diameter 16.0 mm) with "visible" luminescent organ. B. Large snail (shell diameter 23.5 mm) with "visible" luminescent organ. C. Large snail (shell diameter 22.0 mm) with "non-visible" luminescence organ. Abbreviations: 1, albumen gland; 2, spermoviduct; 3, sperm duct; 4, penial apparatus; 5, spermatheca; 6, duct of spermatheca; 7, vagina; 8, dart sac; 9, dart gland; 10, duct of dart gland; 11, common gonopore. Scale: 1 cm = 1 mm.

tion (Tompa, 1984). A group of spermatozoa surrounding a Sertoli cell is shown in Figure 2A and a cross section of a flagellum at higher magnification in Figure 2B. The Sertoli cells are the largest of the four general cell types found in the acinus (sperm, oocytes, follicle cells, and Sertoli cells) (Tompa, 1984). Normally, stylommatophoran oocytes range from 50–200 μm (Tompa, 1984). No cells of that size were found in the ovotestis.

Luminescent Organ: Organ of Haneda: All luminescent organs (N = 2 large-sized snails with "visible," N = 2 large-sized snails with "non-visible," and N = 2 small-sized snails with "visible," luminescent organs) showed an integument of dorsal ciliated epithelium, a ventral simple squamous epithelium, and large granular photocytes surrounded by connective fibers (Figs. 3, 4).

Photocytes were recognized by the large secretory droplets that comprised much of the cytoplasm (Bassot & Martoja, 1968; Martoja & Bassot, 1970). The size and appearance of the droplets varied among the different snail groups. The average droplet size for the large snails with a "visible" luminescent organ was 0.14 μm ± 0.02 S.D. (N = 15) (Fig. 3C) and 2.4 μM ± 0.56 S.D. (N = 15) for large snails with a "non-visible" luminescent organ (Fig. 3D). For small snails, the average droplet size was 5.8 μm ± 2.15 S.D. (N = 15) (Fig. 4C, D).

The substance in the droplets of the large snails with "visible" luminescent organs was homogeneous and was only slightly electron-dense (Fig. 3B, C), whereas the material in the droplets of the large snails with "non-visible" luminescent organs contained a granular substance (Fig. 3D). The substance in the droplets of the small-sized snails was homogeneous and electron dense (Fig. 4B, C).

Structures that have the ultrastructural characteristics of axon terminals (Tauc, 1977; Heuser & Reese, 1974) were found between and directly beneath the integumentary epithelium in one large snail with a "visible" luminescent organ (Fig. 5A, B). Connective fibers (Fig. 5B) were also found that show the characteristic striated feature of collagen in longitudinal section at high magnification (Porter & Bonneville, 1968).

When dissected, the organ of Haneda was shaped like a flattened discus. It was yellowish in appearance, and consisted of an epithelial integument which surrounded photocytes. A reconstruction of the entire luminescent organ is shown in Figure 6.

DISCUSSION

Sexual Maturity and the Luminescent Organ

The reproductive systems of large *D. striata* (both with and without a "visible" luminescent organ) were well developed (Fig. 1), suggesting that reproductive maturity is not obligatorily linked to the loss of the organ of Haneda. In Figure 1, the large snail with a "visible" luminescent organ had a dart in its dart sac, suggesting a propensity for mating (Tompa, 1984). Using the red spermatheca as a criterion for prior mating (Tompa, 1984), both large snails shown in Figure 3 had already mated at least once. The small-sized individuals, an example of which is shown in Figure 1A, possessed luminescent organs, undeveloped genitalia, and undeveloped dart glands and, thus, were probably sexually immature (juvenile).

Using TEM, sperm was found in large-sized snails that had "visible" luminescent organs (and in those with "non-visible" luminescent organs as well) (Fig. 2). Taken together, we conclude that luminescence occurs in sexually mature individuals. This contradicts earlier studies, which described luminescence in *D. striata* as juvenile luminescence and indicated that luminescence was lost at sexual maturity (Haneda, 1981; Martoja & Bassot, 1970).

It is possible that in the previous studies too few large-sized snails were found for adult luminescence to have been seen (i.e., sampling bias). For example, we searched for snails for 1–2 hours every other day for two weeks at one collection site at the Institute of Education, National University of Singapore. At this site, 59 small snails were found. The ratio of those with a "visible" luminescent organ to those with a "non-visible" luminescent organ was 3.5:1. At the same site, 21 large snails were found, and the ratio of "visible":"non-visible" luminescent organ in these snails was 0.4:1 (Copeland & Maneri, 1984). The number of snails collected at this site was about average, as was the size distribution. Had we only collected a small number of snails of both size, the probability of finding a large snail with a "visible" luminescent organ might have been low. Additionally, adult snails flash less often than juvenile snails (Copeland & Daston, 1989), so adult luminescence might be easily overlooked. Also, we used an ultraviolet light to determine that snails possessed a luminescent organ.

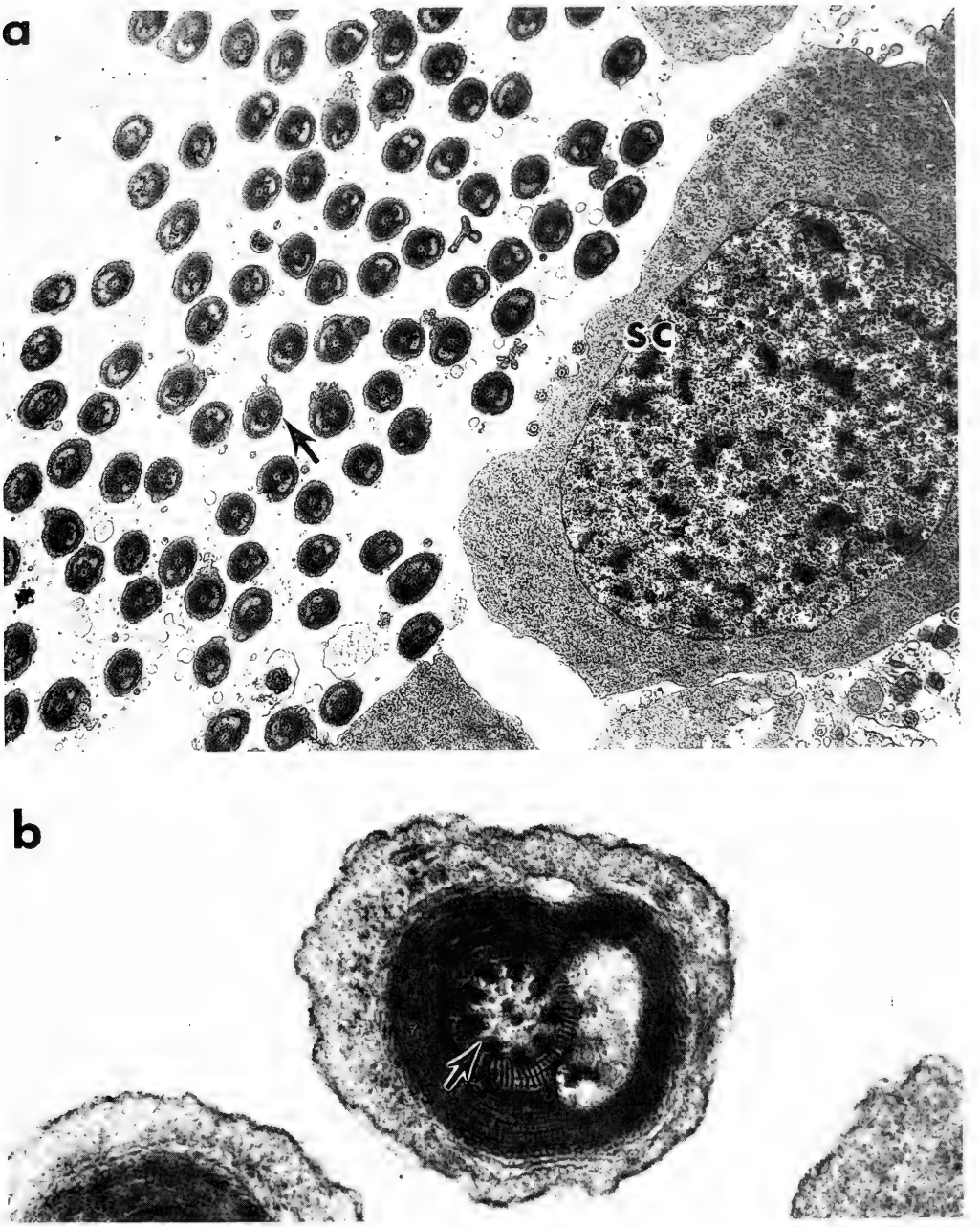

FIG. 2. Ovotestis of an adult snail. A. Sertoli cell (sc) with a group of sperm tails (arrow) (6300×). B. High magnification view of sperm tails in cross-section showing the axoneme (arrow) (54,300×).

Cellular Structure and Function of the Organ of Haneda

The organ of Haneda is discus-shaped and yellow. It consists of a dorsal ciliated epithelium, a ventral simple squamous epithelium, and large granular photocytes surrounded by connective fibers (Figs. 3–5). This confirms the morphology described by Bassot & Mar-

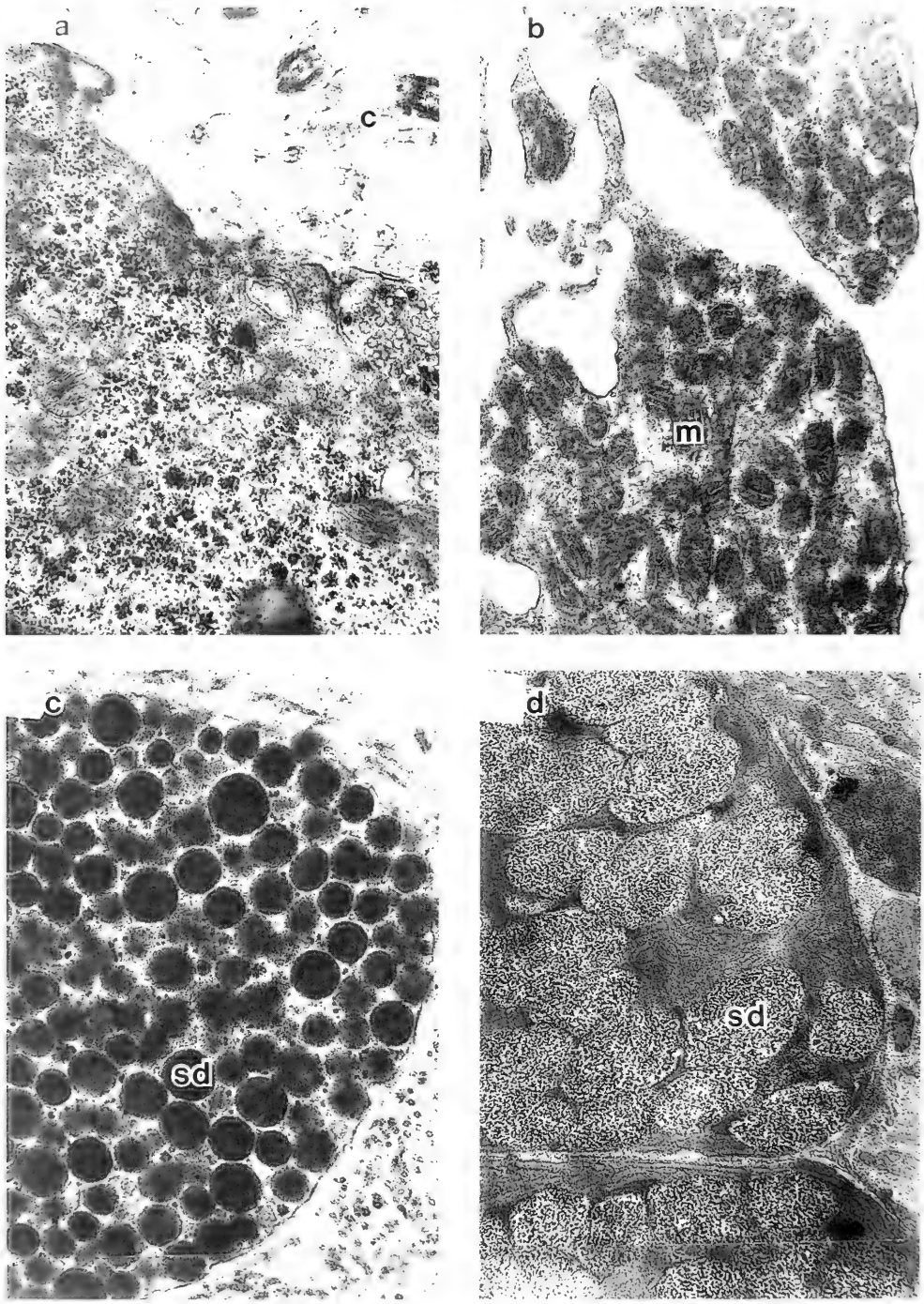

FIG. 3. Luminescent organ of adult snails. A. Ciliated epithelial cells; c, cilia (35,700). B. Photocyte with numerous mitochondria (m) (49,500×); C. Photocyte with secretory droplets (sd) (42,000×); D. Photocyte with secretory droplets (sd) (7,500×). B, C, snail with "visible" luminescent organ; D, snail with "non-visible" luminescent organ.

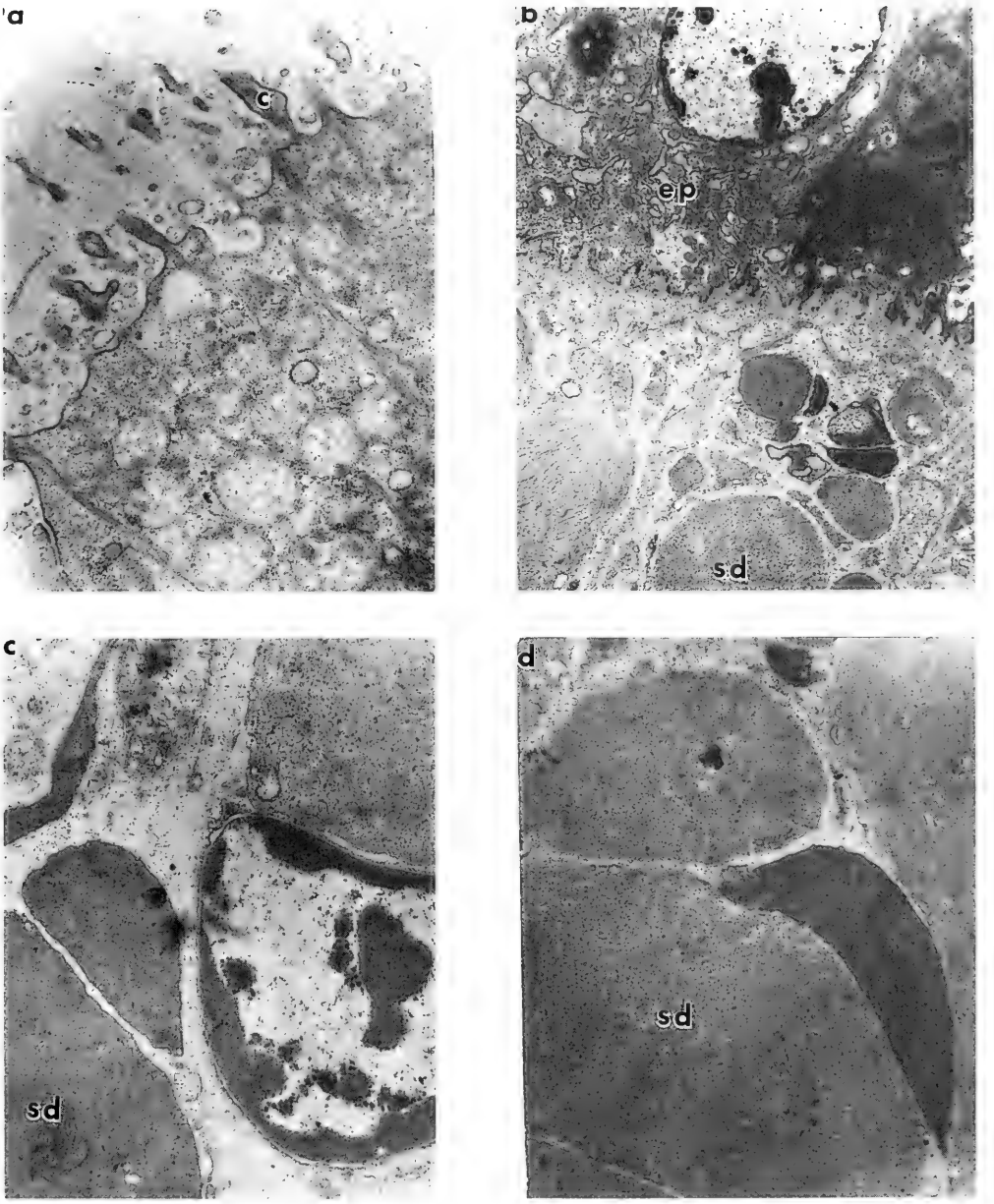

FIG. 4. Luminescent organ of a juvenile snail with a "visible" luminescent organ. A. Ciliated epithelia cells; c, cilia (17,900×). B. Border between ciliated epithelium (ep) and photocytes (sd, secretory droplets (4,000×). C, D, material within the photocytes (C = 15,000×; D = 13,000×).

toja (1968) and Martoja & Bassot (1970) using light microscopy.

Little is known about the mechanisms of light production in *D. striata.* The luminescence is thought to be intracellular, but this belief is inferential: a substance stored in the secretory droplets of the luminescent organ is believed to contain the luminescent substrate and enzyme, and the reaction is suspected to take place inside the photocytes (Bassot &

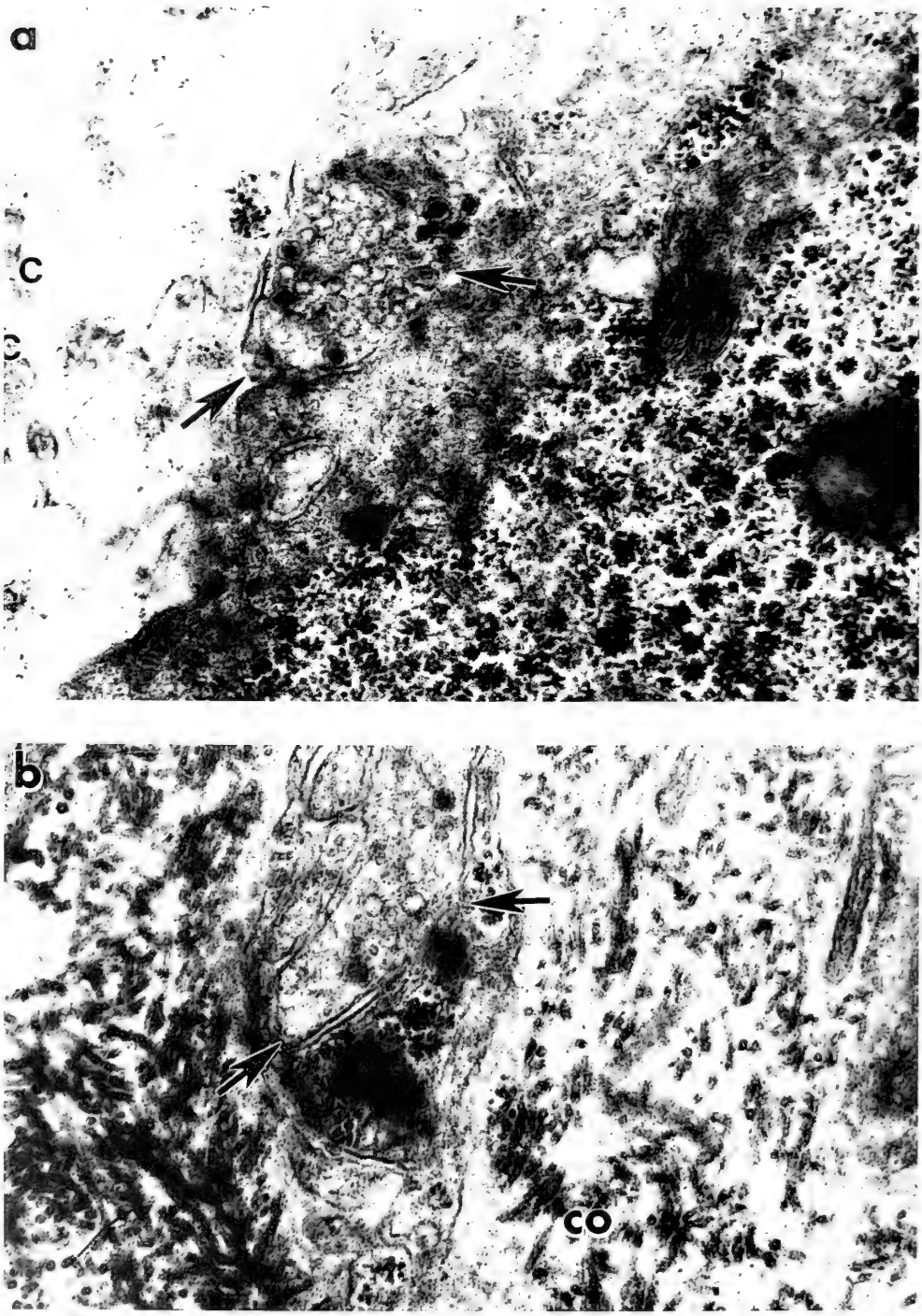

FIG. 5. Evidence for neural innervation of the luminescent organ. Axon terminals (arrows) from the luminescent organ of an adult snail. A. Ciliated epithelial cells (53,000×). B. Beneath the ciliated epithelium, collagen fibers are seen (72,000×). Abbreviations: c, cilia, co, collagen fibers.

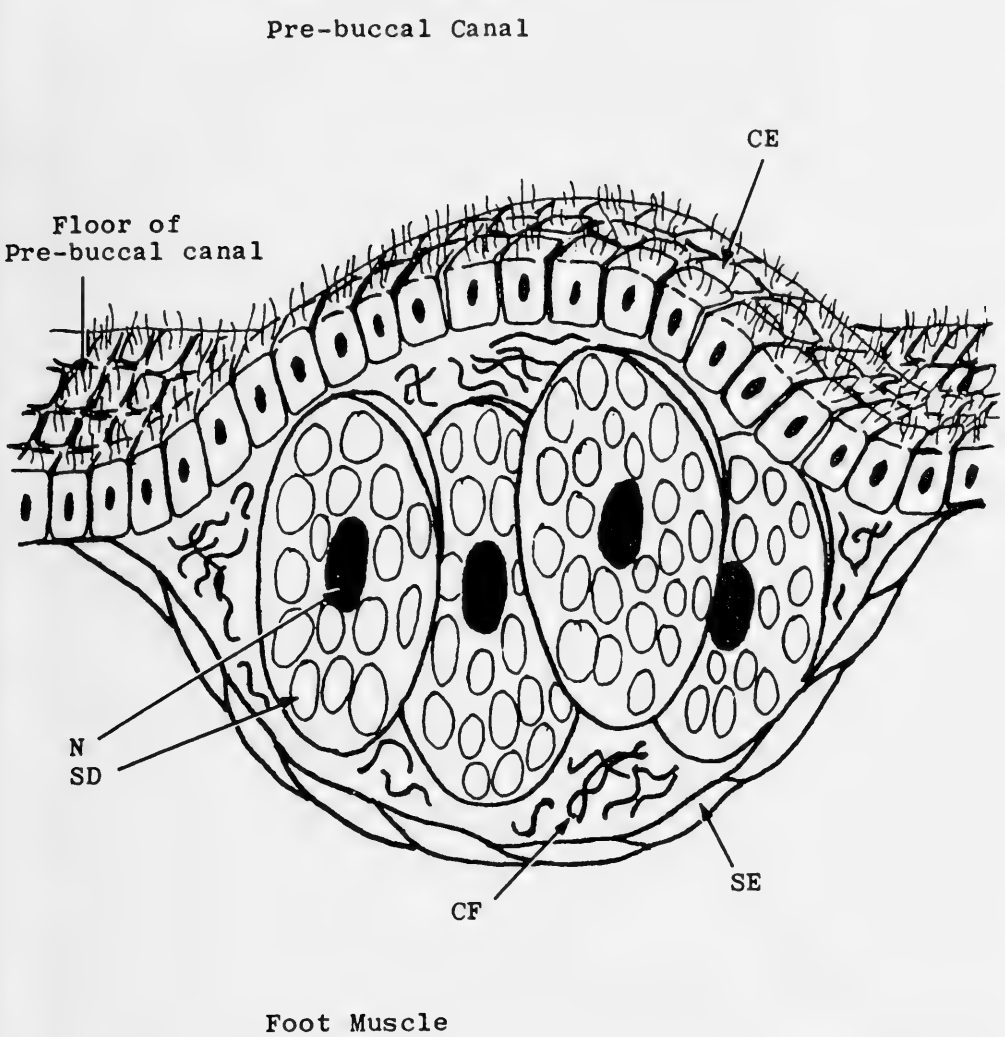

FIG. 6. Reconstruction of a luminescent organ (organ of Haneda) in cross section. CE, ciliated epithelium; SE, simple squamous epithelium; N, nucleus; SD, secretory droplets; CF, collagen fibers. Scale; width of organ of Haneda = 1 mm.

Martoja, 1968; Martoja & Bassot, 1970; Haneda, 1963, 1981). What is known is that the luminescent substance in *D. striata* tests negatively to a luciferin-luciferase reaction (Haneda, 1963) and, from spectrophotometric evidence that used extracted luminescent organs, that the luminescent substance of *D. striata* is different from firefly luciferin (Isobe et al., 1988).

The organ of Haneda is part of the pedal gland complex of *D. striata.* This pedal complex is larger in *D. striata* than it is in other stylommatophorans, in which only the dorsal gland and the pedal gland have been found (Martoja & Bassot, 1970). Glands of the pedal complex usually secrete mucus extracellularly for use in locomotion (Barr, 1926; Martoja & Bassot, 1970; Kater, 1977).

The structure of the organ of Haneda is similar to the structure of the luminescent organ in the two other known luminescent noncephalopod mollusks (Nichol, 1960; Bowden, 1950). In these other mollusks, the luminescence is associated with the secretion of mu-

cus from glands. In *Pholas dactylus,* a marine bivalve, the luminescent organ consists of a ciliated columnar epithelium that lies over the glandular cells which expel their secretions through the surface epithelium. The glandular cells are of three types: mucus secreting cells and two types of photocytes. Here, the luminescence is under the control of the nervous system and is thought to be extracellular (Nichol, 1960). *Latia neritoides,* a freshwater limpet, has photocytes that are histologically similar to *P. dactylus* and *D. striata.* However, instead of being confined to a discrete organ, the photocytes are scattered over the body of the limpet in small clusters that lie beneath the surface cuboidal epithelium within the loose subepithelial tissue. Mucocytes, melanophores, and muscle fibers are found intermingled among the photocyte clusters. Luminescence in *L. neritoides* is extracellular and does not involve the nervous system (Bowden, 1950).

The histological similarity between *D. striata, P. dactylus,* and *L. neritoides* could indicate similar function: extracellular secretion of a luminescent mucous. Thus, although luminescence in *D. striata* might be intracellular (Haneda, 1963, 1981; Martoja & Bassot, 1970), it could also be extracellular and even intraglandular. It is possible that the luminescent substance is secreted from the photocytes and remains localized within the organ of Haneda.

The difference in the appearance of the secretory droplets in the photocytes in the three types of snails examined (Figs. 3, 4) could be correlated with differences in the intensity of luminescent activity (Copeland & Daston, 1992, this issue). For example, Copeland & Daston show that small snails have brighter flashes than large snails when the flashes are viewed either by eye or with a photomultiplier. Small snails have the largest secretory droplets (Fig. 4). The secretory droplets in small snails possess a substance that was homogenous but not electron-dense. Large snails with "non-visible" luminescent organs have intermediate-sized secretory droplets, but these are granular and non-homogenous (Fig. 3D). The granular appearance could represent a degenerative form of the luminescent substance.

There was no indication of the phagocytosis of the photocytes described earlier (Bassot & Martoja, 1968; Martoja & Bassot, 1970). Some of the large snails with a "visible" luminescent organ had photocytes with a highly convoluted plasma membrane (Fig. 3B), but unlike the findings of Martoja & Bassot (1970), no phagocytes were found in the indentations (Fig. 3B).

One of the adult snails with a "visible" luminescent organ exhibited variability in the appearance of the photocytes: in some cases, the cytoplasm was crowded with mitochondria and the plasma membrane was convoluted, whereas in other cases the photocytes had secretory droplets in the cytoplasm and even a membrane. Some of the possible explanations for this phenomenon are: (1) there are two types of photocytes; (2) the two forms represent cells in different phases of a production-secretion cycle; or (3) they represent a concentration of different organelles in different regions of a single cell.

Thus, mature gametes, photocytes, plus the presence of secretory droplets and numerous mitochondria (Figs. 2, 3), suggest that luminescence can perist into adulthood in *D. striata.*

Luminescence, Gonadal Maturity, and Behavior

Stylommatophorans usually exhibit simultaneous hermaphroditism or protandry (Tompa, 1984). In terms of gonadal maturation, oocytes usually start to differentiate first, but the sperm develop faster and, thus, are first to reach maturity (Runham & Hunter, 1970).

In *D. striata,* we found that the large snails have large, well-developed gonads and mature sperm (Figs. 1, 2), and are, therefore, adults. Small snails have undeveloped gonads (Fig. 1), and are, thus, juveniles. Somewhere along the continuum of snail sizes, sexual maturity is reached, but an external marker for sexual maturity is not yet known.

Because luminescence in *D. striata* is not a juvenile-only luminescence (Haneda, 1981; Martoja & Bassot, 1970), as was previously thought, it is possible that it might play a role in mating behavior in *D. striata.* The presence of two types of adult snails, some with a "visible" luminescent organ and some with a "non-visible" luminescent organ, and the commonplace nature of simultaneous hermaphroditism or protandry in stylommatophorans, is a stimulus for further research on analysis of communication by bioluminescence in *D. striata.* As yet, the behavioral significance of the flash of *D. striata* remains enigmatic.

ACKNOWLEDGMENTS

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A POPULATION STUDY OF THE BIVALVE *IDAS ARGENTEUS* JEFFREYS, 1876, (BIVALVIA: MYTILIDAE) RECOVERED FROM A SUBMERGED WOOD BLOCK IN THE DEEP NORTH ATLANTIC OCEAN

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ABSTRACT

A large population of the wood-associated, deep-sea bivalve *Idas argenteus* was recovered from a wood block submerged for 11 years at 3,600 m depth at Deep Ocean Station 2 (DOS 2) in the western Atlantic south of New England. Acetate peels of the inner shell layer revealed a series of annual growth lines which were utilized to establish a relationship between shell length and age. Individuals recovered from wood panels also deployed at DOS 2 but submerged for much shorter periods were also examined using the acetate peel technique, and the number of growth lines generally coincided with the length of time spent on the bottom. Evidence for seasonality in the deep sea is reviewed, and the annual variation in the settlement of organic material from overlying photosynthetic layers is invoked as an important environmental cue to deterministic growth of the filter feeder *I. argenteus.* Analysis of a crystal size gradient in the region between successive growth lines in the inner shell layer lends support to gradual environmental change at DOS 2 and also to the Lutz-Rhoads (1980) model of annual shell deposition. Age-size frequency analysis revealed numerical dominance by the third and fourth year classes, perhaps due to what Roughgarden et al. (1985) characterized as "limit cycles." The *I. argenteus* living on the wood block functioned as protandric hermaphrodites, spending their first six years as males and the remainder of their existence as females. Increase in shell length of *I. argenteus* fits both the Gompertz and Power function growth models. The analysis of size-specific growth rates indicates that *I. argenteus* lacks the high growth rate displayed during the first year but shows a slower decrease in size-specific growth rates with age compared to shallow-water and freshwater bivalves. Specimens from the wood panels were larger than equal-aged individuals from the wood block, most likely due to a higher food quality and quantity on the wood panels. *Idas argenteus* is capable of colonizing patches of organic material in the deep sea probably a consequence of high reproductive potential and a planktotrophic larval stage. Whereas shallow-water opportunists are capable of a rapid increase in population size following settlement of a new site, *I. argenteus* can only increase population size upon reaching sexual maturity the year following settlement.

Key words: deep-sea ecology, bivalve, opportunist, growth line analysis, protandry, population structure, size frequency analysis, growth rate, shell microstructure, seasonality, larval settlement.

INTRODUCTION

Many known deep-sea bivalves (with the exception of those living at the hydrothermal vents and sulfide/methane seeps) are small, with low metabolic and growth rates, and apparently require a long time to reach maturity (Turekian et al., 1975; Grassle, 1978; Smith & Hinga, 1983; Grassle, 1986). Recolonization studies of sediment trays in the deep sea indicate low recruitment rates as well as low rates of population increase (Grassle, 1977; Levin & Smith, 1984). There is increasing evidence, however, that what have been described by Pearson & Rosenberg (1978) as "enrichment opportunists" occur in the deep sea and survive by specifically finding and exploiting organically enriched sites (Grassle & Morse-Porteous, 1987; Smith & Hessler, 1987; Desbruyères & Laubier, 1988).

Turner (1973) was the first to describe deep-sea opportunistic species associated with organic material. Turner (1973, 1977, 1981) found that wood placed on the deep-sea floor was rapidly colonized by pholad bivalves belonging to the subfamily Xylophagainae, a group of obligate deep-sea wood borers. Large numbers of these opportunistic borers rapidly colonize submerged wood, and probably reach sexual maturity rapidly—esti-

mated by Turner (1973) to take as little as three months—and render the nutrients in cellulose accessible to other deep-sea species. Desbruyères et al. (1980, 1985) reported rapid colonization of organic aggregates and flocs by the polychaete *Ophryotrocha* sp., whereas Grassle & Morse-Porteous (1987) found *Ophryotrocha* sp. and *Capitella* spp. most abundant in those sediment trays containing decaying *Sargassum.* More recently, Desbruyères & Laubier (1988), working in the deep Atlantic, reported a new genus and species of scale worm recovered from organically enriched substrates. The settlement of organic material in the deep sea appears to be a type of disturbance that provides an important source of spatial heterogeneity in what was previously viewed as a uniform homogeneous environment (Grassle & Morse-Porteous, 1987).

In June 1986, a wood block was recovered from DOS 2 (38°18.4′N, 69°35.6′W) 350 km south of Cape Cod by the research vessel DSRV/ALVIN as part of Turner's ongoing study of deep-sea wood-boring pholads. This block was riddled with mostly abandoned pholad burrows within which lived a large number (7,872) of the wood-associated deep-sea bivalve *Idas argenteus* (family Mytilidae). Recovery of this material provided a unique opportunity to study several aspects of the life history and population biology of a bivalve inhabiting an organically enriched environment in the deep sea.

MATERIALS AND METHODS

Living specimens of *I. argenteus* (Figs. 1, 2) were taken from a wood block (I.D. number N-17) approximately 30 cm on a side that had been placed at DOS 2 as part of a 12-block "wood island" in July 1975 and retrieved on 28 June 1986. Each block was enclosed in a plastic mesh bag to hold together the crumbling wood during recovery. Block N-17 was removed from the wood island using ALVIN's mechanical arm, placed in a vinyl-lined milk crate, and brought to the surface in ALVIN's collecting basket.

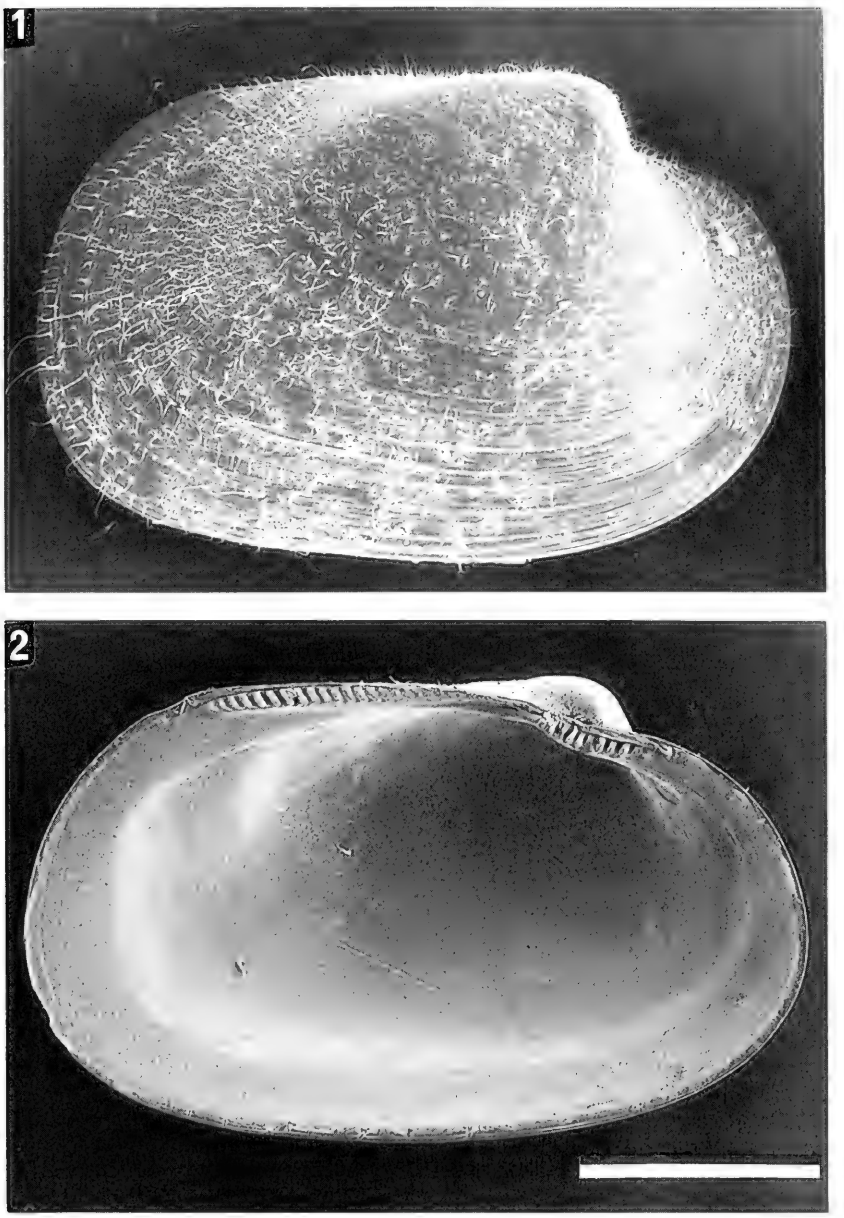
Aboard ship, many specimens of *I. argenteus* were immediately removed from the wood block and placed in 5% buffered formalin. The block was then broken into small pieces and also fixed in 5% buffered formalin. After fixation, all samples were washed and transferred to 95% ethanol. In the laboratory, both the wood block and the panels were dissected using a Stanley knife, and all specimens of *I. argenteus* visible through a 10× lens were removed from the wood chips.

Specimens of *I. argenteus* were also recovered from nylon mesh-covered wood panels (57.6 × 14.5 × 2.3 cm) that had been exposed for periods of 11–47 months (Table 2) near the wood island. Once extracted from the sediment, the panels were placed in retrieval boxes equipped with a locking top to prevent loss of material during their return to the surface (Turner, 1977). These wood panels were fixed while on the bottom with glutaraldehyde, which was released upon closure of the retrieval box lid, or on board ship with either 5% buffered formalin or 2% glutaraldehyde.

Length measurements of the shells represent the maximum distance between the anterior and posterior margin of the valves taken parallel to the ventral margin. All length measurements were made using a Wild M-8 dissecting microscope equipped with an ocular micrometer (at 50× each unit of measure was equal to 19.4 μm). Direct length measurements were made of all wood block specimens ≥ 2.72 mm in length and ≤ 0.97 mm. Individuals between 0.97–2.72 mm in length (N = 6,196) were randomly subsampled and the size frequency distribution of this subsample (N = 770) was adjusted to the total sample size of 7,872 in order to construct the size frequency distribution of the entire wood block population. The U.S. National Marine Fisheries Normal Distribution Separator Program (NORMSEP) was used to divide the size frequency distribution into age classes based on the results of growth line analysis.

Growth line studies were made of the inner shell layer of 102 specimens recovered from the wood block. Valves were removed from fixed individuals, air dried, and embedded in EPO-TEC 301, a transparent epoxy. The embedded valves were filed down along the axis of maximum growth and the exposed surface polished with 240, 800 and 3200 grit polishing compounds. The polished cross sections were etched using 2% HCl (by volume) for 5 to 8 minutes. Once dry, the etched surface was flooded with acetone and a sheet of acetate placed over the surface. Following evaporation of the acetone, the acetate sheet was peeled off, mounted in EPO-TEC 301, and growth lines in the inner shell layer examined using light microscopy.

Thirty nine individuals from the panels were



FIGS. 1, 2. Scanning electron micrographs of specimens of *Idas argenteus* recovered from the wood block. 1. Exterior of left valve showing dense periostracal hairs. 2. Inner surface of right valve. Scale bar = 1.0 mm.

analyzed in order to confirm the annual nature of the growth lines. Valves from the larger individuals found on six wood panels were polished and acetate peels made using the procedures described above.

Some polished and etched valve surfaces were also examined with the scanning electron microscopy (SEM). The embedded valves were mounted on aluminum stubs with double-sided tape, coated with a 700 Å layer of gold-palladium, and viewed using an AMR-1000 electron microscope. The analysis of

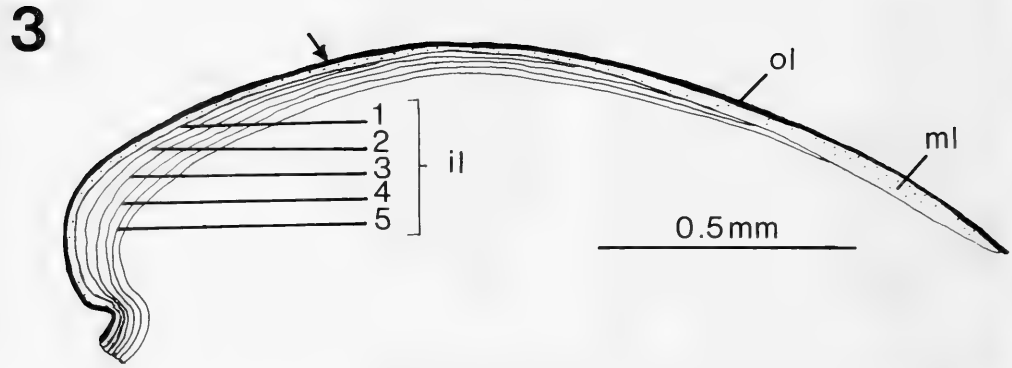


FIG. 3. Camera lucida drawing of an acetate peel taken from the polished surface of the valve of *Idas argenteus.* Five growth lines within the inner shell layer are indicated.

calcium carbonate crystal size was conducted using an enlargement of the SEM micrograph shown in Figure 5. Thirty-one equally spaced transects were drawn perpendicular to these two growth lines, and the length of the transect across each individual crystal was recorded. The relationship between these estimates of crystal size and the distance of each crystal from the older of the two growth lines was analyzed using linear regression.

During the removal of valves for growth line analysis the reproductive state of each specimen was noted using a dissecting microscope. Occasionally, gonadal smears were examined under a compound microscope to confirm the identification of their sexual state.

Analysis of shell growth rates was carried out using the statistical package FISHPARM (Saila et al., 1988). Specific growth rate (the rate of growth divided by size, G) was estimated using the equation:

$$G = (S_2 - S_1)/S_1,$$

where S_1 = shell length at the beginning of time interval T, and S_2 = shell length at the end of time interval T (Kaufmann, 1981).

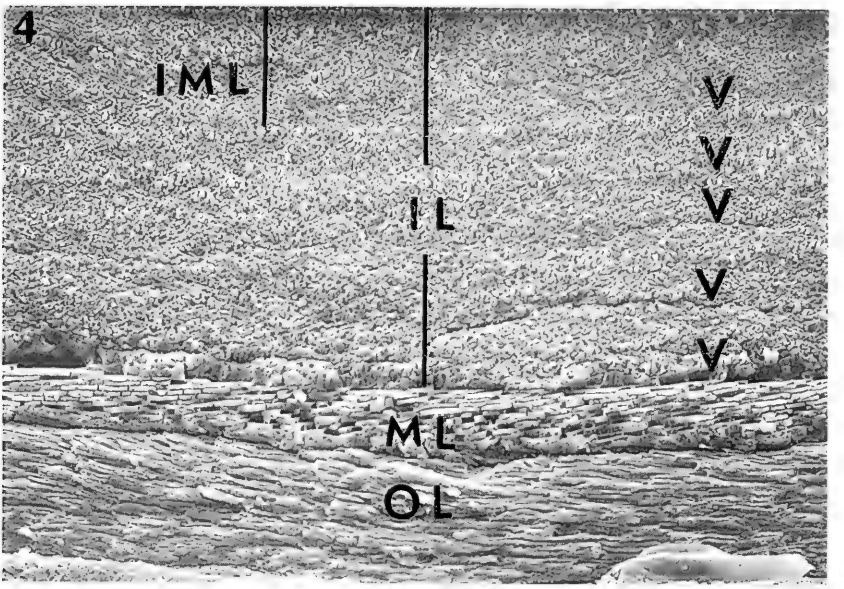
RESULTS

The shell of *I. argenteus* is composed of three separate crystalline layers (Figs. 3, 4). The outer layer consists of irregular simple prisms (*sensu* Carter, 1980) approximately 12 μm long and 1.7 μm in diameter, oriented roughly parallel to the shell surface (Fig. 4). This outer layer forms a series of closely spaced concentric lines on the exterior surface of the valve, but distinctive growth layers associated with these external lines were not apparent.

The middle shell layer is composed of sheets of nacreous tablets varying from 0.4 to 0.8 μm in thickness. This layer is relatively thin in the umbonal region of the valve; it expands, however, to make up much of the thickness of the shell at the valve edge (Fig. 3). No growth lines were apparent in this sheet nacreous layer.

The inner layer of shell has a fine, complex crossed lamellar microstructure (Figs. 4, 5). This layer is divided into a series of bands by fine lines running parallel to the shell growth axis (Fig. 3). The bands of shell material between each pair of lines extend along the axis of growth, with each successive growth band extending somewhat further from the umbonal region than its antecedent (Fig. 3). SEM examination revealed little that was remarkable about the crystalline microstructure of the inner shell layer in the vicinity of these lines (Fig. 5). These fine lines (hereafter referred to as growth lines), present in the inner shell layer of *I. argenteus,* were used to determine the ages of these clams.

Growth lines in the inner shell layer were counted in valves of known length to establish a relationship between size and age (Table 1). The smallest specimens examined displayed a single growth line, whereas the largest individual in the wood block population (7.15 mm in length) possessed nine growth lines in its inner shell layer. The number of fine lines in the inner shell layer of *I. argenteus* increases in concert with increase in valve length. Although there is some size



FIGS. 4, 5. Scanning electron micrograph of a cross section of the shell of *Idas argenteus* from the region indicated by the arrow in Fig. 3. Arrows indicate five growth lines in the inner shell layer. 5. Scanning electron micrograph of the fine complex crossed lamellar inner shell layer of *Idas argenteus*. Arrows indicate two growth lines. ol = outer shell layer; ml = middle shell layer; il = inner shell layer; iml = innermost growth layer. Scale bars = 10 μm.

TABLE 1. Results of the growth line analysis from acetate peels of sectioned valves of specimens recovered from wood block N-17. The size range of individuals encountered, as well as the number of specimens analyzed (N), is given for each age/growth line class.

Number of growth lines	Shell length (mm)		Number of specimens
	Minimum	Maximum	
1	0.91	1.26	6
2	1.35	1.70	10
3	1.44	1.90	9
4	1.91	2.62	12
5	2.40	3.75	15
6	3.04	4.29	15
7	4.08	5.88	24
8	5.44	6.85	10
9	7.15	7.15	1

overlap, age classes based upon growth line number form distinct shell length size classes.

Figure 6 includes the reconstructed size frequency distribution (solid line) of the population of *I. argenteus* taken from wood block N-17. Also included in this figure are the nine component normal distributions (dotted lines) generated by the normal distribution separator program NORMSEP. This program fits normal curves to the size frequency data based upon the size range of each age class derived from growth line analysis (Table 1). The number of individuals in each age class (the area under each of the nine normal curves) and the mean size of each year class are also included in Figure 6.

Growth line counts were also made of larger specimens recovered from wood panels submerged for periods of 11 to 47 months. This allowed the scrutiny of growth line production over much shorter periods of time than the eleven years of wood block submergence and was used to corroborate the interpretation of these fine lines as annual growth markers. Results indicate that the number of growth lines in *I. argenteus* is indeed congruent with a yearly deposition of shell layers in the inner shell (Table 2). Only specimens taken from a panel submerged for 35 months and a panel submerged for 47 months possessed a number of growth lines other than would be predicted based upon the number of years submerged. In these two cases, there were fewer growth lines than expected, perhaps a consequence of a delay in the time of initial colonization by *I. argenteus* or of an increased death rate due to higher predation by epifaunal organisms on the less protected wood panels (Williams & Turner, 1986).

To determine the reproductive strategy of *I. argenteus,* 101 specimens of known age (based on the results of acetate peel analysis) were dissected and the reproductive state of the gonads recorded (Table 3). All members of the first year class examined were found to be sexually immature. Sexually ripe males were present in the second to seventh year classes whereas ripe females occurred in the sixth to eighth year classes. Specimens with unripe gonads were present over the entire size range of the clams analyzed. Four hermaphroditic individuals were encountered possessing both ripe ovaries and testes. In these four instances, the ovaries were well developed while the testes were quite small but still contained spermatozoa (confirmed with gonadal smear analysis).

DISCUSSION

Shell Fine Structure

The shell fine structure of *I. argenteus* is similar to that reported in other members of the family Mytilidae (Taylor et al., 1969) and agrees with an earlier description (Carter et al., 1990) of a single specimen of *I. argenteus* (Yale Peabody Museum 9596) collected from 2,900 m depth "off Marthas Vineyard." Carter et al. (1990) reported that the simple prismatic outer shell layer of this species was calcitic whereas the nacreous middle shell layer and inner fine complex crossed lamalla of the inner shell layer was composed of aragonitic crystals. The presence of a calcitic outer shell layer has been noted in several subfamilies of the Mytilidae, especially in mytilid species from cold water habitats. (Taylor et al., 1969; Carter, 1980: fig. 5). These authors report that

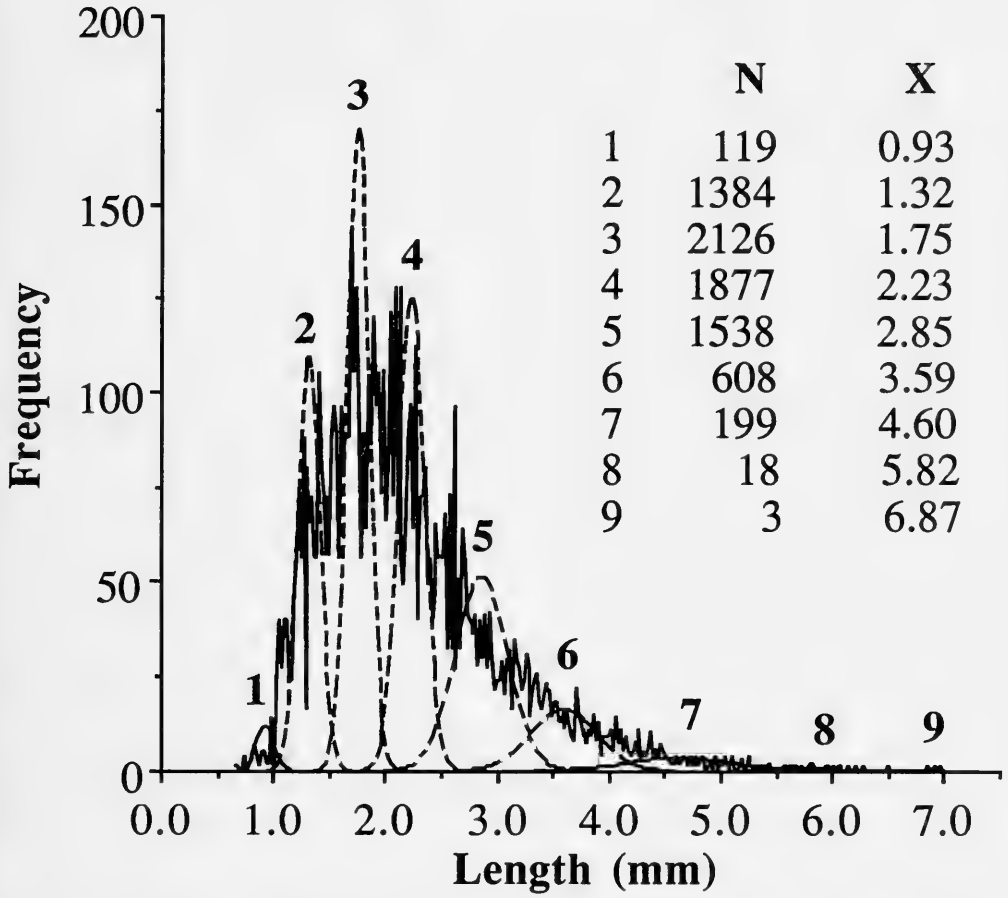


FIG. 6. Size frequency analysis of the wood block population of *Idas argenteus.* Solid line is the size frequency derived from direct measurement of shell length (all specimens ≥ 2.72 mm and ≤ 0.97 mm) or derived from direct measurement of a random subsample (specimens > 0.97 mm and < 2.72 mm). Dashed lines are the age classes derived from the normal distribution separator program NORMSEP based upon the size ranges of each growth line class. N = the number of individuals in each age/growth line class based on the normal curves (dotted lines) derived from NORMSEP. $\bar{X}$ = mean valve length of each age/growth line class.

tropical or warm-water mytilids generally possess shells composed entirely of aragonite. *Idas argenteus,* living in the cold waters of 3,600 m depth, has a prismatic, outer calcitic layer similar to that in other mytilids from colder regions.

The greater width of the innermost band of fine complex crossed lamella in the aragonitic inner shell layer (Fig. 4, iml) tends to support the general description of annual growth line deposition by Lutz & Rhoads (1980). This model postulates that an extended period of shell deposition is followed by a period of dissolution of a portion of this newly laid down shell material. The Lutz-Rhoads hypothesis suggests that during extended shell closure a buildup of organic acids due to anaerobic conditions leads to a reduction in pH of the extrapallial and mantle fluids to such levels that calcium carbonate crystals are dissolved. A concentration of less soluble organic matrix would occur in the region between two depositional periods resulting in what would then be recognized as a growth line.

The innermost growth band of *I. argenteus,* which is wider relative to those laid down previously, may be the current year's deposit of calcium carbonate crystals produced during a

TABLE 2. Results of the growth line analysis from acetate peel of sectioned valves of specimens recovered from the panels. The valve length and the number of growth lines in the inner shell layer is given for the largest individuals on the wood panel successfully analyzed. The number of months of panel submergence and the number of individuals (N) of *Idas argenteus* recovered from each panel are also included. *, See text.

Length (mm)	Number of lines	Length (mm)	Number of lines
Panel N-37	11 months N = 6	Panel N-76	35 months N = 1577
1.05*	1	2.16	3
		2.23	3
Panel N-39	23 months N = 221	2.23	3
		2.25	3
1.35	1	2.27	3
1.47	1	2.43	3
1.51	1	2.78	3
2.00	2		
Panel N-30	24 months N = 129	Panel N-78	35 months N = 363
		2.18	3
1.47	1	2.33	2
1.82	2	2.47	3
		2.61	3
		2.66	2
		2.86	3
		2.90	3
Panel N-93	25 months N = 71		
1.29	1		
1.45*	2		
1.51*	2		
		Panel N-55	47 months N = 2068
Panel N-82	35 months N = 79	2.47	3
		2.48	3
1.59*	2	2.57	3
1.82	2	2.58	2
1.84	2	2.67	3
		2.72	3
Panel N-83	35 months N = 424	2.76	3
1.90	2	2.98	3
1.90	2	3.10	3
2.18	3	3.68	3

TABLE 3. Results of the gonadal analysis of specimens prepared for growth line analysis. The number of individuals examined (N) and their reproductive state are presented for each age/growth line class.

Number of Lines	Number of Specimens	Male	Female	Hermaphrodite	Unripe
1	5	—	—	—	5
2	6	2	—	—	4
3	6	2	—	—	4
4	12	10	—	—	2
5	14	8	2	—	4
6	14	7	1	3	3
7	23	1	16	—	6
8	9	—	6	—	3
9	1	—	—	—	1

period of growth prior to collection of the block. This band of crystals would have been partially eroded during a subsequent non-growth period to a width similar to the previously formed growth bands seen in the inner shell layer. This scenario is strongly supported by examination of the crystal size gradient in this innermost growth band (dis-

cussed below relative to deterministic growth in the deep sea), which indicates the occurrence of a period of shell crystal deposition extending beyond that seen in previously laid down growth bands. An expected concentration of organic material at each growth line was not evident upon SEM examination of the shell of *I. argenteus* (Fig. 5), and this aspect of the Lutz-Rhoads hypothesis of shell growth is not supported by these results.

Growth Lines

Growth lines, such as those seen within the inner shell layer of *I. argenteus,* have been interpreted as being produced annually in many shallow-water bivalves (Rhoads & Panella, 1970; Lutz & Rhoads, 1980; Fritz & Lutz, 1986). This has been documented in mark-and-recovery experiments with *Mercenaria mercenaria* (Linné) (Panella & MacClintock, 1968), *Spisula solidissima* Dillwyn (Jones et al., 1978), *Anadara granosa* (Linné) (Richardson, 1987), *Mya arenaria* Linné (MacDonald & Thomas, 1980), *Mytilus edulis* (Linné) (Lutz, 1976), and *Corbicula fluminea* (Müller) (Fritz & Lutz, 1986). Further support for yearly deposition of growth lines has been given by Jones et al. (1983), who analyzed annual cycles in oxygen isotopic variations in the shell growth increments of *Spisula solidissima.*

Whereas internal growth lines within the inner shell layers have been reported from deep-water bivalves, it has not been demonstrated that these growth lines represent yearly depositional events. Work with *Yoldia thraciaeformis* from a submarine canyon off the southeastern Grand Banks of Newfoundland at 895–1,500 m by Hutchings & Haedrich (1984) and Gilkinson et al. (1986) noted the presence of distinctive growth lines, but they could only assume that they were laid down annually. The data presented here for *I. argenteus* provide the first strong evidence for annual growth patterns in deep-sea bivalves.

Wood block N-17 provided a large number (7,872) of specimens of *I. argenteus,* thus allowing growth line analysis over a wide range of shell lengths (Table 1). The results of these analyses present a very clear picture of a direct relationship between the number of growth lines and shell length, as well as an estimate of the size range of individuals in each age class based upon growth line number. The largest individual in the population exhibited nine growth lines, indicating that it was collected while in its ninth year, two years less than the period of submergence of the wood block. *Idas argenteus* may not have colonized the wood block until some time after the deep-sea wood boring pholads had colonized and begun the conversion of the wood block to more accessible forms of organic material (Turner, 1977, 1981). Additionally, large numbers of *I. argenteus* would not be available for settlement until a pioneering colony of adults had become established on the isolated wood island. Finally, given the low number of individuals in the older year classes, any individuals that could have colonized the wood block immediately after submergence would probably have had little chance of survival to their tenth or eleventh year due to high annual mortality rates. The absence of a tenth and eleventh age class is thus not surprising, and a population age structure of nine year classes strongly supports the interpretation of the growth lines as representative of some annual cycle in shell growth.

More telling evidence of the annual nature of the growth lines in *I. argenteus* are the results of the analyses of the largest individuals recovered from wood panels submerged close to the wood block but for much shorter periods of time. One would expect rapid colonization of these panels by both the pholads and *I. argenteus* soon after emplacement due to the large numbers of larvae emanating from the previously established wood island, and there should be close agreement between the number of growth lines in the shells of larger specimens of *I. argenteus* and the number of years submerged. The maximum number of growth lines observed in specimens from seven of the nine panels examined did indeed parallel the number of years the panel was on the bottom (Table 2). The larger individuals from panel N-82, which was submerged for 35 months, possessed only two growth lines, whereas those from panel N-55, which was submerged for 47 months, exhibited a maximum of only three growth lines. These two exceptions may perhaps be the result of susceptibility of *I. argenteus* to predation by epifaunal organisms on the wood panels (Williams & Turner, 1986) either prior to the exposure of the pholad tunnels upon breakdown of the panel surface or perhaps following the eventual crumbling and disintegration of the panel. Most important is that there is generally a one-to-one relationship between the number of growth lines in the inner shell layer and the number of years

of submergence of the wood, thus providing powerful supporting evidence for annual growth periods in *I. argenteus.*

Deterministic Shell Growth in the Deep Sea

Seasonal variation as well as annual spawning cycles have been implicated in shell layer deposition by bivalve mollusks. For many shallow-water temperate species, growth lines appear to reflect periods of little or no shell growth during the winter when temperatures are at a minimum (Panella & MacClintock, 1968; Williamson & Kendall, 1981; Jones et al., 1983; Fritz & Lutz, 1986). Richardson (1987) suggested that growth lines in the shells of the subtropical *Anadara granosa* may reflect exposure to low salinity waters during the annual intermonsoon period. Both Turekian et al. (1982) and Trutschler & Samtleben (1988) noted that the growth lines in *Arctica islandica* Linné and *Astarte elliptica* (Brown) were produced coincident with seasonal minima in their food supply and may simply be a reflection of slow growth due to nutritional deficiency. Cessation of shell growth during spawning periods when available energy is channelled toward the production of sperm and eggs may also result in growth lines (Pannella & MacClintock, 1968; Thompson et al., 1980; Gallucci & Gallucci, 1982).

In the deep-sea environment, both temperature and salinity change very little (Sanders et al., 1965; Mantyla & Reid, 1983; Grassle & Morse-Porteous, 1987) and cannot be invoked to explain annual shell growth events. In the only previous studies of growth lines in a deep-sea bivalve, Hutchings & Haedrich (1984) and Gilkinson et al. (1986) assumed that *Yoldia thraciaeformis* formed these lines either in response to seasonal fluctuations in food supply or as a "marker" of the reproductive cycle (Gilkinson et al., 1986). These two factors may also provide an explanation for seasonal shell growth by *I. argenteus.*

The specimens of *I. argenteus* observed in this study were apparently filtering suspended material from the water column. Many specimens, especially those taken from the wood panels, were observed with ingested material within the stomach and in the posterior portion of the intestine. SEM study revealed that the ciliation patterns of the gill filaments with long latero-frontal cilia, are typical of those seen in other filter feeding bivalves (Fiala-Métivioni et al., 1986). There were also substantial amounts of what are presumed to be food particles on the frontal cilia of the gill surface and in the ventral food groove similar to that seen in other bivalves known to be actively engaged in filter feeding (Foster-Smith, 1975). Based on these observations, it is believed that *I. argenteus* is filtering suspended material either drifting down from the overlying waters or derived from the actions of the wood-boring pholads and other organisms associated with the wood island.

Recently, specimens of *Idas washingtonius* (Bernard, 1978) with symbiotic bacteria in their gill filaments were reported from the deep Pacific Ocean attached to the bones of a whale carcass (Smith et al., 1989). These authors suggested that *I. washingtonius* may be augmenting its nutrient intake by sulfate reduction in a manner similar to that described by Felbeck & Somero (1982) and Grassle (1986) for several deep-sea vent species. The relative importance of such a chemoautotrophic food source to the total energy budget of these deep-sea bivalves and to that of shallow-water bivalves known to possess the enzymes necessary for sulfate reduction is unknown (Somero et al., 1983). If such a symbiotic relationship does exist for *I. argenteus,* it could perhaps explain the large number of individuals (7,872) on a single wood block. Regardless of any possible contribution by sulfate reduction to the energy budget of *I. argenteus,* any appreciable energy intake gained through suspension feeding could impart a seasonal component to its overall energy budget.

There is growing evidence for appreciable seasonal variability in the deep-sea environment (see Tyler, 1988, for a review). Perhaps most cogent to this discussion is evidence of a rapid transport of organic matter from the surface waters resulting in annual pulses in food supply to the deep-sea benthos. Turner (1973) and Wolff (1979) first called attention to a seasonal influx of plant remains to the deep sea, and sediment trap studies have indicated that particulate material settling on the bottom at depth is coupled to the seasonal plankton blooms in the overlying surface waters (Honjo, 1980; Deuser et al., 1981; Ittekkot et al., 1984; Matsueda et al., 1986). Photographic records and direct sampling have recorded the settlement of large amounts of phytodetritus on the bottom shortly after phytoplankton blooms in the surface waters (Billett et al., 1983; Lampitt, 1985; Riemann, 1989). Several studies have documented

what is usually a rapid response by deep-sea benthic communities to these pulses of food material (Turner, 1973, 1977, 1981; Gooday, 1988; Gooday & Lambshead, 1989; Graf, 1989; Lambshead & Cooday, 1990; Gooday & Turley, 1990).

The seasonal phytoplankton bloom in the northwestern Atlantic occurs from November to April (Menzel & Ryther, 1961), whereas sediment trap studies conducted southeast of Bermuda indicate that the highest influx of organic material reached 3,200 meters from January to May or June (Deuser et al., 1981). *Idas argenteus* is most likely exposed to greatest food supplies from January to June as a result of the rapid settlement of increased amounts of organic material derived from photosynthetic activities occurring in the surface waters.

The availability of an enriched food supply in the deep sea may also extend beyond the time of high productivity in the surface waters due to both the fall phytoplankton bloom and the intermittent resuspension of previously settled particulate matter similar to that documented at the HEBBLE site by Lampitt (1985) and recorded at DOS 2 by Rowe & Gardner (1979). Bottom currents are capable of creating a nepheloid (cloudy water containing suspended solids) layer close to the bottom with a higher suspended load than the overlying waters (Jumars & Gallagher, 1982). Temporal variation in these deep-sea currents has been well documented (Dickson et al., 1982; Grassle & Morse-Porteous, 1987, for the DOS 2 sample site; Csanady et al., 1988), as have abyssal storms associated with the Gulf Stream Current (Hollister & McCave, 1984). These deep-sea currents are of magnitudes capable of resuspending particulate matter, allowing deep-sea suspension feeders an extended period of increased food availability perhaps greater than that indicated by sediment trap studies conducted well above the bottom. Such resuspended material, which would enrich the near-bottom nepheloid layer, as well as the particulate material settling from the overlying surface waters, could result in a seasonal variation in food supply to such deep-sea benthic organisms as *I. argenteus.*

The presence of annual growth lines in *I. argenteus* could also be the result of seasonal spawning events. The presence of small numbers of first-year clams on the wood block indicates that some spawning and settlement must have occurred previous to the collection date of June 28th. Settlement must occur at least through September because there was a large number of sexually mature individuals on the wood block and a large number of very small, presumably recently settled clams on the panels recovered between late July to early September. Inspection of the 39 larger specimens taken from the panels disclosed that only one individual (recovered in late July) possessed a ripened gonad; the other 39 specimens were unripe. These observations indicate that spawning of *I. argenteus* may perhaps be completed by late July, at least in the wood panel populations. If shell growth in *I. argenteus* does cease during an annual spawning season or at least during a season of maximum spawning (Rokop, 1974), then the growth lines visible in the shell could be a reflection of a spawning period rather than a cycle of food availability.

The pattern of crystal deposition at a growth line has been found to differ between a growth line associated with spawning and one attributed to seasonal change in the environment (Kennish, 1980). Lutz (1976) and Lutz & Rhoads (1978, 1980) have characterized the microstructure of spawning breaks in *Geukensia demissa* (Dillwyn) and *Mytilus edulis* as consisting of a series of normal width nacreous crystal tablets that are interrupted abruptly by a growth line break. This growth break is succeeded by deposition of a series of thin crystals laid down during a period of reproductive stress followed by a return to normal width crystals once spawning is completed. Annual growth lines associated with variation in an environmental factor, such as water temperature, are associated with gradual, rather than abrupt, change in crystal deposition (Wada, 1961; Kennish, 1980). Lutz & Rhoads (1980), for example, described regular hexagonal nacreous tablets in the inner shell layer of *G. demissa* that gradually became smaller and less regular as water temperature declined.

The shell microstructure of *I. argenteus* is similar to that noted in response to long-term seasonal changes by shallow-water bivalves (Lutz & Rhoads, 1980; Kennish, 1980). Figure 7 shows the running average (N = 3) of crystal size measured as crystal overlap along 31 transects drawn perpendicular to the two growth lines shown in Figure 5. The crystals gradually increase in size along these transects in the direction of growth away from a growth line (upward in Figs. 4 and 7). Additionally, a linear regression of crystal size

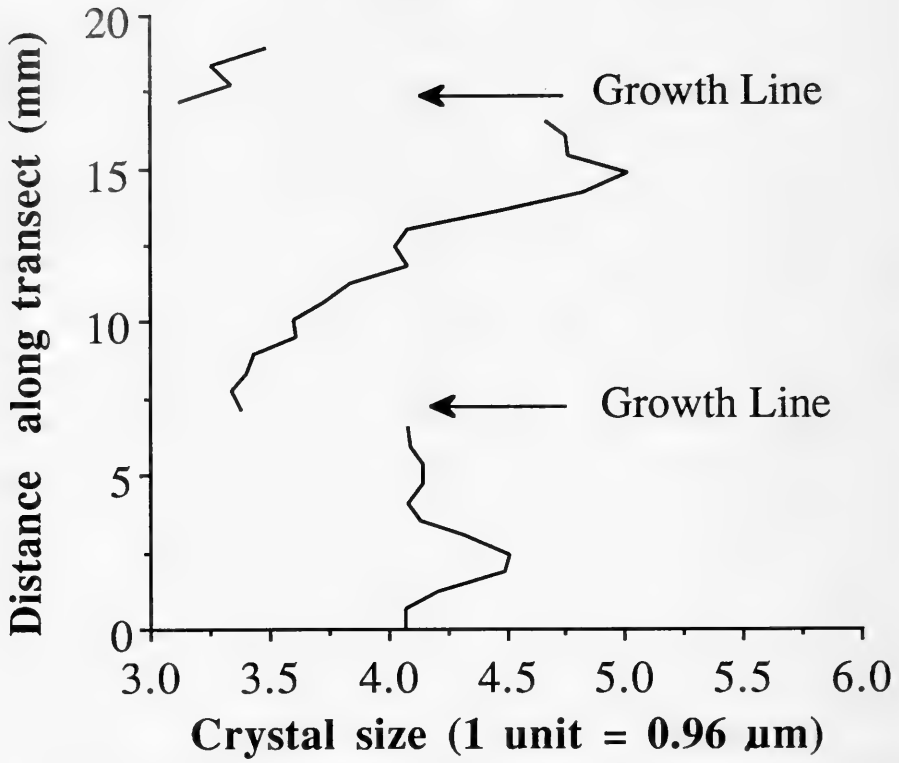


FIG. 7. Running average (N = 3) of the length of crystal overlap in the fine complex crossed lamellar inner shell layer of *Idas argenteus* along transects drawn across the two growth lines in Fig. 5.

for the region between these two growth lines with distance from the older (lower) growth line was found to be highly statistically significant ($p < 0.0000$). Based on these observations, it seems that following the establishment of an annual growth line small crystals are deposited, with crystal size becoming increasingly larger as shell growth progresses.

Based on the analysis of crystal size in the most recently deposited growth band (the innermost band adjacent to the mantle), the peaks in crystal size approaching each growth line in Figure 5 are thought to represent true maxima. Bands of shell material are much narrower between successive growth lines, presumably due to dissolution of a portion of these older bands following their seasonal deposition, as postulated in the Lutz-Rhoads (1980) hypothesis. The newly deposited layer of crystals in the innermost layer has not yet been subjected to the erosion thought to occur at the mantle-shell interface during extended periods of shell closure between growth periods. The crystals in this band have a similar size distribution to those found between the growth lines; however, the right tail of the curve, indicating decreasing crystal size following a seasonal maximum, is more extensive. As mentioned above, variation in crystal size deposition by shallow-water bivalves has been correlated with environmental conditions, with crystal size being reduced in times of stress and reduced growth (Wada, 1961; Kennish, 1980; Lutz & Rhoads, 1980). If crystal size gradients in the shell layers of *I. argenteus* reflect seasonal trends in relative environmental conditions and coincident growth, then it is apparent that some sort of seasonal optimum had occurred prior to retrieval of the wood block.

The shell microstructure in the inner shell layer of *I. argenteus* indicates shell deposition in response to a seasonal gradual change in the environment. As previously noted, the most apparent environmental variable capable of imposing this type of effect upon shell

growth at DOS 2 is food availability. The gradual increase in crystal size deposition following production of a growth line may reflect increased food supply due to submergence of organic material produced in the photic zone during the spring phytoplankton bloom. The reduction in crystal size following a seasonal maximum (seen best in the innermost growth band) may reflect a decreased food availability later in the growth period.

Because food is a factor in the regulation of gametogenesis (Giese & Pearse, 1974), it is probable that there is a coupling of food availability with the spawning period as well as with the production of shell growth lines in the deep sea. The peak in crystal size between successive growth lines noted in the inner shell layers could reflect a shift from the channeling of available energy to the production of the metabolically expensive organic matrix (Palmer, 1983) necessary for shell growth to the production of gametes. To attribute the production of growth lines in the shell of *I. argenteus* entirely to deviations in food supply would be to neglect the metabolic stress of reproduction. Variation in food supply and the channeling of available energy to reproductive processes is most likely an interactive relationship, and presumably both would affect the shell growth pattern of *I. argenteus.*

Population Size Frequency

As may be seen in Figure 6, the wood block population is numerically dominated by the third and fourth year classes. This size frequency distribution is believed to be a true representation of the wood block population rather than a sampling artifact. Although some individuals may have been washed off the block during retrieval, it is doubtful that such loss would occur preferentially to the smallest individuals in the population, that is that 1.3 mm specimens would be preferentially dislodged from the wood block relative to 1.75 mm specimens. The very low number of newly settled, first-year individuals suggests that retrieval of the wood block occurred prior to the period of greatest larval settlement. Many of the individuals in the block had ripe gonads and were about ready to spawn at the time of retrieval in late June. The abundance of very small, newly settled young on panels recovered in late August and September suggests that the major settlement of larvae occurs some time in late summer and that the dearth of first-year individuals is not the result of sampling.

Numerical dominance by older age/size classes is not unusual for populations of marine organisms (Gaines & Roughgarden, 1985; Hughes, 1985, 1990; Roughgarden et al., 1985; Breen et al., 1991) and has been reported for several deep-sea invertebrate populations (Allen & Sanders, 1973; Rex et al., 1979; Tyler & Pain, 1982). This type of age-size frequency distribution was also reported for the deep-sea bivalves *Nuculana pernula* and *Yoldia thraciaeformis* by Hutchings & Haedrich (1984). These authors suggested that intense predation by boring gastropods and benthic fish selects for fast growing individuals that quickly reach a size refuge from predators. This explanation, however, does not address the predominance of older age classes (five to ten years based on external or internal shell growth lines) in their collections.

Roughgarden et al. (1985) and Gaines & Roughgarden (1985) have postulated that populations limited by habitat space and having high, density-independent larval settlement rates would exhibit what they termed "limit cycles." In this model, a wave of numerically dominant year classes moves through the population with time, appropriating much of the available habitat. In the case of *I. argenteus,* the third and fourth year classes may inhabit many of the life-sustainable sites on the wood block, thus preventing the successful recruitment of younger age classes. As these dominant age classes move through the population and become less numerous due to density-dependent mortality, a larger amount of suitable habitat becomes available for successful larval settlement, leading to the eventual establishment of another generation of numerically dominant age classes.

Reproductive Strategy

Analysis of gonadal development (Table 3) indicates that the *I. argenteus* in the woodblock population at DOS 2 are protandric hermaphrodites. In the four year classes following the first year of sexual immaturity, those individuals observed with ripe gonads were exclusively males. Females occurred in the fifth and sixth year classes, but the majority of sexually ripe individuals in these age classes were males. With a single exception, all individuals in the seventh year class and older were females. It appears that members of the

wood block *I. argenteus* population spend their first five or six years as males and subsequent years as female. The environment has been shown to be a major determinant of the sexual strategy of an opportunist such as *I. argenteus* (Charnov & Bull, 1977), and protandry would not necessarily be the optimum strategy in all environments. In a newly colonized habitat where there are no preexisting females, it would be expected that some of the first sexually mature individuals of *I. argenteus* would be female.

According to the size-advantage model of Ghiselin (1969), protandric mollusks generally have a very patchy distribution with only limited adult mobility. These generalizations seem true of *I. argenteus,* which is characterized as living associated with sunken wood (Dell, 1987; Warén, 1991) and is nonmotile as an adult. Males living in such small, isolated communities are thought to have limited opportunity for successful mating because the restrictive factor is the number of eggs produced by the females of the population (Wright, 1988). Under such conditions, there would be little gained by producing large amounts of sperm, and there would be no reproductive advantage to being a large male. There is usually a direct relationship between female fecundity and female size in the Mollusca (Hoagland, 1978). *Idas argenteus* may be viewed as maximizing its reproductive success by being male when small and switching its sex later in life when its larger size would maximize its output of eggs.

Growth Rates

Estimates of annual growth in *I. argenteus* were derived from the mean valve lengths of the nine age classes shown in Figure 6. The change in length from one year class to the next was divided by the size at the beginning of the growth period, resulting in a size-specific growth rate that could be compared with similarly derived growth rates from other bivalves much different in size. The assumption is made that variations in growth rate due to year-to-year environmental variability are negligible and that each individual follows the same schedule of growth during its lifetime. As has been noted (McNew & Summerfelt, 1978; Kaufmann, 1981), the use of the mean length for each year class tends to dampen any yearly variations in growth, making this a resilient method for the analysis of the growth strategy of a species.

The resultant annual size-specific growth rates for *I. argenteus* were found to change little over the eight growth intervals, exhibiting only a slight downward trend with increasing age (Fig. 8, solid line). This growth pattern exhibited a statistically highly significant fit with the Gompertz (R^2 = .998) and Power curve (R^2 = .995) growth models, whereas the Exponential (R^2 = .914), Logistic (R^2 = .926) and Von Bertelanffy growth models (R^2 = .800) fit less effectively. Both the Gompertz and Power growth models include a reduction in growth rate with age, but the former assumes asymptotic growth to a size maximum and the latter is an indeterminant growth model. Due to the low number of individuals and greater standard deviations of the older age classes commonly encountered in size frequency distributions (MacDonald & Pitcher, 1979; Gage, 1985), it is not possible to determine whether the growth of *I. argenteus* is determinate or indeterminate from these data.

Also included in Figure 8 are the size-specific growth rates derived from previously published age-length data for two freshwater species (*Lampsilis radiata* and *Anadonta grandis* from McCuaig & Green, 1983) and three shallow-water marine species (*Cerastoderma edule* and *Modiolus modiolus* from Seed & Brown, 1978, and *Spisula solidissima* from Jones et al., 1978). The size-specific growth pattern of *I. argenteus* differs greatly from these bivalves, which all exhibit elevated growth rates in their first year followed by a precipitous drop in growth by the second year. By the third or fourth year, the size-specific growth rates of all five of these freshwater and shallow-water species are lower than those of *I. argenteus.* Only *M. modiolus* (the only other member of the family Mytilidae in Figure 8) approached the rate of growth exhibited by *I. argenteus* in the older age classes. The deep-water bivalve *I. argenteus* lacks the rapid growth exhibited early in life by the shallow-water marine and freshwater species but experiences a slower reduction in growth with increasing age.

It is difficult to make comparisons of the growth rates of *I. argenteus* with other deep-sea bivalves not associated with the vents and seeps as so few such studies have been conducted. Early growth estimates were carried out on *Tindaria callistiformis* collected from 3,800 m depth in the North Atlantic by Turekian et al. (1975). These authors employed radio-chemical dating techniques to establish a life span of approximately 100

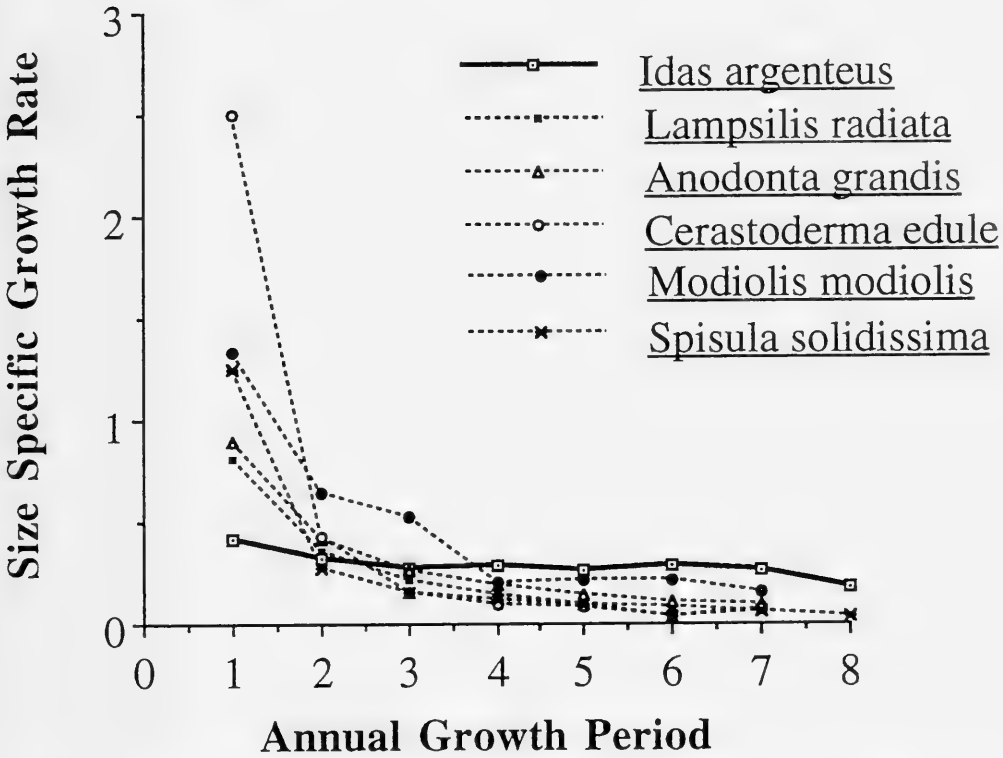


FIG. 8. Size specific growth rates of *Idas argenteus* (solid line) and five species of marine shallow-water and freshwater bivalves (dotted lines). *Lampsilis radiata* Gmelin and *Anodonta grandis* Say from data in McCuaig & Green (1983); *Cerastoderma edule* (Linné) and *Modiolus modiolus* (Linné) from data in Seed & Brown (1978); *Spisula solidissima* Dillwyn from data in Jones et al. (1978).

years and a resultant very slow growth rate of 0.084 mm/year. Unfortunately, the variance in their data (s.d. = 38 years) plus the use of external rather than internal growth lines as annual markers (see Lutz & Rhoads, 1980) makes their estimates of longevity and growth rate highly questionable.

Hutchings & Haedrich (1984) included age determinations based on internal growth lines for *Yoldia thraciaeformis* collected 895–1,500 m deep in the northwestern Atlantic Ocean, making it possible to derive size specific growth rates from their data. The size-specific growth rate of four- to eight-year-old specimens of *Y. thraciaeformis* ranged from 0.07 to 0.18. These growth rates are comparable to those of the similarly aged fresh and shallow-water species included in Figure 8 but are lower than those for specimens of *I. argenteus* of comparable age from the wood block population.

Rhoads et al. (1982) carried out *in situ* measurements of growth for specimens of the large mussel, *Bathymodiolus thermophilus* Kenk & Wilson, 1985, from the Galapagos Rift, and size-specific growth rates were generated using estimated values from their figure 4. Comparisons were made between individuals collected from a densely populated area and from a less densely populated region peripheral to the mussel beds. For two specimens from the dense mussel bed, estimated to be five years old based on growth lines, the size-specific growth rates were 0.27 and 0.29, whereas a specimen estimated to be eight years old had a specific growth rate of 0.14. Eight- to fourteen-year-old specimens of *B. thermophilus* taken from the less densely populated peripheral region had size specific growth rates ranging from 0.04–0.15. Lutz et al. (1985, 1988) have indicated that this correlation between growth rates and proximity to

the hydrothermal vents are most likely the consequence of an elevated food supply.

The size-specific growth rates for the mussel bed specimens of the Galapagos Rift are comparable with, while those specimens from the periphery of the mussel bed are lower than, those of *I. argenteus* taken from the wood block at DOS 2. Apparently, these high size-specific growth rates for *I. argenteus* are the consequence of the organic enrichment of the region surrounding the wood island due to the actions of the wood-boring pholads (Turner, 1973, 1977, 1981).

The analysis of specimens from the panels also presents evidence that food availability may be a major determinant of growth for *I. argenteus.* Included in Table 2 are the lengths of specimens with ages determined by growth line analysis, and it is apparent that these clams are larger than their age cohorts growing on the block. Those specimens with shell lengths that do not exceed the range of the normal curve (and thus fall within the size range) for their age class in the wood block population have been marked with an asterisk in Table 2. Growth of *I. argenteus* is apparently more rapid in specimens inhabiting the panels than in specimens living on the block.

The major difference between the wood panels and the wood block was that the wood panels contained large numbers of pholads that were providing copious supplies of fecal material to the organisms on and around the panels (Turner, 1981). The posterior intestines of the majority of specimens examined from the wood panels were filled with yellowish fecal material, in contrast to the specimens from the wood block, which usually had little or no visible material in their guts. Additionally, after eleven years of submergence and processing by benthic organisms, the organic material derived from the wood block was probably of much lower quality than that of the younger (one to four years) wood panels. Alongi (1992), in his study of deep-sea benthic communities in the western South Pacific, found that much of the wood and plant material encountered was well aged, with C:N ratios exceeding 300:1 (as compared to 18:1 for fresh algal material), indicating low nutritional value. Food therefore seemed to be more abundant on the panels and may have been of higher quality, resulting in higher growth rates and indicating that food availability is a limiting factor to the growth of *I. argenteus* in the deep sea.

Opportunists in the Deep Sea

Two life history traits that give opportunistic species an ability to colonize under-exploited areas of suitable habitat are a high dispersive capability and a facility to rapidly increase population size (Turner, 1973, Grassle & Grassle, 1974). These traits allow long distance movement by pioneering individuals and the ability to maximize the exploitation of that resource. The results of the present study indicate that *I. argenteus* possesses both of these attributes.

The small prodissoconch I (length = 110 μm) of *I. argenteus* indicates an egg size associated with bivalves possessing planktotrophic larvae, and the well-developed prodissoconch II (approximately 500 μm) is an indication of an appreciable free-swimming phase (Turner & Lutz, 1984). Individual reproductive output is apparently quite large, with an estimated 3,000 eggs in varying stages of development observed within the ovaries of a single female 5.26 mm in length. By broadcasting large numbers of free-swimming larvae into the water column with the capability of remaining suspended for an extended period of time, *I. argenteus* has the dispersal capabilities necessary for successful colonization of an ephemeral deep-sea habitat.

Based on what has been learned from the wood block and panel studies, *I. argenteus* increases its population size by means of larval settlement. The abundance of small individuals found on several of the wood panels (1,500–2,200 specimens <1.2 mm in length on two panels colllected in late July) indicated dense settlement by larvae undoubtedly originating from the previously established wood island population. Grassle & Morse-Porteous (1987) also reported large numbers of juvenile specimens of *I. argenteus* in the organically enriched sediments surrounding the wood island at both DOS 1 and DOS 2. Whereas the larvae of *I. argenteus* have the capacity to colonize distant isolated patches, it may often be more advantageous to settle close to the home site when unexploited substratum remains available. It is known that the planktonic larvae of shallow-water invertebrates often display great variability in the length of the competent phase, which may be greatly affected by the presence of an appropriate settlement site (Scheltema, 1986; Knowlton & Keller, 1986). The high reproductive capacity of *I. argenteus* ensures dense settlement of the wood island area by those larvae remain-

ing close to the homesite, perhaps due to chemosensory cues similar to those described for shallow-water species (Burke, 1986).

Results of this study indicate that while *I. argenteus* has a high reproductive potential and is capable of rapid population increase by dense larval settlement of an established site, it lacks the capacity seen in shallow-water opportunists immediately following the colonization of a new site. The generation time of a shallow-water opportunist, such as *Capitella* sp., for example, is approximately 30 to 40 days (Grassle & Grassle, 1974), whereas at DOS 2 *I. argenteus* is not capable of reproduction until the year following settlement. The few pioneering larvae that successfully colonize an isolated patch of organic matter would experience a delay prior to the full exploitation of the available resource. Population size could not increase until the pioneering individuals were sexually mature and able to produce large numbers of larvae.

Colonization rates of organically enriched sediment trays in the deep sea are quite low when compared to similar studies in shallower waters (Levin & Smith, 1984; Desbruyères, 1985; Grassle & Morse-Porteous, 1987). For many species, the pattern of colonization on sediment trays deployed by Grassle & Morse-Porteous (1987) at DOS 2 was a small initial settlement followed by increasing densities with time. For four of the more common species colonizing these sediment trays, Grassle & Morse-Porteous (1987) indicated maximum times to maturity much greater than those of similar opportunists from shallower waters. The bivalve *Nucula cancellata* collected from these trays was, for example, estimated to have a maximum maturation time of two years. The dependence upon colonization by planktonic larvae and the preliminary delay in population increase due to slow maturation time was used by Grassle & Morse-Porteous (1987) to explain the slow colonization rates reported for the deep-sea benthos. The sexual maturity of the deep-sea organic enrichment opportunist *I. argenteus,* which occurs a year after initial settlement, lends further support to the view that deep-sea opportunists differ from those in shallow water in the rate of their response to patches of organic enrichment.

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EVOLUTIONARY RELATIONSHIPS AND EXTREME GENITAL VARIATION IN A CLOSELY RELATED GROUP OF *PARTULA*

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ABSTRACT

The land snails *Partula otaheitana, P. jackieburchi,* and *P. affinis,* endemic to Tahiti, are genetically very similar species with complex morphological relationships. There is great variation among the species in the morphology of the reproductive system, *P. jackieburchi* having originally been placed in the genus *Samoana* because of its genital characters. Individuals with characteristics intermediate between the species have been found in several populations. Multivariate analysis of morphological variation among 108 individuals from 14 sites shows that different combinations of the species may be distinct in sympatry, but that the distinctions break down at some sites. The morphology of genitalia is correlated with the morphology of shells in comparisons between species, and in comparisons between various intermediate forms, but not in comparisons within species. This pattern suggests that the correlation is due to intergradation between species, rather than to geographic variation within the separate species. Laboratory hybrids between *P. otaheitana* and *P. jackieburchi* have genitalia with characteristics similar to those of many intermediate individuals found in the wild. Quantitative comparisons with the related genus *Samoana* show that the differences in genital anatomy between species in the *P. otaheitana* group are as great as, or greater than, the overall differences between genera. Our results show that even large differences in genital anatomy do not necessarily bring about reproductive isolation, and they demonstrate the complexity of relationships within the endemic radiation on Tahiti.

INTRODUCTION

Land snails of the genus *Partula* have radiated on many high islands of the Pacific, and show their greatest diversity in the Society Islands (Cowie, 1992). The radiation on Moorea has been studied in the most detail, and has revealed complex patterns of variation in reproductive relationships, morphology, and molecules (e.g. Crampton, 1932; Murray & Clarke, 1980; Johnson et al., 1986a; Murray et al., 1991). The species on Tahiti apparently represent a more recent radiation derived from a Moorean ancestor (Johnson et al., 1986b). Although the Tahitian species have not been as thoroughly studied, they too display a challenging array of diversity. The most confusing variation is in the *Partula otaheitana* group.

This group, which is endemic to Tahiti, is now considered to include the three species *P. otaheitana* (Bruguière, 1789), *P. jackieburchi* (Kondo, 1980), and *P. affinis* Pease, 1868 (Kondo & Burch, 1979, 1983; Kondo, 1980; Johnson et al., 1986c). On the basis of their shell morphology, Crampton (1916) apportioned the variation represented by these taxa among eight subspecies of *P. otaheitana,* and this assignment was adopted in a recent analysis of geographical variation (Emberton, 1982). However, *P. o. affinis,* the most distinctive of the "subspecies," is widely sympatric with *P. o. rubescens* Reeve, 1850, "its very antithesis in most respects" (Crampton, 1916: 185). Whereas *P. o. rubescens* is large, almost entirely sinistral, and generally yellow or red, *P. o. affinis* is generally small, usually dextral, and typically brown (Crampton, 1916, color plates). The two sympatric forms also have distinct genital anatomies (Kondo & Burch, 1979; Kondo, 1980), supporting the view that they are separate species.

Although the morphology of the reproductive system can often be useful in clarifying relationships (e.g. Reid, 1986), this appears not to be so for the *P. otaheitana* group, in spite of the differences between *P. affinis* and *P. otaheitana.* It was on the basis of genital morphology that *P. jackieburchi* was separated from *P. o. rubescens.* Although the shells of the two taxa are virtually indistinguishable, the anatomical differences are so

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striking that *P. jackieburchi* was initially described as a member of the genus *Samoana* (Kondo, 1980). Later studies of allozymes, however, showed that *P. jackieburchi* is very similar to other species of *Partula,* and very different from *Samoana* (Johnson et al., 1986c). Indeed, *P. otaheitana, P. jackieburchi,* and *P. affinis* cannot be distinguished by their allozymes or their mitochondrial DNA (Murray et al., 1991).

The genital characteristics of *P. jackieburchi* show a strong convergence toward the genus *Samoana,* resulting in great anatomical diversity within this closely related group of *Partula* species. While attempting to discover the relationships of *P. jackieburchi* and *P. otaheitana,* we have found another level of complexity. At several sites there are snails that do not fit the anatomical descriptions of any species. This finding was perhaps anticipated by Kondo's (1968) summary of unpublished observations: "A curious instance of a species having 3 distinct forms of genitalia occurs in Tahiti. Five of the 8 varieties (or subspecies) of *P. otaheitana* dissected show that two of them vary in anatomy according to valleys."

We have tried to find out whether the peculiar anatomical types represent geographic variation within, or genetic exchange between, taxa. Few studies of reproductive anatomy in gastropods quantify the variation within or between taxa. In the highly variable *P. otaheitana* group, however, such quantification is essential. In this paper we report the results of multivariate analyses of genital morphology and shell characters in samples of *P. otaheitana, P. jackieburchi, P. affinis,* and various types of intermediates, and compare them with data from laboratory hybrids between *P. otaheitana* and *P. jackieburchi.* We also compare the *Partula* species with two species of *Samoana.*

MATERIALS AND METHODS

Samples

We examined 108 adult *Partula* from 14 sites. Their locations are shown in Figure 1, and a summary of the samples is given in Table 1. The snails were initially identified using the anatomical drawings by Kondo & Burch (1979) and Kondo (1980). The samples contain 24 obvious *P. otaheitana,* 22 *P. jackieburchi,* 17 *P. affinis,* and 45 specimens of uncertain placement (Table 1). The sampling localities are concentrated in the eastern half of Tahiti Nui, the region where *P. otaheitana* and *P. affinis* are sympatric. All the securely identified *P. otaheitana* are *P. o. rubescens,* except those from Sample 801 (*P. o. crassa* "Pease" Garrett, 1884) and Sample 778 (*P. o. amabilis* Pfeiffer, 1846). All are sinistral, except two dextrals in Sample 778. All the *P. affinis* are dextral, except three sinistrals in Sample 791. As well as the samples of *Partula,* three individual *Samoana diaphana* Crampton & Cooke, 1953, from Moorea (one from Uufau; two from Faatoai) and seven *S. attenuata* (Pease, 1864) (five from Hotutea on Moorea; two from Tiarei on Tahiti) were included to allow comparison between the two genera.

Hybrids were obtained from laboratory matings between *P. otaheitana* from Papehue (Sample 801) and *P. jackieburchi* from Mahaena (Sample 780). Experimental matings within and between the species were set up to test the relative fertility of the interspecific matings, and the viability and fertility of the hybrids. The parents of the matings were wild-caught juveniles reared to maturity in isolation. Laboratory conditions were as described in earlier studies (Murray & Clarke, 1966). Unfortunately, neither the experimental matings nor the controls were very successful. Not enough young were produced to allow comparisons of fertilities. Nevertheless, mature offspring were produced by two interspecific matings. From one mating, both parents and three mature offspring were dissected. The parents of the second mating died, and were in too poor a condition for measurement of the anatomical traits, but two mature offspring of that mating were dissected.

Measurements

Seventeen anatomical characters were measured in each snail (Fig. 2): length of vas deferens (LVD), coded as 0 (stretched taut between penis and oviduct), 1 ("normal"), or 2 (heavily convoluted); length of penis (LPEN), including epiphalus, from its tip to the junction with the vagina; angle of retractor (ARET), measured on the side of entry of the vas deferens, between a line along the outside of the retractor and a line tangent to the penis at the point of attachment (to nearest 15°); angle of insertion of vas deferens (AVD) (to nearest 15°); distance from vas deferens

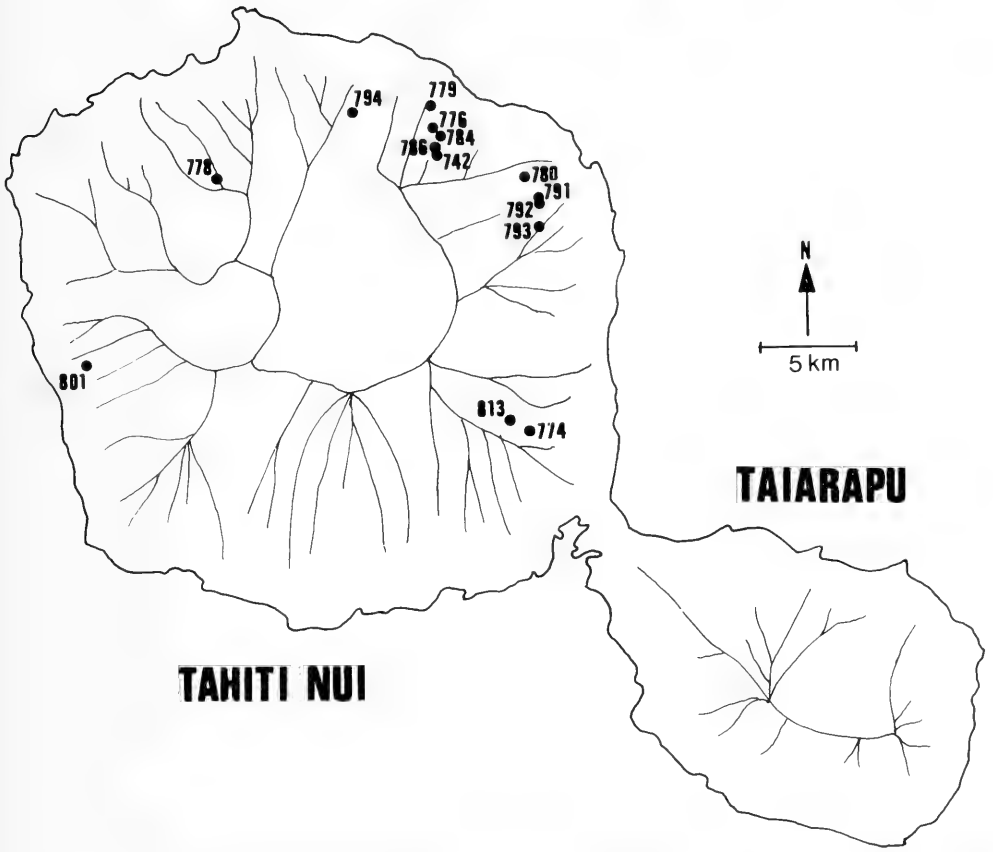

FIG. 1. Map of Tahiti, showing sampling sites for the *Partula otaheitana* group. Sample codes as in Table 1.

TABLE 1. Samples dissected for quantitative study of genital morphology in the *Partula otaheitana* group on Tahiti. Sample codes as in Fig. 1.

Sample	Valley	*P. otaheitana*	*P. jackieburchi*	*P. affinis*	unplaced
801	Papehue	4			3
778	Hamuta	6			
794	Papenoo	1		1	10
779	Faarumai	7		4	
776	Tiarei	2		1	
784	Tiarei	3			
786	Tiarei		1		
742	Tiarei	1	9		
780	north Mahaena		9		1
791	south Mahaena			7	
792	south Mahaena			4	25
793	south Mahaena				3
774	Faone		3		
813	Faone				3
TOTAL		24	22	17	45

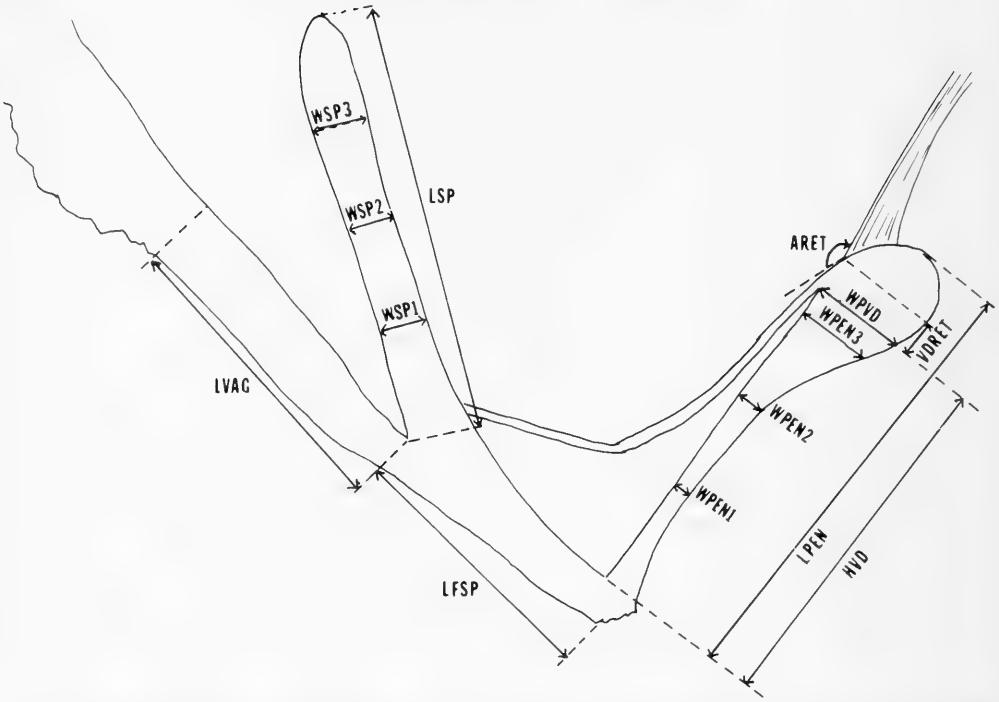

FIG. 2. Diagram showing the traits measured in the analysis of genital morphology. The traits LSG and LALB are not shown. See text for explanation.

to retractor (VDRET), measured on the proximal side of each; length of spermatheca, from its tip to junction with vagina (LSP); distance from the genital pore to junction of the spermatheca with the vagina (LFSP); length of vagina from its junction with the spermatheca to the beginning of the oviduct (LVAG); width of penis at the vas deferens (WPVD); width of penis at one quarter of its length from the genital pore (WPEN1); width of penis at three quarters of its length (WPEN3); distance from entry of vas deferens to the junction of the penis with the vagina (HVD); width of the spermatheca at its midpoint (WSP2); width of the spermatheca at one quarter of its length (WSP1); width of the spermatheca at three quarters of its length (WSP3); length of shell gland (LSG); length of albumen gland (LALB).

Although our interest in this group of species was initiated by Kondo's (1980) description of *P. jackieburchi,* we soon became aware that the overal variation of genital morphology transcends the specific problems raised by that work. It is this overall variation, and not the specific taxonomic questions, that is the focus of this study. We did not select the anatomical traits specifically with the *P. otaheitana* group in mind, so they do not replicate the set of traits used by Kondo (1968, 1980). Except for one addition (LFSP), they are the traits used previously to represent variation in *Partula* on Moorea (Murray & Clarke, 1980). Therefore, our selection of characters should not introduce any bias stemming from our perception of variation in the *P. otaheitana* group. Nevertheless, the set of traits is sufficiently comprehensive that it should reflect the major variations described by Kondo.

The shells of all but eight of the dissected *Partula* were also measured, producing 13 variables (for detailed descriptions, see Murray & Clarke 1980): length of shell (SHLEN); width of shell (SHWID); length of aperture (APLEN); width of aperture (APWID); length of spire (SPILEN); width of spire (SPIWID); width of upper suture (SUTWID); width of lip (LIPWID); thickness of lip (LIPTHIC); height of shell (SHHT); height of spire (SPHT); angle between columella and long axis of aperture (APANG); number of whorls (WHORL).

Measurements were made with vernier calipers to the nearest 0.1 mm. Anatomical measurements of the genitalia were made on camera lucida images, projected on a ground glass screen at a magnification of 5. All measurements were made by one person to ensure the consistency of any individual bias. The anatomical data are given in the Appendix.

Analyses

In morphometric studies, variation in size can overwhelm other components of variation. In order to minimize redundancy among the characters, it is important to correct for the underlying effect of size, and there are several possible approaches to this problem. Ratios are sometimes used, but they have severe statistical problems, and can produce misleading results (Atchley & Anderson, 1978). A more reliable approach is to use regression analysis, and adjust the variables to a standard size. Here, the relevant regression is that within species, rather than that in the total sample. A variable independent of size within species but correlated with size among species should not be "corrected" for size, because we are interested in species differences. We have used the length of the shell (SHLEN) as a measure of size. Within each species, each anatomical and shell variable was tested in a regression against SHLEN. If the average of the three intraspecific r^2 values was greater than 0.5, the variable was transformed. The transformed value was:

$$y' = y + m(\text{Average SHLEN} - \text{SHLEN})$$

where y is the original measurement, and m is the weighted average of the slopes of the within-species regressions (weighted by r^2).

Seven of the thirteen shell characters were transformed: SHWID; APLEN; APWID; SPILEN; SPIWID; SUTWID; SHHT. None of the genital traits required correction, as they were not significantly correlated with SHLEN within species. Three transformations were made to reduce redundancy among the anatomical characters themselves. HVD was scaled by its intraspecific regression on LPEN, in the manner described above. Because HVD is a part of LPEN, the transformation is an obvious one. Since WSP1, WSP2, and WSP3 are the widths of the spermatheca at different positions, a clearer indication of the relative widths is provided by expressing WSP1 and WSP3 as their differences from WSP2.

Because of damage, some anatomical measurements were missing in nine specimens of *Partula* (three with one missing value, two with two, and four with three). Missing values exclude an individual from many types of multivariate analysis. To avoid losing information, missing values were replaced by estimates derived from a multiple regression. Each variable with a missing value was used as the dependent variable with all of the other characters as independent variables in a multiple regression, calculated from all the specimens without missing values. Each missing value was then replaced by a calculated one based on the data available for the individual concerned. To test the usefulness of this approach, we tested the regression equations on the individuals for which we had complete data. For all the relevant characters, the correlation between actual values and the values predicted by the regressions was greater than 0.8, indicating that the estimates were reasonably accurate.

The modified data were analysed by two kinds of multivariate techniques. We used a principal components analysis of the genital characters to give a summary of the variation that was independent of our initial classification of the specimens. We used varimax rotation to produce axes that were the most easily interpretable in terms of the original variables. After the principal components had confirmed that the differences between species could be quantified, we used discriminant functions to maximize the separation between the groups. The functions then gave scores for the individuals initially classified as "unplaced." The data on shell variation were subjected to a separate discriminant analysis. The analyses were carried out using the SPSS-X routines at the University of Virginia.

RESULTS

Differences Between the Species

The principal components confirmed our visual impressions about the range of variation in genital anatomy. The first two axes (representing 37.2% and 10.6% of the original variation) show a clear separation of *P. otaheitana* from *P. jackieburchi* and *P. affinis,* and a weaker separation of *P. jackieburchi* from *P. affinis* (Fig. 3). Factor 1 separates *P. otaheit-*

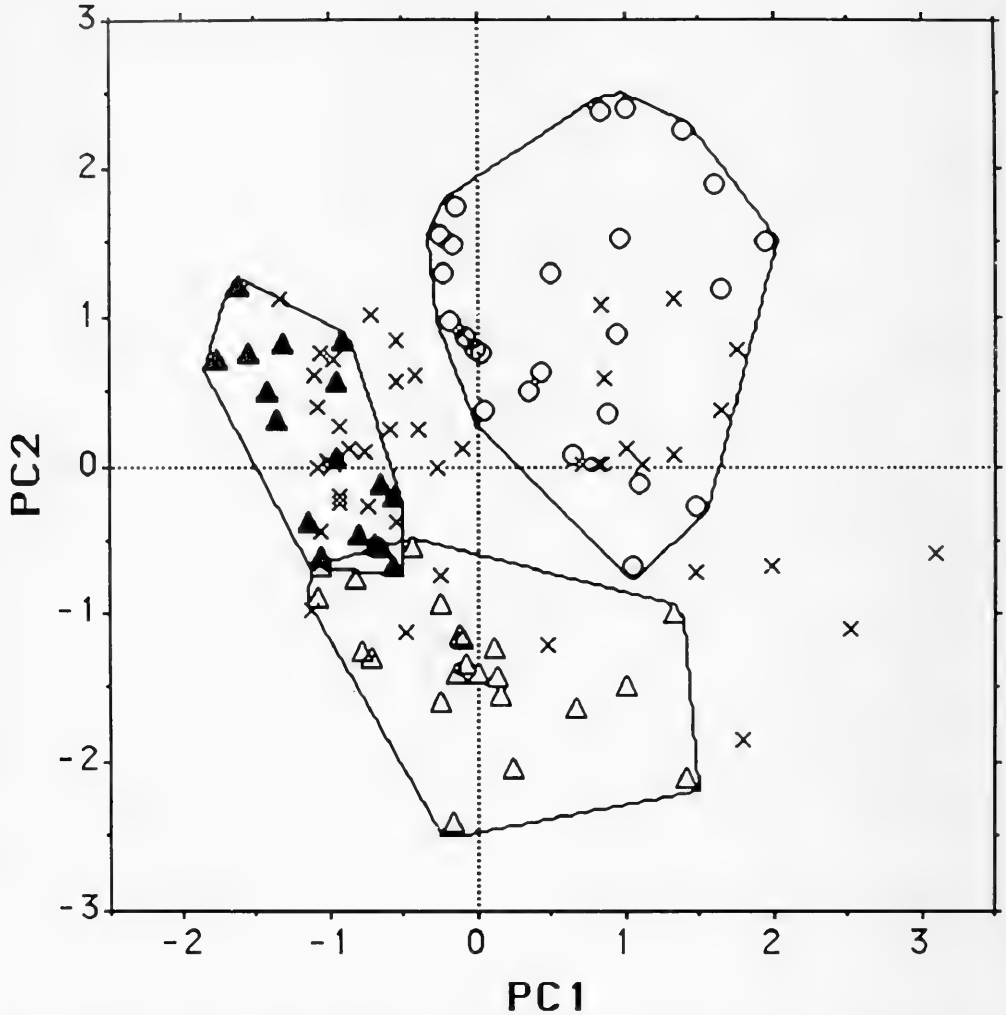

FIG. 3. Results of the principal components analysis of variation in genital morphology. Polygons enclose conspecifics of readily identifiable individuals. Circles = *P. otaheitana;* open triangles = *P. jackieburchi;* filled triangles = *P. affinis;* X = unknown.

ana from *P. affinis. Partula jackieburchi* broadly overlaps the others, but with intermediate average scores. High scores on this axis reflect the large, chunky shape of the *P. otaheitana* penis, with strong positive loadings for LPEN and WSP2, and reasonably strong ones for some other traits (Table 2). Factor 2 separates *P. jackieburchi* from the others. The strong negative loading of HVD and the positive loadings of VDRET, WPVD, and WPEN3 give *P. jackieburchi* negative scores, which reflect the distal insertion of the vas deferens into the relatively narrow penis. Populations within a species overlap each other on both axes, indicating that geographic variation is small compared to the differences between the species. Two more factors have eigenvalues greater than one, but they do not improve the separation of *P. jackieburchi* from *P. affinis.* The "unplaced" snails are variously intermediate, but spread over a wide range (Fig. 3).

The principal components illustrate two important points that underly later analyses. First, both the differences between species and the peculiarities of the "unplaced" snails

TABLE 2. Varimax factor loadings of traits in the principal components analysis of genital morphology in the *Partula otaheitana* group. Only traits with loadings greater than 0.5 on either of the first two principal components are included.

Variable	PC1	PC2
LPEN	0.735	0.334
VDRET	0.506	0.729
LSP	0.694	0.280
LFSP	0.646	0.146
WPVD	0.373	0.718
WPEN3	0.312	0.745
HVD	0.018	−0.843
WSP2	0.830	0.195
LSG	0.830	0.066

are shown clearly. Because the analysis does not use our a priori groupings, it confirms that the difficulty of identifying specimens was genuine. Second, the measured characters do a reasonably good job of quantifying the visual classification. Thus we can be confident, in moving to the discriminant analysis, that we are not making artificial groups. The principal components show that the specific groups are objectively recognizable, and the discriminant functions can be used to express their differences most effectively.

Discriminant analysis of *P. otaheitana, P. jackieburchi,* and *P. affinis* gives a picture similar to that given by the principal components, but, as expected, a clearer separation of the species (Fig. 4). The first discriminant function separates *P. otaheitana* from the others. This function is positively correlated with WPVD, WPEN3, and VDRET and negatively correlated with HVD, so that high scores represent the club-like shape of the penis in *P. otaheitana,* and its proximal insertion of the vas deferens. The second discriminant function separates *P. jackieburchi* and *P. affinis,* mainly by the smaller size of *P. affinis* (Table 3).

The discriminant functions based on genitalia correctly group all the members of the three species identified in the initial classification. Those based on shell characters do not do so well. The shells of 24 *P. otaheitana,* 17 *P. jackieburchi,* and 17 *P. affinis* were analyzed, and the discriminant analysis incorrectly classified 12% of the specimens from each species. Nearly all the separation between the species was by the first function, on which *P. jackieburchi* is intermediate between *P. otaheitana* and *P. affinis,* which do not overlap. The variable most strongly correlated with this function is shell length (Table 4).

Connections Between the Species

The possiblity of genetic exchange between anatomically different species is demonstrated by the hybrids between *P. otaheitana* and *P. jackieburchi* from the laboratory crosses. In the discriminant analysis of the genital morphology, the parents of mating MJ430 lie with their respective conspecifics, whereas the offspring are almost exactly intermediate (Fig. 4). Drawings of the genitalia of these hybrids, their parents, and a representative *P. affinis* are shown in Figure 5. The parents of the second mating (MJ431) could not be dissected, but the two mature offspring of that mating have scores on the first discriminant function that lie between those of the parental species. One of the offspring is close to the group from MJ430, but the other has a lower score for the second discriminant function, placing it between *P. otaheitana* and *P. affinis.* Although all of them lie between the parental species, the hybrids span a wide range of discriminant scores.

In the analysis of genital morphology, the "unplaced" snails also show a wide range of intermediate values, overlapping the specific groups, and bridging the gaps between them (Figs. 2, 3). We were able to measure the shells of 44 "unplaced" snails and assign them scores from the discriminant functions based on the identified groups. The relationship between the variation in genital morphology and the shells can be seen by comparing the individual scores on the first discriminant functions for each set of traits (Fig. 6). Taken together, these two functions completely distinguish *P. otaheitana,* and nearly separate *P. jackieburchi* and *P. affinis.* The scores on the two functions are significantly correlated both for the combined sample of identifiable individuals ($r = -0.74$, $P<0.001$) and for the "unplaced" snails ($r = -0.57$, $P<0.001$). Nevertheless, it is clear from Figure 6 that many of the unknowns have shells like *P. otaheitana* but intermediate genitalia. Furthermore, the association of the two sets of traits is between groups, most clearly between *P. otaheitana* and *P. affinis.* They are not correlated within any of the three species (Fig. 6).

Using these analyses, we can look in detail at each of the samples with "unplaced" snails. Discriminant scores for the genital morphology of these snails blur the distinc-

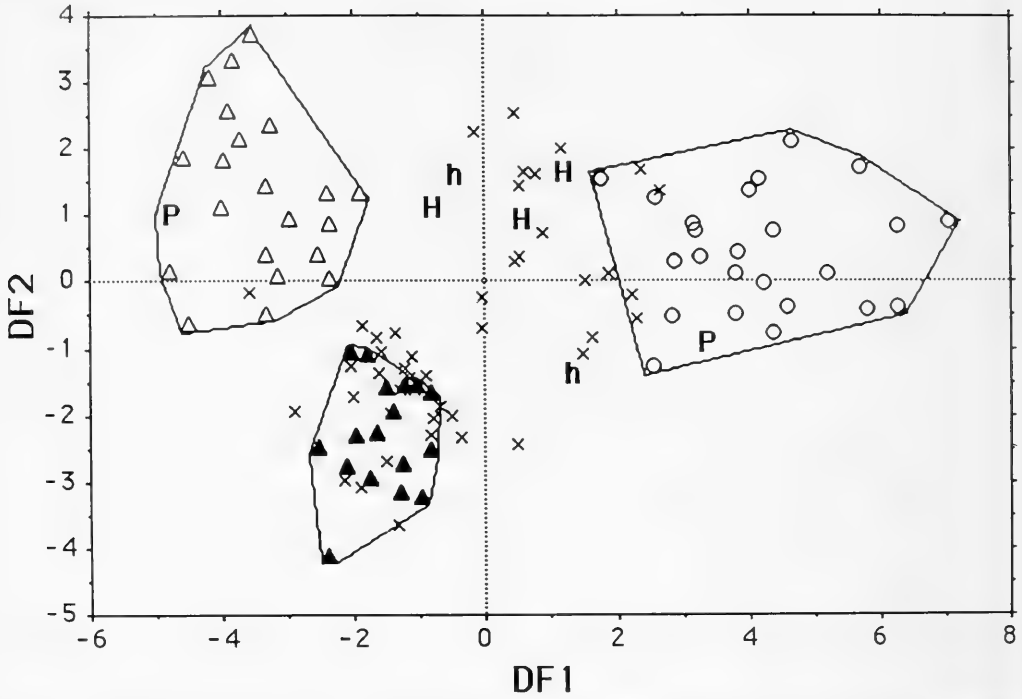

FIG. 4. Discriminant scores from the analysis of genital morphology. Symbols as in Fig. 3. Additional symbols: P = parents for mating MJ430; H = F_1 from MJ430; h = F_1 from MJ431.

TABLE 3. Pooled within-groups correlations between the traits and the discriminant functions in the analysis of differences in genital morphology between *P. otaheitana, P. jackieburchi,* and *P. affinis.* Only traits with a correlation of at least 0.4 with one of the two functions are included.

Variable	DF1	DF2
WPVD	0.743	0.042
WPEN3	0.581	−0.049
VDRET	0.534	0.129
HVD	−0.404	0.190
WPEN1	0.080	0.489
LPEN	0.341	0.477
LSP	0.219	0.438

TABLE 4. Pooled within-groups correlations between the traits and the discriminant functions in the analysis of differences in shells between *P. otaheitana, P. jackieburchi,* and *P. affinis.* Only traits with a correlation of at least 0.4 with one of the two functions are included.

Variable	DF1	DF2
SHLEN	0.857	−0.451
SPWID	−0.039	−0.485
APWID	−0.251	0.420

tions between the three species, but each sample has its own characteristics (Fig. 7).

Sample 801 from Papehue on the western side of Tahiti is the source of the *P. otaheitana* parents in the experimental matings. The sample has seven snails, all of which are sinistral. Four of them are clearly *P. otaheitana.* One of the "unplaced" snails also falls within *P. otaheitana,* but the other two are intermediate between *P. otaheitana* and the other two species (Fig. 7).

Sample 794 is from the lower section of the large central valley of Papenoo. It includes typical *P. otaheitana,* but it also spans the range of intermediates, suggesting connections between *P. otaheitana* and either *P. affinis* or *P. jackieburchi,* or both (Fig. 7). With one exception, the individuals with intermediate genitalia have shells that resemble *P. otaheitana.*

The sample from north Mahaena (780) is not problematical. The one doubtful individual is clearly *P. jackieburchi,* making a total of ten *P. jackieburchi.* Sample 793 from south Ma-

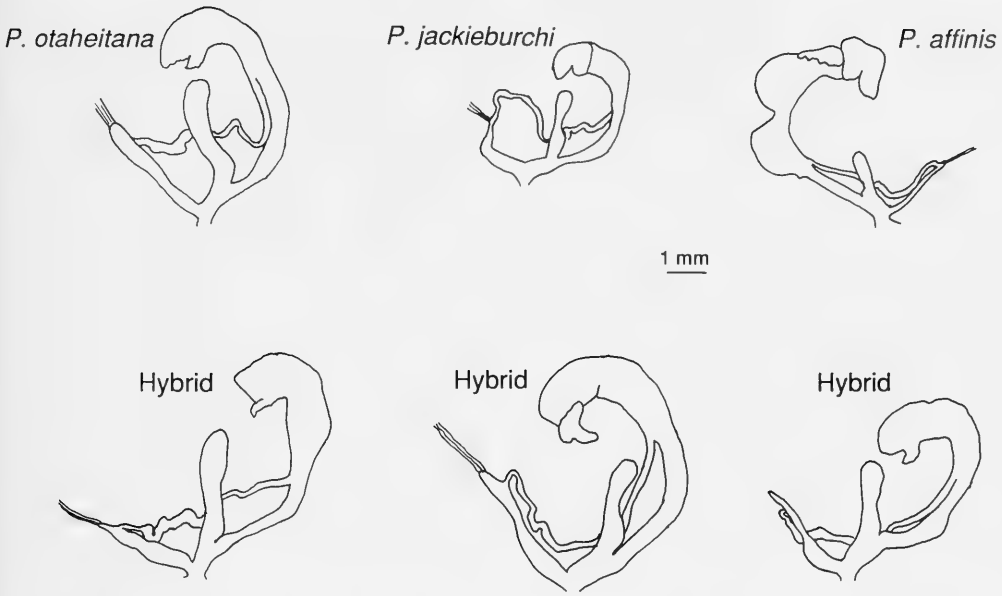

FIG. 5. Reproductive anatomies of the parents (*P. otaheitana* and *P. jackieburchi*) and the F_1 hybrids of laboratory mating MJ430, drawn from camera lucida images. A typical *P. affinis* from sample 779 is included for comparison.

haena, however, does have peculiar individuals. This sample contains three large sinistral snails with pink shells, taken from a high ridge. One lies within *P. otaheitana,* but the other two are anatomically intermediate (Fig. 7).

Sample 792, also from south Mahaena, is a more complicated mixture. With the exception of four variously intermediate individuals, the discriminant analysis of the genitalia made this group overlap, but offset from, unambiguous *P. affinis* (Fig. 7). There is a range of shell types connecting *P. affinis* with the other species. The group is polymorphic for the direction of coiling. Seven individuals are dextral, including the four snails that were clearly *P. affinis* on visual inspection of their genitalia. These four also have shells that are typical of *P. affinis,* so they pose no problem. The multivariate analyses showed that the other three dextrals are also *P. affinis,* although the shell of one of them is not clearly so.

Among the sinistrals, variation connects all three species. Several have genitalia similar to *P. affinis,* but most of these are displaced from the clear *P. affinis* group containing the dextral individuals (Fig. 7). Others have shells like *P. otaheitana* but genitalia of intermediate character. Within the group of sinistrals, scores on the first discriminant functions for genitalia and shells are significantly correlated ($r = -0.474$, $P = 0.026$). To examine this variation more closely, a separate principal components analysis was made using the genitalia of Sample 792 alone (Fig. 8; Table 5). The first axis, representing 22.5% of the variation, separates two of the sinistrals from all the others. With high loadings from LPEN, LFSP, WSP2, and LSG, this component is similar to the first component in the analysis of all specimens (Table 2). The high scores of the two distinct individuals reflect their larger size and greater similarity to *P. otaheitana.* They have large, yellow shells with a pink apex, typical of *P. o. rubescens* or *P. jackieburchi.* The second principal component (16.7% of the variation) confirms the difference between the dextrals and the sinistrals. The dextrals, which include typical *P. affinis,* all have relatively high scores. The sinistrals, in contrast, span the range of scores, but are concentrated at the lower end (Fig. 8). A low score on the second component indicates a penis that is relatively thick in the middle region and thin at the distal end, and a relatively long spermatheca (Table 5), suggesting some similarities to *P. jackieburchi.* The snails with low scores tend to have shells with some

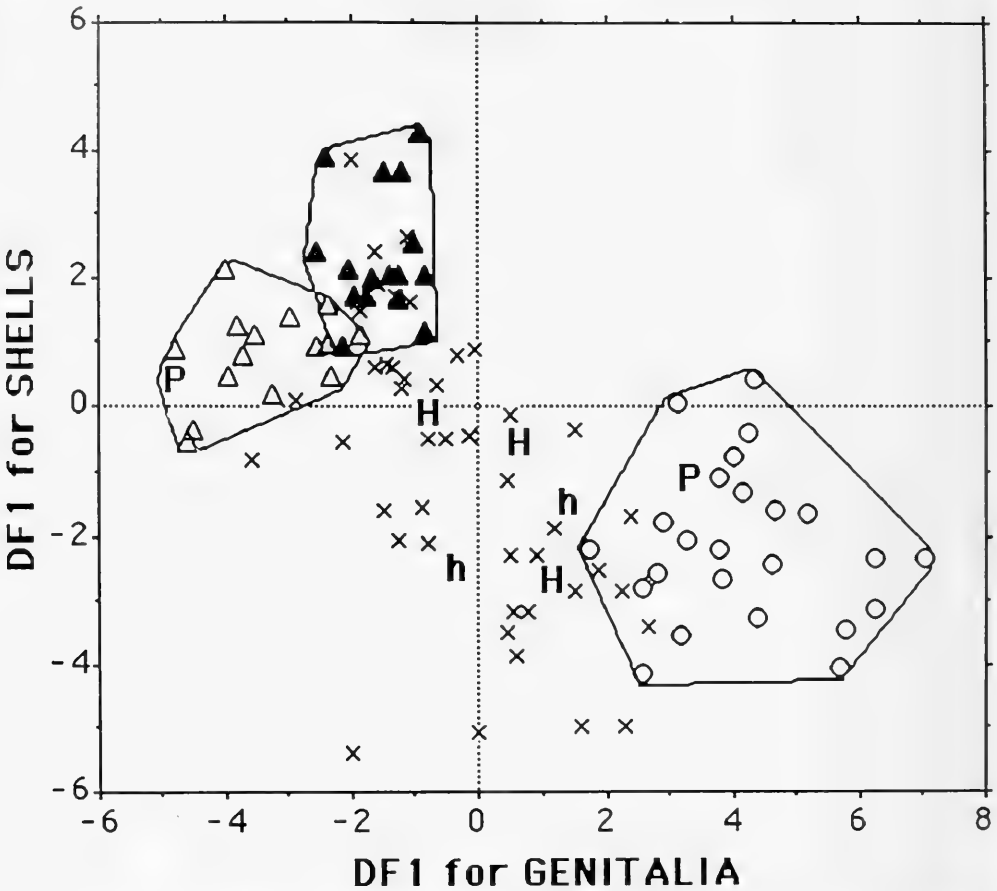

FIG. 6. Relationship between the discriminant scores based on analyses of shells and genitalia. Symbols as in Figs. 3 & 4.

yellow or pink, similar to *P. o. rubescens* or *P. jackieburchi.* From this analysis, it is clear that this is a heterogeneous sample, which cannot be explained simply as aberrant *P. affinis.*

The final sample with individuals that were difficult to identify is number 813, in the southeastern valley Faone. This sample includes seven snails, only three of which could be dissected. Two shells are brown dextrals, typical of *P. affinis.* The dissected dextral also has genitalia typical of *P. affinis* (Fig. 7). The other five snails are large sinistrals, with the appearance of either *P. o. sinistrorsa* "Pease" Garrett, 1884, or *P. a. producta* Pease, 1864, which are sympatric and conchologically indistinguishable in southwestern portion of Tahiti Nui (Kondo & Burch, 1983). Four of these have the cestata banding morph, whereas the fifth is apex, both morphs being common in *P. o. sinistrorsa* (see Crampton, 1916). One of the dissected sinistrals has genitalia intermediate between *P. affinis* and *P. otaheitana,* whereas the other is within the range of typical *P. affinis* (Fig. 7).

Taken together, these samples suggest connections between *P. affinis* and *P. otaheitana,* and possibly *P. jackieburchi.* Although each sample has its unique features all the samples with anatomically intermediate snails contain individuals that lie unambiguously within one of the three species. Thus, we have not found any purely intermediate populations.

Comparisons Between *Partula* and *Samoana*

In order to see how the differences between the species of *Partula* compare with

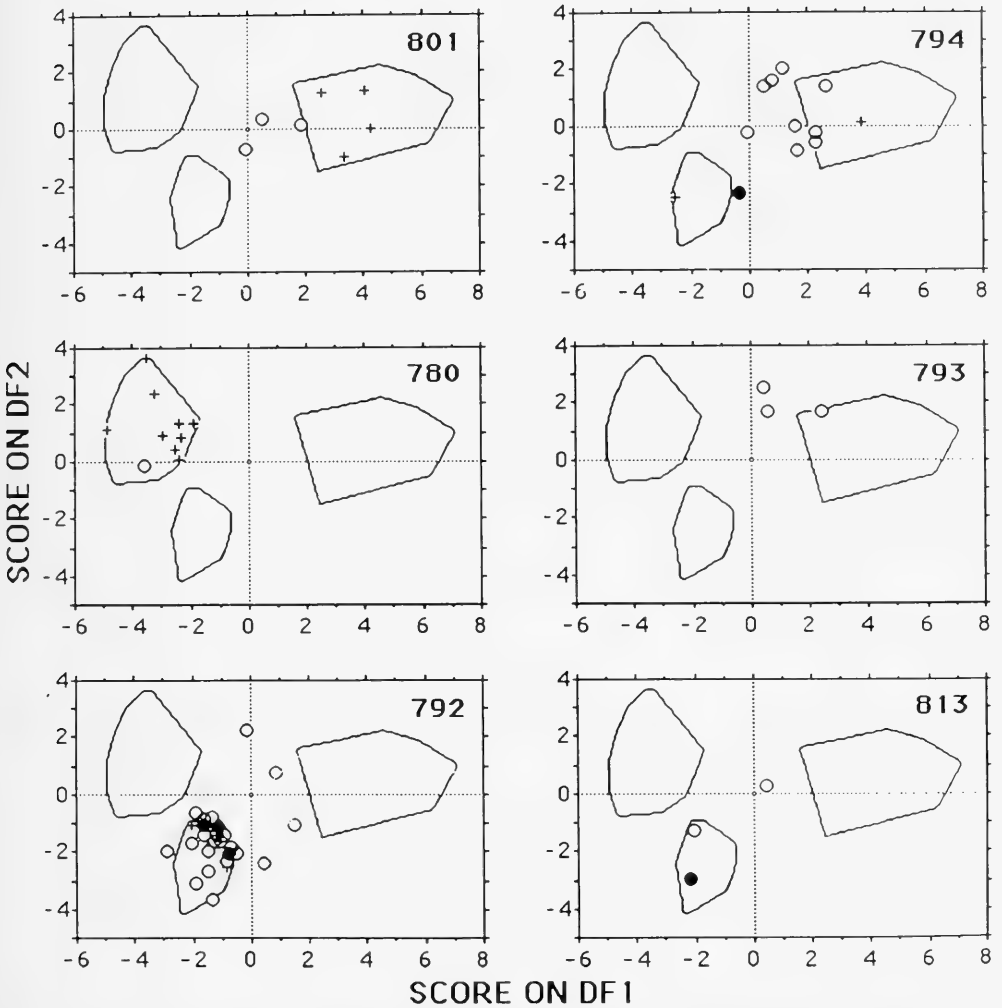

FIG. 7. Discriminant scores from the analysis of the genital morphology for samples with "unplaced" snails. Sample codes as in Fig. 1 and Table 1. Polygons indicate areas occupied by typical *P. otaheitana, P. jackieburchi,* and *P. affinis* as in Fig. 4. Open circles = sinistral unplaced; filled circles = dextral unplaced; + = individuals originally in the known groups.

the differences between the genera, a discriminant analysis of the genitalia was made, using the four groups *P. otaheitana, P. jackieburchi, P. affinis,* and the combined samples of *Samoana attenuata* and *S. diaphana.* The overall separation of these groups is good, and all the snails were correctly placed in their prescribed groups. The separation on the first two axes is essentially the same as in the earlier analysis of *Partula* alone: *P. otaheitana* is separated from the others on the first, whereas *P. jackieburchi* and *P. affinis* are separated on the second (Fig. 9). The two species of *Samoana* are intermediate but overlapping with *P. jackieburchi* and *P. affinis.* Thus, the major separation is between the species of *Partula,* not between the genera. This is not surprising for *P. jackieburchi,* which was at one time placed within *Samoana,* but it was not expected for *P. affinis.* On the third discriminant axis there is partial separation of *Samoana* from *P. jackieburchi* and *P. affinis* (Fig. 9). The trait contributing the most to that separation is the relative width of the proximal

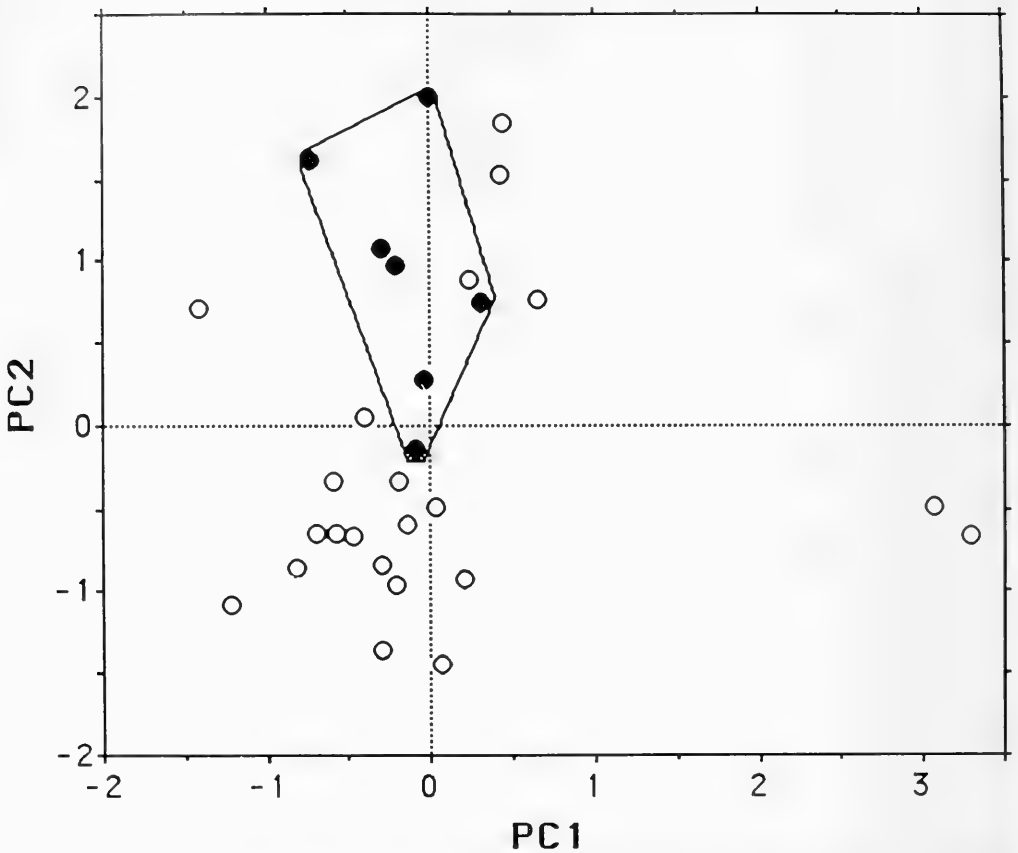

FIG. 8. Principal components scores for the analysis of genital morphology within Sample 792. Polygon encloses dextral individuals. Open circles = sinistrals; filled circles = dextrals.

TABLE 5. Varimax factor loadings of traits in the principal components analysis of genital morphology in Sample 792. Only traits with loadings greater than 0.5 on either of the first two principal components are included.

Variable	PC1	PC2
LPEN	0.634	0.049
LSP	0.356	−0.644
LFSP	0.752	−0.200
WPVD	−0.101	0.772
WPEN1	0.080	0.884
WPEN3	−0.154	0.845
WSP2	0.783	−0.140
LSG	0.877	−0.074

section of the penis (WPEN1). The low scores of *S. attenuata* and *S. diaphana* reflect the stout penis with thickened middle region.

DISCUSSION

The complexity of variation revealed in this study is important both for understanding the radiation of *Partula* on Tahiti and for tackling general problems of snail systematics. Our interest began with Kondo's (1980) discovery of a dramatically different anatomical form within *P. o. rubescens,* and his description of that form as *Samoana jackieburchi.* Comparisons of allozymes showed this placement to be incorrect, as this taxon clearly lies within *Partula,* and is genetically very similar to *P. otaheitana* and *P. affinis* (Johnson et al., 1986c). Later work on mitochondrial DNA has confirmed the close association of these three species (Murray et al., 1991).

The present study shows clearly that the overall differences in genital morphology are between the species, and not between the

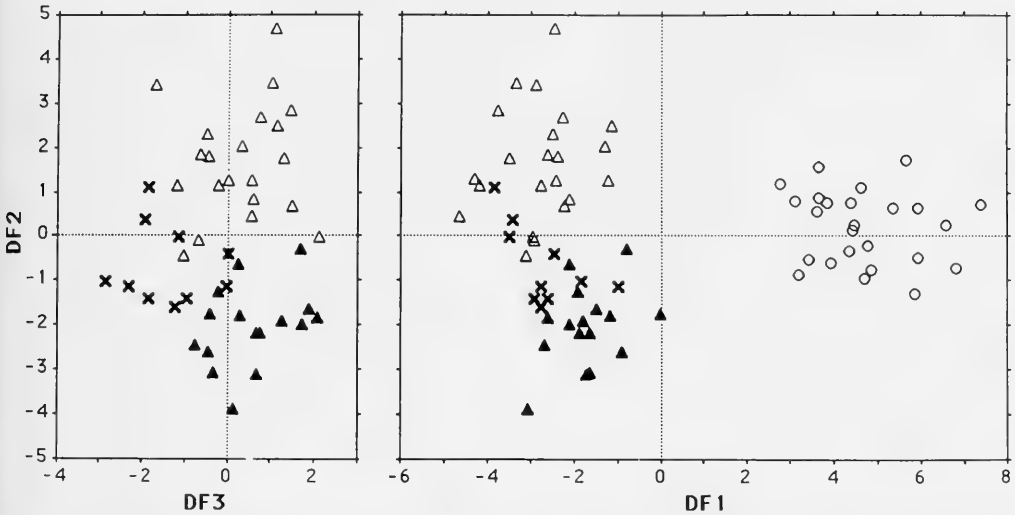

FIG. 9. Discriminant scores for the analysis of genital morphology in *P. otaheitana* (circles), *P. jackieburchi* (open triangles), *P. affinis* (filled triangles), and *S. attenuata* and *S. diaphana* (X). Scores for *P. otaheitana* on the third discriminant function span a wide range, and are omitted for clarity.

genera. There are two conclusions to be drawn from the comparison of *Partula* and *Samoana*. First, if there are consistent differences separating the genera, we have not measured them. However, because the analyses within *Partula* discriminate the main groups already recognized, our chosen set of characters has provided a reasonable description of the variation. The multivariate analyses show that the definition of the groups does not depend on some special weighting of certain "important" characters. The second conclusion is that, regardless of whether there are other anatomical differences between the genera, there is convergence of anatomical characteristics between *P. jackieburchi* (and *P. affinis*) and *Samoana*. Convergence, rather than retention of ancestral characteristics, is indicated by the fact that the Tahitian species of *Partula* are apparently derived from Moorean ancestors (Johnson et al., 1986b), but none of the Moorean species share the anatomical characteristics with *Samoana* (Murray & Clarke, 1968, 1980).

Even more interesting than this convergence is the demonstration, by the experimental matings, that snails with "generically different" genital morphologies can interbreed, producing viable hybrids. It is significant in this respect that the laboratory hybrids between *P. jackieburchi* and *P. otaheitana* have intermediate morphologies. They show no sign of aberrant genitalia that might suggest developmental problems (cf. Murray & Clarke, 1980). As discussed below, the field results also suggest that these species can exchange genes, despite their anatomical differences. A similar situation occurs on Moorea, where *Partula aurantia* Crampton, 1932, has a large, club-like penis, which distinguishes it from all other species on the island, but does not prevent its hybridization with *P. suturalis* Pfeiffer, 1855 (Murray & Clarke, 1968). It is clear that, in *Partula* at least, differences in genital morphology have little impact on reproductive isolation, and do not necessarily have special value as taxonomic characters. In this light, we must view with caution the proposed taxonomic revision of the Tahitian Partulidae based solely on reproductive anatomy (Kondo & Burch, 1983).

The complexity of the *P. otaheitana* group has long been recognized on the basis of the variation in their shells (Crampton, 1916). Rather than simplifying the complexity, our results increase it. It is important, however, to exclude possible artefacts before attempting to interpret the multivariate patterns of variation in genital morphology. Measurement errors, state of preservation, and reproductive state can have marked effects on analyses of genital morphology (e.g. Emberton, 1985, 1989). Some of the variation of discriminant

scores within the clearly defined groups or among siblings from the laboratory crosses might be due to such errors. However, the ability of our multivariate analyses to recognize the groups described by Kondo (1968, 1980; Kondo & Burch, 1983) indicates that the major variations are real. Furthermore, the intermediacy of the laboratory hybrids provides strong evidence that we are looking at heritable differences between groups. Thus, we can be confident that any spurious variation in our measurements is small enough to justify examination of the geographical and taxonomic patterns of the variation in the *P. otaheitana* group.

Based on our analyses, it is clear that some combinations of species are distinct in sympatry, without any sign of interbreeding. *Partula affinis* can coexist with either *P. otaheitana* or *P. jackieburchi.* The situation between *P. otaheitana* and *P. jackieburchi* is not as clear. Tiarei is the only valley in which both have been found, and they are found together only in Sample 742. Even that case is marginal, however. The genitalia of 34 individuals from that site were examined (ten of which were measured for this study). Only one was *P. otaheitana,* and 33 were *P. jackieburchi.* About 1.5 km lower down the valley, near site 776, a sample of 17 individuals was examined (but not measured), and all were *P. otaheitana.* Attempts to collect along a transect between the sites were not very productive, because the snails were scarce, but the few snails obtained were *P. otaheitana.* In our samples outside Tiarei, distinct *P. otaheitana* were found only to the north and west, and distinct *P. jackiebruchi* only to the south (Table 1). Thus, it appears that *P. otaheitana* and *P. jackieburchi* are, at least locally, parapatric replacements. However, there is some uncertain evidence for the occurrence of *P. otaheitana* to the south in Mahaena (see below), and much more sampling would be needed to describe the geographical distributions of the two species.

In contrast to the coexistence, or abrupt transition, between species is the existence of variously intermediate individuals at several sites. It is difficult to know how much of this intermediacy is due to geographic variation within species and how much to exchange of genes between species. The possibility of gene exchange is shown by the laboratory hybrids between *P. jackieburchi* and *P. otaheitana,* and by the fact that in the discriminant analysis the hybrids lie amongst the "unplaced" snails from the field samples (Fig. 4). Gene exchange is also suggested by the correlation between genital anatomy and shell shape among the "unplaced" snails and between species, but not within species (Fig. 6). However, the strength of the evidence for hybridization differs from sample to sample.

One difficulty is that hybrids are not easy to identify. Although they are intermediate in their anatomy, even the sibling hybrids show a wide range of discriminant scores (Fig. 4). It is therefore difficult to separate hybrids of *P. otaheitana* and *P. jackieburchi* from hybrids of *P. otaheitana* and *P. affinis.* In Sample 794 from Papenoo, for example, the snails vary from obvious *P. affinis,* with small, brown, dextral shells, to *P. otaheitana,* with large, pink or yellow, sinistral shells. All the individuals with intermediate genital morphologies, however, have shells like *P. o. rubescens,* with no sign of introgression from *P. affinis.* Since typical *P. otaheitana* occur on either side of this valley, it seems unlikely that the intermediates represent an unusual geographic variant of *P. otaheitana.* It is not clear, however, whether *P. otaheitana* is exchanging genes with *P. affinis* (without any apparent effect on the shells) or with *P. jackieburchi* (which has not been reported from Papenoo).

Similar problems apply to other samples. In Sample 801 from Papehue, for example, there are typical *P. otaheitana* and apparent hybrids, but the shells are all typical of *P. otaheitana.* Furthermore, neither *P. affinis* nor *P. jackieburchi* is known from the western series of valleys. Similarly, Sample 793 from Mahaena includes *P. otaheitana* and possible hybrids with *P. jackieburchi,* but the presence of *P. jackieburchi* has not been established. Although exchange of genes between species seems to be the most likely explanation for these samples, we cannot exclude the possibility of local differentiation.

The most convincing evidence for hybridization is in Sample 792, also from Mahaena. In this chirally polymorphic population, the dextrals are typical *P. affinis,* but the sinistrals show a spread between *P. affinis* and *P. otaheitana* for both genital and shell morphology. Taken together, samples 792 and 793 suggest that a thorough search would reveal typical *P. otaheitana* in Mahaena.

Another connection between *P. affinis* and *P. otaheitana* is suggested by Sample 813 from Faone, the southernmost valley in this study. Whereas the dextral individual is clearly *P. affinis,* with a small, brown shell, the

sinistrals have shells typical of *P. o. sinistrorsa* (Crampton, 1916, plate 30), and genitalia either like *P. affinis* or intermediate between *P. affinis* and *P. otaheitana.* Crampton (1916) did not find *P. o. sinistrorsa* in Faone, but reported large numbers from the valleys that connect to its southern ridge. Kondo & Burch (1983) also found large sinistrals with genitalia like *P. affinis* in Faone. They considered these to be the subspecies *P. a. producta,* which they say is conchologically indistinguishable from *P. o. sinistrorsa.* If their interpretation is correct, their subspecies *P. a. affinis* and *P. a. producta* are sympatric. In either case, the sinistral individual with intermediate genitalia indicates a connection between *P. affinis* and *P. otaheitana* at the southern end of Tahiti Nui.

These results pose more questions than they answer. Regardless of how we explain the existence of intermediate specimens, the variation in genital morphology fills the gaps between the currently recognized species. Although these species retain their distinctness in some areas, the connections demonstrate the complexity of the group. Faced with this variation, it is clear that only comprehensive study, based on intensive geographic sampling, dissection of large samples, and quantitative analysis will resolve the relationships within the *P. otaheitana* group. These species are now almost certainly extinct in the wild (Murray et al., 1988), so that further work must rely on preserved specimens.

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APPENDIX. Data for analysis of genital morphology in the *P. otaheitana* group. See text for explanation of variables.

Site	Snail	Sp	LVD	LPEN	ARET	AVD	VDRET	LSP	LFSP	LVAG	WPVD	WPEN1	WPEN3	HVD	WSP2	WSP1	WSP3	LSG	LALB
801	5	unk	1	434	170	30	91	268	80	191	40	23	42	362	49	44	51	190	206
801	6	ota	2	268	170	120	41	273	81	174	36	33	37	209	46	53	77	199	173
801	7	unk	1	430	180	90	55	245	77	210	41	30	40	375	42	52	47	222	201
801	8	ota	2	320	180	15	86	233	106	213	33	31	34	242	57	51	73	193	170
801	9	unk	1	465	180	30	82	271	76	170	36	26	53	377	56	60	77	232	214
801	10	ota	1	326	170	120	57	283	101	208	27	29	39	274	49	56	66	202	128
778	1	ota	1	458	180	120	129	288	192	324	72	28	76	324	52	73	83	211	117
778	2	ota	1	418	135	90	96	311	160	287	78	38	75	335	41	59	60	205	133
778	4	ota	1	311	150	15	83	224	111	230	40	22	37	218	44	60	63	136	202
778	5	ota	1	341	195	90	80	262	141	195	51	31	47	269	42	61	67	204	221
778	7	ota	1	487	165	30	118	321	225	389	73	33	78	346	50	78	75	233	134
778	8	ota	1	368	150	15	82	221	117	237	53	30	53	280	37	60	58	186	218
794	1	unk	2	322	135	150	78	267	106	131	29	31	25	241	40	47	62	188	97
794	2	unk	2	279	125	30	62	307	90	133	39	28	31	204	62	81	80	186	90
794	3	unk	1	280	180	135	52	287	95	191	36	29	36	219	48	52	51	235	161
794	6	unk	1	298	150	135	52	261	110	176	32	32	34	250	50	77	80	227	149
794	7	unk	1	403	120	150	73	293	121	218	31	33	31	341	48	62	72	238	90
794	8	aff	1	157	195	180	12	118	85	190	12	15	12	157	20	20	35	147	115
794	9	unk	1	207	165	135	48	197	75	140	15	17	15	150	47	50	60	171	198
794	22	unk	2	273	165	15	84	284	97	132	32	25	32	194	68	72	86	202	99
794	23	unk	1	316	165	105	69	277	96	176	35	25	35	242	44	52	50	218	138
794	26	unk	1	313	165	120	54	256	105	183	30	28	32	257	43	75	76	224	142
779	1	ota	1	357	165	15	78	337	127	270	56	41	56	261	31	38	66	160	195
779	2	ota	1	353	150	15	76	304	103	258	65	45	61	252	50	54	84	206	161
779	3	ota	1	376	165	15	77	311	123	234	50	53	45	303	37	45	52	174	141
779	4	ota	1	361	150	15	82	310	116	201	73	43	84	287	30	44	50	169	177
779	5	ota	1	355	180	15	81	254	113	166	91	51	91	266	41	63	62	210	198
779	7	ota	1	288	165	15	61	253	127	248	74	44	73	213	41	66	57	182	191
779	9	ota	1	374	180	15	78	309	123	215	58	42	48	293	36	46	72	178	174
779	12	aff	1	191	180	135	12	129	61	223	15	19	16	178	32	32	37	137	163
779	13	aff	1	217	180	15	15	132	60	225	20	27	21	191	23	19	34	120	165
779	22	aff	1	180	180	105	11	112	56	216	13	20	15	167	19	32	38	156	166
779	23	aff	1	219	180	15	22	123	76	270	17	25	18	192	32	26	39	108	161
776	2	aff	1	158	135	2	15	159	100	144	16	19	21	150	41	30	49	149	231
776	1	ota	1	398	135	15	141	325	146	247	72	48	73	258	66	84	94	256	173
776	21	ota	1	439	135	15	135	318	146	256	70	45	73	288	53	77	74	219	179
784	1	ota	1	455	165	90	138	332	219	345	54	35	58	317	45	63	62	228	185

784	2	ota	1	444	165	60	120	319	176	318	62	36	60	332	43	61	71	183	212
784	3	ota	1	452	120	15	85	290	106	234	78	57	76	342	40	78	64	200	249
786	1	jac	1	292	180	90	24	111	95	206	8	33	8	268	25	22	25	127	113
742	1	jac	1	210	150	15	12	116	73	235	6	32	6	192	35	30	57	104	206
742	2	jac	1	195	150	15	11	89	81	196	8	38	8	187	28	18	42	137	164
742	4	jac	1	258	150	15	12	197	133	421	7	49	6	254	27	24	52	170	268
742	5	jac	1	210	180	15	15	49	151	400	18	55	16	190	44	41	40	175	182
742	6	jac	1	265	150	15	12	256	114	234	11	51	9	254	25	34	32	167	162
742	7	jac	2	204	180	15	15	133	126	157	14	37	18	189	34	36	47	132	182
742	8	jac	2	248	180	15	12	211	83	151	7	39	10	235	29	29	30	146	191
742	9	jac	2	257	180	15	11	121	72	138	11	55	8	246	44	34	45	180	206
742	10	jac	1	259	180	15	12	189	79	183	13	47	10	247	28	26	29	133	215
742	30	ota	1	325	135	2	108	306	308	96	72	45	86	206	57	68	91	208	163
780	2	jac	1	326	180	60	26	283	202	297	15	42	17	303	46	51	68	194	221
780	3	jac	1	223	180	135	8	218	89	197	19	30	8	217	30	40	50	175	245
780	4	jac	2	305	180	90	16	216	60	123	12	27	24	287	31	40	54	140	195
780	21	jac	1	223	180	30	10	255	102	247	12	31	25	213	26	27	50	170	184
780	22	jac	1	253	180	90	26	268	81	241	13	35	13	230	31	42	52	192	221
780	23	jac	1	290	180	60	29	363	127	268	12	26	8	267	30	40	57	146	191
780	25	jac	1	372	180	90	40	298	168	305	8	28	8	329	31	40	37	148	177
780	26	jac	1	333	180	135	32	283	131	250	9	21	11	302	42	40	45	158	104
792	4	unk	1	252	180	135	69	211	84	240	13	26	15	181	21	26	41	149	125
792	5	unk	1	309	180	135	75	255	125	201	15	22	16	242	50	52	82	255	191
792	6	unk	1	240	180	90	70	169	81	163	15	25	13	175	29	26	45	125	205
792	7	unk	1	264	180	150	81	164	86	238	23	37	23	186	31	31	54	132	246
792	8	unk	1	217	180	120	37	195	83	225	15	24	20	181	21	26	48	143	297
792	10	unk	2	200	180	120	41	187	84	181	13	24	19	164	25	28	36	178	234
792	11	unk	1	277	180	90	80	203	67	114	23	28	25	197	31	34	52	188	188
792	12	unk	1	245	135	165	50	169	71	167	16	30	31	191	20	28	42	122	134
792	13	unk	2	254	180	45	32	195	120	209	17	23	15	226	51	56	63	275	217
792	15	unk	1	207	180	180	48	172	52	115	16	18	16	161	28	29	34	107	160
792	16	unk	1	243	180	135	70	250	111	232	14	25	14	175	26	43	41	139	181
792	17	unk	1	234	180	90	28	162	69	195	19	31	26	203	24	25	47	140	173
792	19	aff	1	247	180	135	54	111	50	111	24	32	28	191	27	28	37	113	191

(*continued*)

APPENDIX (Continued)

Site	Snail	Sp	LVD	LPEN	ARET	AVD	VDRET	LSP	LFSP	LVAG	WPVD	WPEN1	WPEN3	HVD	WSP2	WSP1	WSP3	LSG	LALB
792	20	aff	1	242	180	135	26	234	72	175	19	28	28	217	26	35	36	131	161
792	21	unk	1	263	180	90	58	208	94	240	18	29	27	204	25	28	39	126	197
792	26	aff	2	217	180	90	33	146	55	99	27	26	30	186	29	30	44	146	196
792	30	aff	1	224	180	135	29	91	70	221	25	32	32	194	32	30	44	142	169
792	34	unk	1	255	180	135	71	196	72	141	14	28	21	180	27	25	31	138	130
792	35	unk	2	142	180	30	36	140	67	117	29	26	29	105	26	32	50	116	121
792	38	unk	1	244	180	165	50	178	77	150	14	21	17	195	22	27	51	136	171
792	39	unk	1	244	180	90	88	250	70	185	14	20	13	161	29	30	28	126	166
792	41	unk	1	290	180	90	58	199	85	176	18	28	28	232	25	26	47	105	218
792	43	unk	1	256	180	120	53	193	69	201	11	21	19	207	25	28	37	124	132
792	44	unk	1	247	180	105	39	219	62	150	15	20	15	215	29	32	61	126	170
792	50	unk	1	220	180	165	38	210	71	131	11	17	18	190	39	29	45	118	150
792	51	unk	1	225	180	90	26	228	64	185	15	20	22	198	22	41	62	123	142
792	52	unk	1	237	180	165	66	157	70	179	13	24	13	168	31	35	54	110	156
792	53	unk	1	219	180	165	37	183	91	216	13	23	18	184	23	32	49	100	156
792	57	unk	1	237	180	120	36	185	85	184	19	18	23	196	20	35	45	133	199
793	1	unk	1	374	180	120	61	275	162	325	23	30	26	313	61	67	72	270	156
793	2	unk	1	412	180	90	83	314	145	260	26	27	26	337	70	60	87	275	100
793	3	unk	1	409	180	30	69	237	154	307	22	23	20	346	58	58	75	179	102
774	4	jac	1	176	180	180	0	140	72	143	5	37	14	176	34	30	34	167	246
774	11	jac	1	181	180	180	7	236	107	230	4	35	4	181	28	31	36	168	191
774	12	jac	1	279	180	90	2	156	125	188	7	41	7	277	45	40	40	160	246
791	1	aff	1	230	180	180	33	121	52	153	37	50	41	205	46	40	48	127	166
791	2	aff	1	170	180	135	37	172	26	106	26	34	32	144	32	29	37	116	139
791	3	aff	1	207	180	150	10	186	46	185	21	31	23	124	20	16	41	124	189
791	4	aff	1	181	180	150	54	172	60	214	28	39	32	122	24	26	42	112	149
791	5	aff	1	179	180	135	39	175	36	161	25	37	33	142	32	33	60	122	183
791	7	aff	1	162	135	150	26	224	29	250	17	33	27	133	29	30	29	126	210

791	8	aff	2	158	165	135	45	226	28	209	19	25	32	122	23	29	31	107	120
780	9	unk	1	184	180	135	16	199	65	231	6	38	8	170	34	36	46	165	213
813	11	unk	1	311	180	120	98	196	53	280	13	44	19	211	30	31	43	208	122
813	16	unk	1	182	120	150	0	135	57	164	14	18	20	171	32	22	44	151	226
813	17	unk	1	216	180	120	31	131	51	133	12	32	27	181	29	29	43	148	185
794	12	unk	1	267	180	15	63	333	68	200	24	25	25	208	35	54	87	253	289
794	13	ota	1	212	150	135	143	281	64	147	15	23	15	173	44	48	59	247	177
Laboratory matings																			
780	10	jac	2	163	180	135	7	170	83	149	7	29	21	161	15	47	37	161	192
801	11	ota	1	321	170	15	82	292	64	148	44	33	44	242	44	50	62	162	198
M430	1	F1	1	279	180	10	50	310	53	144	23	43	30	223	39	39	63	202	209
M430	2	F1	1	362	170	115	68	264	89	189	36	45	33	303	43	55	60	226	156
M430	3	F1	1	273	180	115	72	222	81	185	17	47	17	199	40	52	62	202	161
M431	1	F1	1	214	180	45	55	225	47	119	18	21	18	154	43	48	57	197	251
M431	2	F1	1	323	180	90	51	336	51	123	21	43	23	271	46	60	56	195	236

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GENITAL MORPHOLOGY OF *CARACOLLINA LENTICULA* (MICHAUD, 1831), WITH A NEW PROPOSAL OF CLASSIFICATION OF HELICODONTOID GENERA (PULMONATA: HYGROMIOIDEA)

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ABSTRACT

The genital system of *Caracollina lenticula* (Michaud, 1831) has been studied in many Iberian populations, revealing a high morphological diversity affecting mainly the stimulatory apparatus. The general pattern (mucous gland plus "appendix" plus dart sac) appears sometimes modified due to the absence of the "appendix" or the mucous gland, or even both of them simultaneously; whenever the "appendix" is absent, the dart sac is also lacking. Observations carried out in serial sections show that the mucous gland is attached to the "appendix" and that the so called "appendix" is an organ where secretion elaborated by the mucous gland is accumulated, thus corresponding to the accessory sac in the sense of Nordsieck (1987).

Caracollina lenticula was placed in the Helicodontinae by Hesse (1918). In this paper, a critical review of the classifications of the Helicodontinae (Nordsieck, 1987, Schileyko, 1991) is made. We agree with Nordsieck in considering the Helicodontinae to be a polyphyletic assemblage of genera and thus an artificial group, but there are two main points of discordance: *Ciliella* is related to Hygromiinae (Hygromiidae) on the basis of its anatomy and shell microsculpture, which implies a nomenclatorial change for the Nordsieck's "Ciliellinae," once *Ciliella* is excluded. Moreover, all genera of this group, including *Caracollina* and *Oestophora* (which were erroneously considered devoid of accessory sac), have a dart sac with accessory sac and mucous gland (except secondary losses) and, therefore, a subdivision based on the stimulatory apparatus alone is unjustified. Consequently, Schileyko's classification of this group in four subfamilies is also rejected.

We propose the division of the "Helicodontinae" into two unrelated families, Helicodontidae and Trissexodontidae. The inclusion of Helicodontidae in the superfamily Hygromioidae is unclear, because it has a penial caecum and lacks a penial papilla, whereas Trissexodontidae is considered a primitive taxon of Hygromioidea, and the general pattern of its stimulatory apparatus next to the plesiomorphic condition of Hygromioidea.

Key words: Helicodontidae, Trissexodontidae, *Caracollina,* anatomy, morphology, classification.

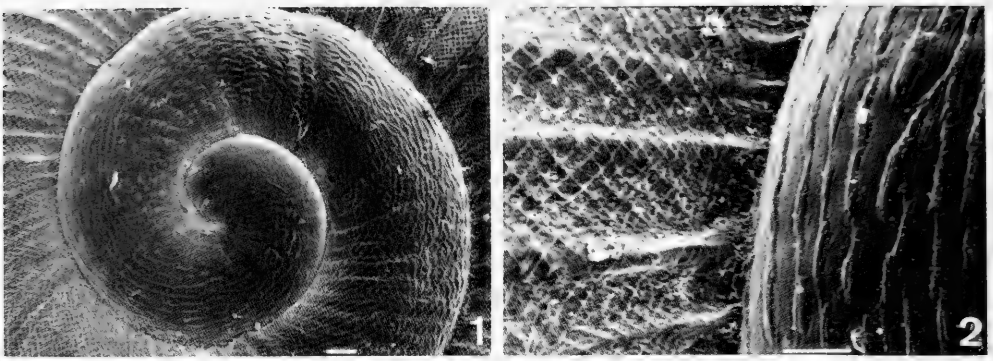
INTRODUCTION

Caracollina Beck, 1837, is a typical Mediterranean genus; its unique species, *C. lenticula* (Miçhaud, 1831), is circummediterranean (Forcart, 1965), also being present in the Canary Islands, Azores, Madeira and Cape Verde islands (Backhuys, 1975).

Caracollina lenticula is an almost unmistakable species; its shell has been fully described by many authors (see below). Its genital morphology is also characteristic, but it shows several morphs. On the other hand, many published interpretations of its genital system, mainly concerning the "appendix" located on the dart sac, are discrepant.

In spite of these disagreements, no studies on variability and taxonomy of *C. lenticula* have been published, and its systematic position has remained in the Helicodontinae from Hesse (1918) until Nordsieck (1987), who proposed the new tribe Caracollinini, placing it together with the Ciliellini and the new tribes Trissexodontini and Oestophorini in the subfamily Ciliellinae. Nordsieck (1987) divided Hesse's Helicodontinae into two subfamiles: Ciliellinae and Helicodontinae. More recently, Schileyko (1991) reunited these two subfamilies into the Helicodontidae, and he raised Caracollinini to subfamilial rank, the Caracollinae.

Routine dissections carried out to identify material collected to study the geographic distribution of *C. lenticula* on the Iberian Peninsula (Puente et al., 1990) have provided new information about its genital morphology and



FIGS. 1, 2. Shell microsculpture of *Caracollina lenticula*. (1) Protoconch; scale, 100 μm. (2) Protoconch and first whorl of the teloconch; scale, 50 μm.

have allowed us to reevaluate the nature of the "appendix" or "upper stylophore" and to suggest a new classification of the Helicodontinae *sensu* Hesse, 1918.

MATERIAL AND METHODS

The studied material of *C. lenticula* has been listed in Puente et al. (1990). Additional material from three localities in Jaén province has been studied: Vilches-Guadalén: 3 km (VH5427), Martos (VG1575), and Jimena (VG5688). Specimens were drowned before being preserved in 70% ethanol. Fresh dissected genital systems of some specimens from Jérica (Valencia, YK0620) were fixed in Bouin's fluid (Culling, 1974), dehydrated with alcohol and embedded in parafin wax; the genital organs between the free oviduct and atrium were serially sectioned at 8 μm and stained with Masson's Haemalum in combination with picroindigocarmine (Martoja & Martoja-Pierson, 1970) for histological observations.

DESCRIPTION

Caracollina lenticula (Michaud, 1831)

Shell

Bibliographical Data: Michaud (1831: 43; pl. 15, figs. 15–17); Moquin-Tandon (1855, t. II: 109; Atlas: pl. 10, figs. 15, 16); Haas (1929: 241, fig. 74); Germain (1930: 236; pl. 3, figs. 69–71; pl. 12, figs. 355, 356); Nobre (1941: 85; pl. 15, fig. 9; pl. 16, figs. 4–6); Zilch (1960: 693, fig. 2418); Gasull (1965: 59); Backhuys (1975: 223; p. 27, figs. 79–80); Gasull (1975: 103; p. 3, fig. 31bis); Mateo (1978: 13; fot. 14); Kerney, in Kerney et al. (1983: 304 + fig.).

Comments: The examined material agrees conchologically with most of the descriptions listed above and, therefore, a new shell description is omitted here. (An error must have occurred in Michaud's original description, because he states "sept tours de spire," but only 4.5 whorls can be counted in his figure.) The shell microsculpture, which has remained unknown until now, is described.

Shell Microsculpture (Figs. 1, 2): The protoconch has one whorl and is characteristically sculptured by small, regularly interrupted spiral crests; from the beginning of the teloconch, these crests change gradually to form a delicate reticulated microsculpture, which is superposed on the typical longitudinal ribs.

Radula

Bibliographical Data: Hesse (1931: 49); Giusti (1970: 102; pl. 14, figs. 1–3).

Genital System

Bibliographical Data: Moquin-Tandon (1855, t. II: 109; Atlas: pl. 10, fig. 14); Schuberth (1892: 9; pl. 1, fig. 9); Hesse (1918: 104); Germain (1930: 235; fig. 182); Hesse (1931: 49; pl. 7, fig. 61a–d); Odhner (1931: 84; fig. 36);

Ortiz de Zárate & Ortiz de Zárate (1961: fig. 3); Giusti (1970: fig. 20); Nordsieck (1987: 30; fig. 22); Schileyko (1991: 208; fig. 8–XVIII).

Description (Figs. 3–7, 12): Right ommatophore retractor muscle between penis and vagina. Atrium, two to four times longer than wide, with an enlarged proximal part and, usually, an outside visible fold; on the opposite side, around the penial orifice, there is internal ring-shaped fold showing some voluminous sub-epithelial goblet-gland cells with narrow necks that open on the epithelial surface (Fig. 12). The penis is cylindrical, with an enlarged distal part, twisted above the atrium, and covered by a penial sheath. In the proximal end of the penis, there is a very small, slender and elongate penial papilla, which is perforated by a central duct. The penial retractor muscle is attached to the diaphragm. The epiphallus is cylindrical, one to three times the penis length, usually double, and elbow-shaped at its middle. There is no flagellum, and the epiphallus/vas deferens transition is evident. The vas deferens is enlarged at its origin and decreases gradually distally. The vagina is thicker than the penis and has an evident muscular protuberance in its distal third, which constitutes a low, broad dart sac containing a small dart. The dart is very small, hook-shaped, with a furrow on its convex side (Fig. 6). The external surface of the dart sac has an U-shaped muscular crest with the U branches directed towards the oviduct; from the U vertex arises an "appendix," very slender at its insertion on the dart sac but greatly enlarged distally, cylindrical, muscular and bent. In the proximal third of the vagina, there is a single mucous gland, generally bifurcated at the middle; the mucous gland duct is attached to the vagina wall until it communicates with the "appendix" duct. The bursa copulatrix is very small, oval or rounded in shape, with a slender duct one to two times the penis length. The free oviduct, which is as long as the atrium, is progressively enlarged from the insertion of the bursa copulatrix duct to the separation of the broaded vas deferens. Running along the free oviduct and the proximal part of the vagina, there is a muscular band originating from the spermoviduct that ends attached to the vagina wall.

Other Morphologies (Figs. 8–11): Besides the morphology of the genital system described above, which is the most frequent and the only one that exists in most of the populations examined, some modifications in the stimulatory apparatus have been observed.

(1) Very reduced mucous gland (Fig. 10): The mucous gland appears as a small rudiment; the other parts appear unaltered. It has been observed from Plasenzuela (Cáceres province, QD5462).

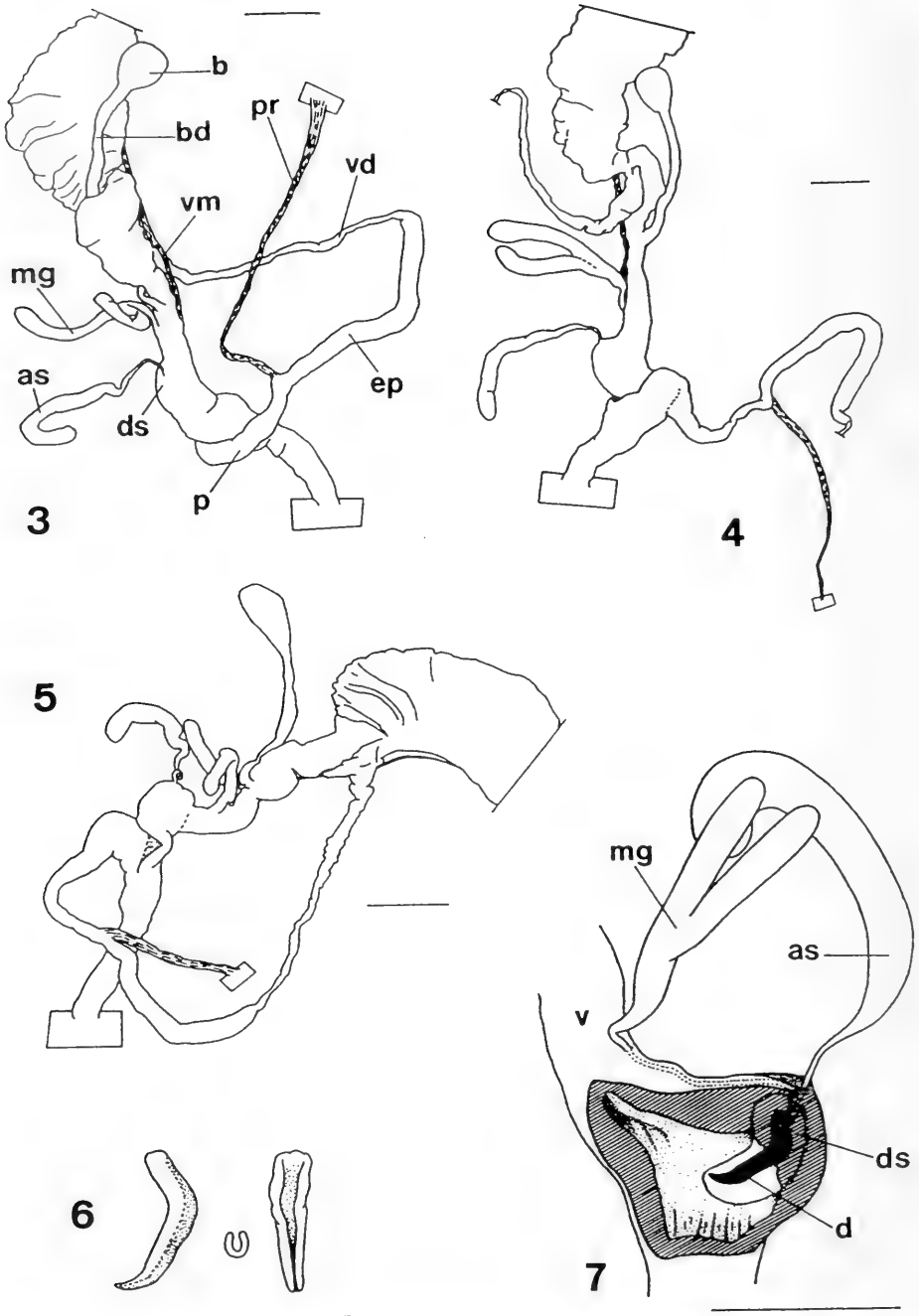
(2) Absence of mucous gland (Fig. 8): This has been observed in three of four specimens collected from Porcuna-Bujalance (Jaén province, VG9492); in two specimens from the same locality, the other parts of the stimulatory apparatus appear unaltered, but in the third, the "appendix" is reduced to a small swelling.

(3) Absence of "appendix" (Fig. 11): Five out of ten specimens examined from Vilches-Guadalén (Jaén province, VH5427) show very variable forms of mucous gland—bifurcate, bifurcate but with reduced branches, simple—but both the "appendix" and the dart sac are absent. In these specimens, the vagina is much shorter than in those specimens from the same locality with complete stimulatory apparatus (four out of ten examined specimens).

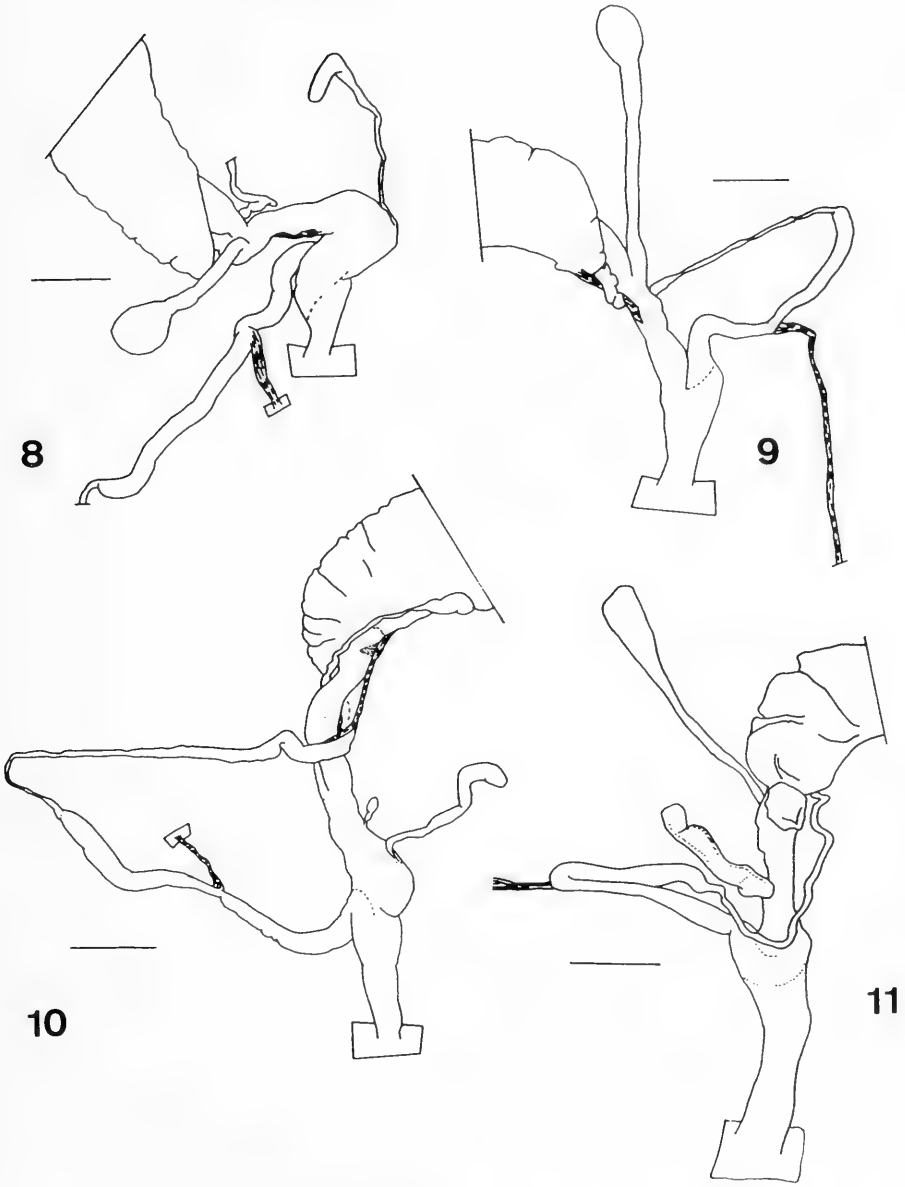
(4) Absence of both mucous gland and "appendix" (Fig. 9): The simultaneous absence of both structures is accompanied by a shortening of the vagina, which causes alterations in the proportions of the genital system: the penis/atrium + vagina length ratio is 1/1, in contrast to 1/1.5–2.5 in typical specimens. As in the previous case, the absence of "appendix" is related to the lack of dart sac. This morphology has been observed in one out of ten examined specimens from Vilches-Guadalén, one of the four specimens collected from Porcuna-Bujalance, and in all the 14 adult and subadult specimens from La Guardia de Jaén (Jaén province, VG3977).

Histological Observations (Fig. 13): The proximal portion of the vagina has a thick muscular and connective wall, with muscular fibres oriented in any direction; the low-columnar epithelium is folded, becoming cuboidal towards the distal portion, where the vaginal wall enlarges laterally due to the presence of a thick dart sac (Fig. 13a).

The mucous gland wall consists of a single high-columnar epithelium, the cells of which have many small mucous secretory vesicles concentrated in the apical region; these vesicles seem to be detaching from the epithelial cells towards the mucous gland lumen, which is full of mucus. A very thin wall of mainly



FIGS. 3–7. Genital system of *Caracollina lenticula*. (3) Dalías (Almería, WF1174). (4) Tavira (Algarve, PB2011). (5) El Villar (Huelva, PB9974). (6) Dart from a specimen of Jerez de la Frontera (Cádiz, QA5163). (7) Scheme of the stimulatory organ. Abbreviations: as, accessory sac; b, bursa copulatrix; bd, bursa copulatrix duct; d, dart; ds, dart sac; ep, epiphallus; mg, mucous gland; p, penis; pr, penial retractor muscle; v, vagina; vd, vas deferens; vm, vaginal muscle. Scale, 1 mm.



FIGS. 8–11. Defective genital systems of *Caracollina lenticula*. (8) Porcuna-Bujalance (Jaén, VG9492), without mucous gland. (9) La Guardia de Jaén (Jaén, VG3977), without mucous gland or accessory sac. (10) Plasenzuela (Cáceres, QD5462), with rudimentary mucous gland. (11) Vilches-Guadalén: 3 km (Jaén, VH5427), without accessory sac. Scale, 1 mm.

connective tissue surrounds the epithelium (Fig. 13a).

The wall of the "appendix" is thick and mainly muscular, with dense muscular fibres mostly circularly oriented; the epithelium is cuboidal, lacking secretory cells (Fig. 13a). Nevertheless, the lumen of this organ is full of secreted material with the same mucous appearance as the mucous gland secretions.

The base of the mucous gland is a narrow

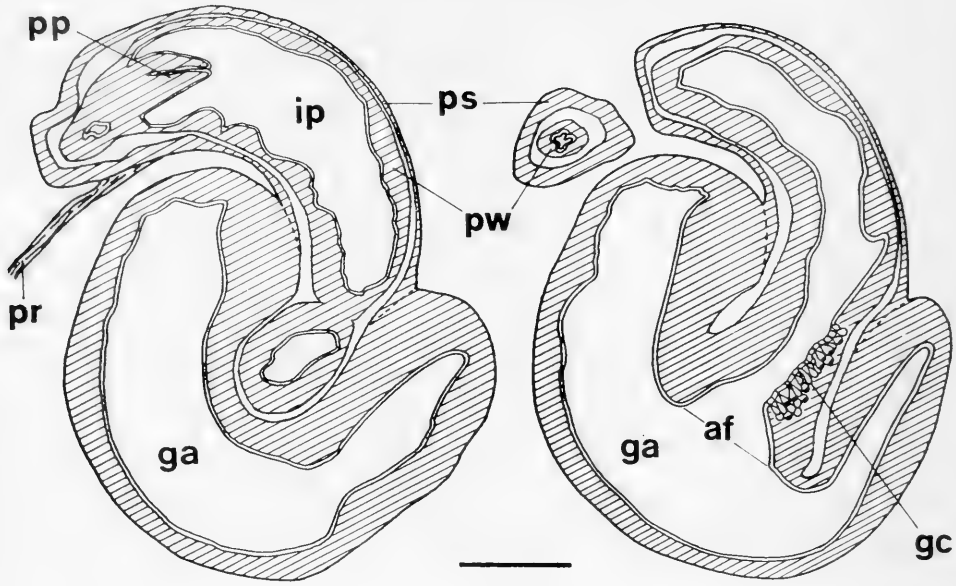


FIG. 12. Two histological sections of the genital atrium and penial distal region of a *Caracollina lenticula* specimen from Jérica (Valencia, YK0620) (left, upper section). Abbreviations: af, annular fold; ga, genital atrium; gc, goblet-gland cells; ip, inner penis; pp, penial papilla; pr, penial retractor muscle; ps, penial sheath; pw, penial wall. Scale, 100 μm.

duct through which the secretory products, elaborated in the upper region, are discharged; the epithelial cells have lost their glandular nature becoming cuboidal (Fig. 13b). This secretory duct fuses with the vaginal wall over the lateral thickening and runs within the vaginal wall as a duct totally independent of the vaginal lumen, which is surrounded by connective and muscular walls (Fig. 13c). More distally, the "appendix" itself, after being bound by muscular bands, fuses with the vagina and, after a short distance in which three lumina run together, the mucous gland duct flows into the lumen of the "appendix" duct (Fig. 13d–f); close to the junction of both ducts (approximately, 25 μm outwards), the upper end of the dart sac cavity begins to appear. The lumina of dart sac and "appendix" duct are covered by dense muscular fibres, mostly circularly oriented, and both are embedded in the enlarged vaginal wall (Fig. 13g). The "appendix" duct evaginates into the dart sac cavity, until the former becomes a very narrow duct that opens into the hollow side of the dart (Fig. 13h–i); the opening of the "appendix" duct is controlled by a thickening of the connective tissue of its walls, which operates as a terminal valve.

DISCUSSION

Morphological Diversity of the Genital System of *C. lenticula*

As it has been stated above, the genital system of *C. lenticula* shows distinct morphologies affecting mainly the stimulatory apparatus. The most frequent morphology is the presence of a complete stimulatory apparatus, that is dart sac plus "appendix" plus forked or simple mucous gland. The different descriptions of the stimulatory apparatus mentioned in the literature and in the material studied are listed in Table 1.

The only descriptions in the literature not observed among our specimens is that depicted by Moquin-Tandon (1855, t. II: 109): "Point de poche a dart. Une seule vésicule muqueuse simple, vermiforme, flexueuse, a peine renflée au sommet (. . .). Vagin assez developpé, se dilatant brusquement en un corps irrégulièrement obové, un peu au dessous de la vésicule vermiforme," and that by Germain (1930: 235): "1 seule glande multifide simple, vermiforme, flexueuse (. . .); pas du sac du dard." Although Moquin-Tandon stated that there is no dart sac, he mentioned

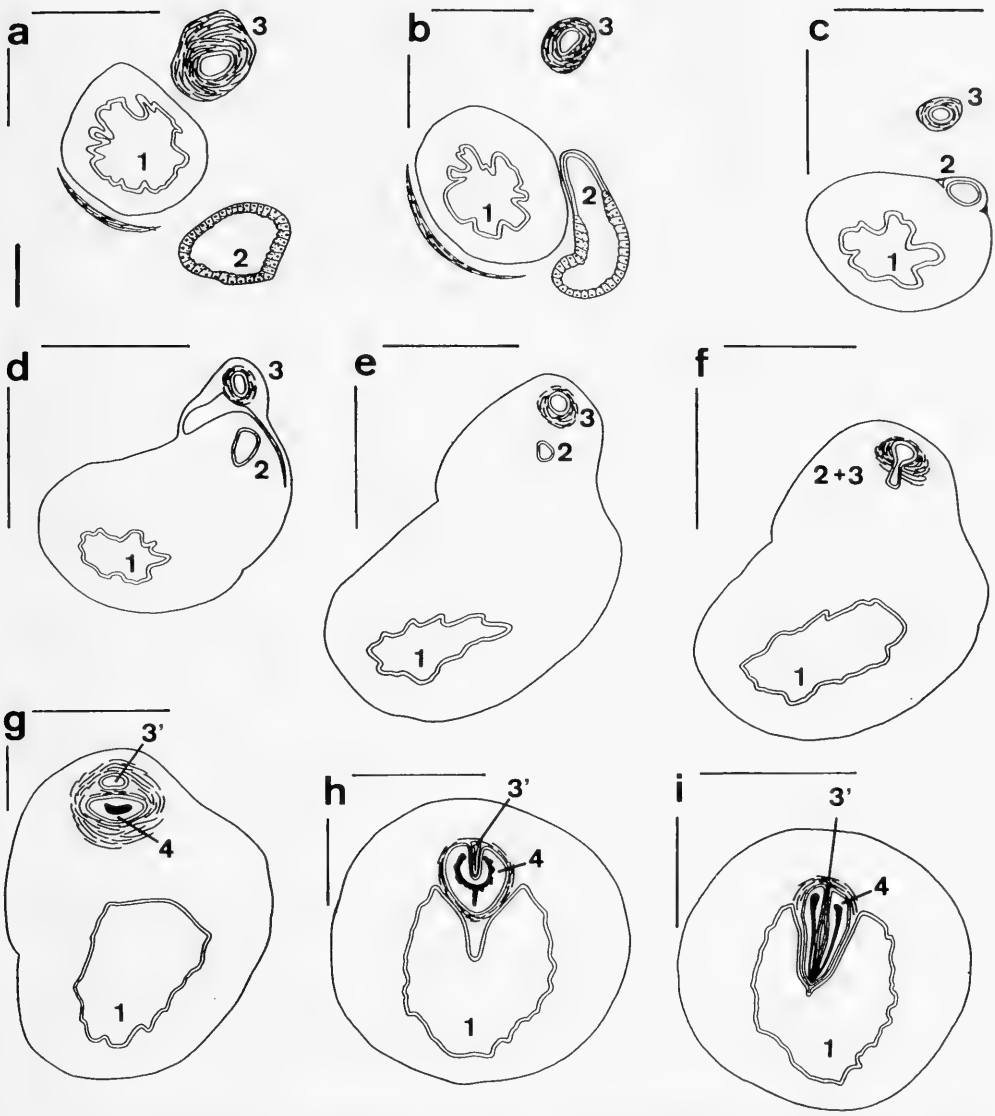


FIG. 13. Microscopical sections of the vaginal structures of *Caracollina lenticula* of a specimen from Jérica (Valencia). (a) Mucous gland, accessory sac and vagina sections. (b) Conversion of the mucous gland into a mucous gland duct. (c) Fusion of the mucous duct with the vagina wall. (d) Binding of the accessory sac to the vagina wall by muscular bands. (e) Fusion of the accessory sac to the vagina wall. (f) Flowing of the mucous duct into the accessory sac duct. (g–i) Accessory sac duct running into the hollow side dart. Symbols: 1, lumen of the vagina; 2, mucous gland and mucous gland duct; 3, accessory sac and accessory sac duct; 3′, accessory sac duct below its fusion with the mucous gland duct; 4, dart sac lumen with the dart. Scale, 100 μm.

a well-developed vagina with a strong dilatation, which can only correspond to the dart sac. This suggests that the "appendix" could had been accidentally lost during the dissection (due to the narrowness and extreme fragility of the lower part of the "appendix") because, according to our observations, the lack of the "appendix" is always related to the absence of the dart sac and reduction of the vagina length.

TABLE 1. Bibliographical descriptions of the genital system of *C. lenticula*.

Appendix	Mucous gland	References and searched localities
PRESENT	BIFURCATE	Schubert (1892): Tanger, Barcelona Hesse (1931): Oran, Mallorca, Tenerife (v. *major*) Odhner (1931): Canary Islands Giusti (1970): Pianosa Island
	SIMPLE	Hesse (1931): Palermo, Tenerife, Gran Canaria O. Zárate & O. Zárate (1961): La Rábida (Huelva)
ABSENT	BIFURCATE	Soos (1933)(+): Maltese Islands
	SIMPLE	Moquin-Tandon (1855): S-France Germain (1930)(*): S-France

(+) taken from Ortiz de Zárate & Ortiz de Zárate (1961)
(*) who states "quelquefois bifide" also.

We have also noticed other variations not described before, such as a extremely reduced mucous gland, the lack of mucous gland, and the simultaneous absence of both mucous gland and "appendix."

Defective morphologies of the stimulatory apparatus have been observed in specimens from three localities, all of them in Jaén province, although specimens from intermediate and neighbouring localities have complete stimulatory apparatus. These observations suggest a tendency towards the reduction of the stimulatory apparatus in this area; it is even completely absent in all the 14 adult and subadult specimens sampled from La Guardia de Jaén. We consider that the distinct described morphologies are within the scope of the polymorphism of *C. lenticula.* Nevertheless, we cannot exclude the possibility that the specimens without stimulatory apparatus could constitute a local subspecies and, thus, the intermediate morphologies would correspond to intermediate forms. Intensive sampling from the Jaén area should be made to solve this question.

Interpretation of the "Appendix"

Authors dealing with the genital system of *C. lenticula* have given different names to the "appendix" on the dart sac, as a result of different interpretations of this organ. Schuberth (1892) regarded it as a somewhat extended dart sac, whereas Odhner (1931) mentioned a long muscular appendix, and Hesse (1931) an appendicula. Giusti (1970), in a drawing of the genital system, pointed out a vaginal diverticulum, and Schileyko (1973) considered it as a second mucous gland. Recently, Nordsieck (1987) indicated that *C. lenticula* has no accessory sac near the dart sac, although there is a dart sac appendix. Finally, Schileyko (1991) emphasized that *Caracollina* "posseses a pair of stylophores," the upper stylophore (= "appendix") being modified into a hydrostatic pump.

Our observations suggest that the muscular "appendix" is an organ where the secretion elaborated by the mucous gland before copulation is stored. The opening of the terminal valve of the "appendix" duct allows the mucous secretion to flow into the hollow dart face. During mating, this secretion would be injected into the haemocoel of the partner through the dart injuries, accompanied by the simultaneous contraction of the muscular wall of the "appendix," in order to stimulate the copulation or to reduce the courtship duration, as it has been stated in other stylommatophores (Tompa, 1984; Adamo & Chase, 1990; Gómez, 1991). On the other hand, the secretions of the goblet-gland cells located in the penial opening seem to aid sperm transfer.

Thus, the muscular "appendix" of *C. lenticula* corresponds to the accessory sac in Nordsieck's terminology. This conclusion is in contrast to Schileyko's idea, regarding the "appendix" in *Caracollina* as a modified upper stylophore. In the remaining Hygromioidea, the homologization of the upper stylophores (never with darts) with true dart sacs, proposed by Schileyko (1991), is very doubtful. In this sense, the structure and function here shown for *Caracollina* and *Hygromia* (Prieto & Puente, in press-2) lead us to support Nordsieck's (1987) hypothesis, which considers the upper sacs as accessory sacs, directly and primarily originated for the accumulation of mucous gland secretions.

Critical Review of the Classifications of the Helicodontoids

The first anatomical diagnosis for Helicodontinae, as a subfamily of Helicidae, was provided by Hesse (1918), and included genera with a dart sac (*Oestophora* Hesse, 1907; *Drepanostoma* Porro, 1836; and *Mastigophallus* Hesse, 1918), as well as genera lacking a dart sac (*Helicodonta* Férussac, 1819; *Canariella* Hesse, 1918; *Caracollina; Soosia* Hesse, 1918; and *Trissexodon* Pilsbry, 1895), plus some *incertae sedis* (*Helix buvignieri* Michaud, *H. hispanica* Gude, and *H. turriplana* Morelet, among others). Some statements about these genera have been later corrected: Hesse (1931, 1934) considered that *Caracollina* is monotypical and possesses a dart sac with dart, which was figured by Odhner (1931), and that *Drepanostoma* and *Lindholmiola* Hesse, 1931, do not have a dart sac.

Later, Gittenberger (1968) showed that *Trissexodon* has a dart sac with dart and a muscular ligament between the stimulatory apparatus (dart and accessory sacs, and sometimes the base of the mucous gland) and the spermoviduct, and he suggested a relation between the mucous gland and accessory sac. He proposed to divide Helicodontinae into two groups that might be unrelated subfamilies, although these were neither named nor formalized. The first group would include *Oestophora, Mastigophallus, Oestophorella* Pfeffer, 1929, *Trissexodon,* and perhaps *Ciliella* Mousson, 1872, whereas *Helicodonta, Drepanostoma, Lindholmiola, Atenia* Gittenberger, 1968, *Soosia,* and perhaps *Caracollina* would constitute the second.

Schileyko (1978: 57) considered Helicodontidae as a family within Helicoidea, and recognized its heterogeneity, subdividing it into four groups headed by *Trissexodon, Lindholmiola, Helicodonta,* and *Oestophora,* respectively. In contrast, Nordsieck (1987) recognized two unrelated lines within "Helicodontinae" (= Helicodontidae *sensu* Schileyko), Ciliellinae and Helicodontinae, both belonging to Hygromiidae. This reorganization agrees in outline with the groups suggested by Gittenberger, except in including *Caracollina* in the Ciliellinae (approximately corresponding to Gittenberger's first group) and *Soosia* into Eloninae (Xanthonychidae). The Ciliellinae was divided into four tribes: Trissexodontini (with dart sac and accessory sac, and a small dart), Oestophorini (without accessory sac, with dart sac and darts of different sizes, or lacking dart sac), Caracollinini (with dart sac, without accessory sac, but with an appendix, and a very small dart) and Ciliellini (without stimulatory apparatus at all). The Helicodontinae was divided into two tribes: Helicodontini (dart sac transformed into an appendix, without dart, and the penial retractor muscle arising from the columellar muscle) and Lindholmiolini (without appendix, the penial retractor muscle arising from the diaphragm). According to Nordsieck (1987), the unique characteristics that relate both subfamilies are the depressed shell and the tendency towards the reduction of the stimulatory apparatus, both conditioned by the endogeous way of life. We agree with Nordsieck's classification in recognizing two unrelated groups, which will be substantiated further as two families within Hygromioidea, and in the generic composition of each group, with an exception for *Ciliella.*

Three features permit us consider the *Ciliella* does not belong to the helicodontoid groups:

(1) The genital system, with a broad penis, wrinkled tongue-shaped penial papilla and short, enlarged flagellum, with a short vagina without stimulatory apparatus and with a wide bursa copulatrix duct (Manganelli et al., 1989), is not related to any genus of these groups.

(2) The shell surface is covered by numerous radially arranged, nail-like scales and rows of minute longitudinal crests (Manganelli et al., 1989), which is very similar to the shell surface of two Hygromiidae genera: *Cryptosaccus* Prieto & Puente (Prieto & Puente, in press-1) and *Mengoana* Ortiz de Zárate, 1949 (Outeiro, 1988). This characteristic is not present in any helicodontoid genus.

(3) The habitat and way of life of *Ciliella* are clearly distinct from those of the helicodontoids; it lives on vegetation near streams in montane habitats (Germain, 1930; Kerney et al., 1983; personal observations) as do other species of Hygromiidae, e.g., *Hygromia, Mengoana* or *Euomphalia.*

Therefore, we consider the *Ciliella* belongs to Hygromiidae and is close to Hygromiinae. This possible new systematic placement of *Ciliella* would require nomenclatorial changes in the classifications of both Nordsieck and Schileyko: the "Ciliellinae" of Nordsieck (1987), minus *Ciliella,* should be named Trissexodontinae, and the "Ciliellidae" of Schileyko (1991), minus *Ciliella,* should be named Halolimnohelicidae.

Nevertheless, we disagree with Nordsieck's diagnosis for Oestophorini and Caracollinini. The former has a stimulatory apparatus consisting of a dart sac with a little dart, and a large accessory sac (Manga, 1983; unpublished data), contrary to the large dart sac with a long dart inside it figured by Nordsieck (1987: fig. 21) based on an erroneous drawing of *Oestophora barbula* (Rossmässler, 1838) by Schileyko (1971); Caracollinini, as indicated by Schileyko (1991) and shown above, is characterized by having a long accessory sac instead of an appendix. Therefore, the diagnosis for both Oestophorini and Caracollinini agree with the one for Trissexodontini and, thus, Nordsieck's tribal division is not longer valid.

Recently, Schileyko (1991) included Ciliellinae and Helicodontinae *sensu* Nordsieck (excluding *Ciliella* and *Canariella*) plus *Soosia* within Helicodontidae, a family of Hygromioidea. The reconstruction of the evolutionary pathways of Helicodontidae and its division into subfamilies and tribes made by Schileyko are unsatisfactory in many aspects:

(1) The attachment point of the penial retractor muscle is unclear in the hypothetical hygromioid ancestral form: it appears attached to the diaphragm in Schileyko's figs. 2-III and 5-III, and to the columellar muscle in his figs. 8-I and 9-I. Moreover, the penial retractor muscle reverses once more to appear attached to the diaphragm in his figs. 8-II (scheme of evolution of the Ciliellidae) and 9-II (scheme of the Hygromiidae); within the Helicodontidae, Schileyko suggests a very unparsimonious way to explain the presence of a penial-columellar muscle in Helicodontinae, with parallel reversions to a penial-diaphragmatic muscle in all the remaining subfamilies.

(2) In Schileyko's fig. 8, both *Caracollina* and *Trissexodon* derive from *Mastigophallus*, but in his classification, *Caracollina* is separated as a subfamily from Trissexodontinae (with *Mastigophallus* and *Trissexodon*). Doubtful as well is the derivation of *Gittenbergeria* Schileyko, 1991, and Helicodontinae from an "intermediate link" common to both, suggesting a close phylogenetic relationship for them, when Schileyko (1991: 206) supposes that "the roots of the origin of *Gittenbergeria* should be looked for among the forms close to *Trissexodon.*"

(3) The most important criticism is that some genital schemes utilized by Schileyko are erroneous. The case of *Oestophora* has been mentioned before; another example is his representation of the genital system of *Gittenbergeria turriplana* (Schileyko, 1971). We have observed in this species a single birramous mucous gland flowing into the vagina and, by a narrower duct, also into the long accessory sac, which is in turn flowing into the vaginal side of the dart sac. Within the dart sac, an annulated papilla, located below the insertion point of the sac accessory has been observed; no dart has been found. The dart and sacs accessory are apically connected with the spermoviduct by means of a conspicuous muscular ligament (unpublished data).

A Proposed New Classification

As a result of these comments, we believe that previous classifications are unsatisfactory in both nomenclatorial and diagnostic aspects, and we propose a new one for the helicodontoid genera.

HELICODONTIDAE Kobelt, 1904

Diagnosis: Shell planorboid (although some genera have a depressed shell) with very open umbilicus and a smooth surface always with hairs. Genital system with a sac (absent in *Lindholmiola, Soosia* and *Atenia*) without dart; one undivided mucous gland beside the sac; penis covered by a sheath, with a small caecum between the slender proximal and the widened distal parts of the penis (Gittenberger, 1968, for *Atenia;* Prieto, 1986: fig. 7B, Gittenberger et al., 1970: fig. 183, and Nordsieck, 1989, for *Helicodonta;* Schileyko, 1971: fig. 2-IV, for *Lindholmiola*); there is neither penial papilla nor flagellum. Penial retractor muscle attached to the columellar muscle, but to the diaphragm in *Lindholmiola;* the attachment point is unknown for *Atenia* (Gittenberger, 1968).

Geographic distribution: Central and southern Europe, with one genus extending to the Iberian Mediterranean region (*Atenia*), where it is endemic.

Composition: Helicodonta Férussac, 1819; *Drepanostoma* Porro, 1836; *Falkneria* Nordsieck, 1989; *Lindholmiola* Hesse, 1931; *Atenia* Gittenberger, 1968; and perhaps *Soosia* Hesse, 1918.

Comments: The following features appear to be synapomorphic: planorboid shell; absence of dart sac; undivided mucous gland; penis

with a small caecum and lacking both flagellum and penial papilla. The lack of these structures is convergent with other groups: the dart sac is absent in some Hygromiidae (Euomphaliinae, Metafruticicolinae, and some Trichiinae and Hygromiinae, and *Ciliella*) and in one genus of Trissexodontidae (see below); either the flagellum or the penial papilla are absent in some genera of Trissexodontidae, and neither of the two is present in *Oestophora* (Schileyko, 1971). The most striking feature is the presence of a small caecum, which is unknown in the remainder Hygromioidea, and could be the main synapomorphic character for this family. It is not clear whether the penial-columellar retractor muscle is synapomorphic for Helicodontidae (modified secondarily to a penial-diaphragmatic muscle in Lindholmiolinae) or for Helicodontinae only (and unchanged in Lindholmiolinae). It is also unclear whether the dartless sac is homologous to the dart sac, as suggested by Nordsieck (1987), or to the accessory sac, although Schileyko (1991) considers it to be a small branch of the mucous gland. In any case, the relationships of Helicodontidae with Hygromioidea are not well supported, and both taxa could be unrelated.

The systematic position of *Soosia* is doubtful; Nordsieck (1986, 1987) considers it to belong to the Eloninae (Xanthonychidae, Helicoidea), whereas it is related to Helicodontinae by Schileyko (1991). The defective genital system of *Soosia,* which lacks accessory sac, mucous glands and flagellum, makes its systematic placement difficult, but the morphology of its genital system, penial-diaphragmatic retractor muscle, shell morphology and geographic distribution (Grossu, 1983) suggest a probable relationship to *Lindholmiola.*

Helicodontidae can be divided into two subfamilies, as already proposed by Schileyko (1978):

HELICODONTINAE Kobelt, 1904

Diagnosis: Planorboid shell. Genital system with accessory sac, tubular mucous gland; penial-columellar retractor muscle; inner penis (only known for *Helicodonta*) with spinulose semicircular folds and a long, strong, longitudinally divided distal pleat (Schileyko, 1971, 1978, 1991). Chromosome number n = 27? (only known for *Helicodonta;* Rainer, 1967).

Composition and Comments: Helicodonta, Drepanostoma and *Falkneria. Atenia* seems to be related to these genera because of its planorboid shell, tubular mucous gland and geographic distribution, but the absence of accessory sac, a condition of Lindholmiolinae, together with the unknown insertion of the penial retractor muscle, make its systematic placement difficult. The synapomorphic features of this group appear to be the planorboid shell and the penial-columellar retractor muscle, although this last character is considered plesiomorphic for Hygromioidea by Schileyko (1991), as it has been previously discussed.

LINDHOLMIOLINAE Schileyko, 1978

Diagnosis: Lenticular shell. Genital system with a corrugate mucous gland (absent in *Soosia*), without accessory sac; penial-diaphragmatic retraction muscle; inner penis with small flaccid folds.

Composition and Comments: Lindholmiola and perhaps *Soosia* (see above). The synapomorphic features of this group are the absence of accessory sac (convergent with *Atenia*) and the corrugation of the mucous gland.

TRISSEXODONTIDAE Nordsieck, 1987

Diagnosis. Shell regularly ribbed and flattened, never with hairs. Genital system with an accessory sac, usually long and large, flowing into the dart sac (except in *Gasulliella* Gittenberger, 1980, in which the stimulatory apparatus is completely absent), with their upper ends connected to the spermoviduct by a muscular ligament (except in *Caracollina,* in which it is attached to the vagina wall; it has not been described for *Mastigophallus,* but its presence is probable); dart short and curved (canaliculate in *Caracollina*); one or two bifurcate mucous glands flowing into the base of the accessory sac (in *Oestophora* they are connected to the vagina); penis covered by a penial sheath, with a penial papilla deeply situated (but absent in *Oestophora*; Schileyko, 1971) and a moderate-sized to long flagellum (reduced in *Oestophorella* and absent in *Caracollina, Oestophora* and *Gittenbergeria;* Schileyko, 1991). Penial retractor muscle attached to the diaphragm. Chromosome number n = 30? (only known for *Oestophora;* Ramos & Aparicio, 1985).

Geographic Distribution: Iberian Peninsula, northwest Africa and ?Macaronese Islands.

Composition: Trissexodon Pilsbry, 1895; *Caracollina* Beck, 1837; *Oestophora* Hesse, 1907; *Mastigophallus* Hesse, 1918; *Oestophorella* Pfeffer, 1929; *Gasullia* Ortiz de Zárate & Ortiz de Zárate, 1961; *Suboestophora* Ortiz de Zárate & Ortiz de Zárate, 1961; *Gasulliella* Gittenberger, 1980; *Gittenbergeria* Schileyko, 1991; and perhaps *Spirorbula* Lowe, 1852, endemic from Madeira Islands and with a stimulatory apparatus that reminds one of that of *Caracollina* (see Schileyko, 1991).

Comments: As it has been commented previously, *Ciliella* is not related to this group and, therefore, the name Ciliellinae, *sensu* Nordsieck, is not available. On the other hand, *Canariella* Hesse, 1918, according to Nordsieck (1987), is related to *Oestophora,* but is included in Ciliellidae by Schileyko (1991) (= Halolimnohelicidae, if *Ciliella* is removed from this family).

In contrast to the Helicodontidae, the synapomorphic features of Trissexodontidae cannot be readily established because the general structure of the genital system that we can deduce for this group (one bifurcate mucous gland flowing into the usually great accessory sac which, in turn, flows into the dart sac, and penis with penial papilla and flagellum) could be the plesiomorphic condition of Hygromioidea. On this assumption, the double stimulatory apparatus present in Hygromiidae (at least, in some subfamilies), as well as in Vicariihelicinae and Halolimnohelicinae (included by Schileyko, 1991, in Ciliellidae, see above), is a derivative condition from a primitive single stimulatory apparatus, represented in Trissexodontidae and Helicodontidae, and (secondarily?) in Hygromiinae. This supposition is contrary to the plesiomorphic condition proposed for Hygromioidea by Nordsieck (1987) and Schileyko (1991), who consider that the single stimulatory apparatus is a convergent derivative condition.

In the resolution of this dilemma, i.e., single vs. double stimulatory apparatus as the plesiomorphic condition for Hygromioidea, other data can be used, e.g., the insertion of the mucous glands and the chromosome number.

(1) Schileyko (1991) considered the primitive position of the mucous glands of Hygromioidea to be around the vagina above the upper sacs. Most Hygromiidae have this arrangement, but there is, at least, one case with another disposition: *Ponentina* Hesse, 1921, with double stimulatory apparatus, shows one bifurcate mucous gland attached to each of the accessory sacs, and these, in turn, are attached to the vaginal side of the dart sacs, which bear darts (Manga, 1983; Prieto, 1986). In "Ciliellidae" *sensu* Schileyko, the two subfamilies with sacs have, according to Schileyko (1991), bifurcate mucous glands attached to the base of the respective dartless sacs, which are very small, but these flow into the sacs in, at least, *Vicariihelix kivuensis* Verdcourt and *Halolimnohelix sericata* Pilsbry (Verdcourt, 1981). In Helicodontidae, there is one mucous gland near the base of the small dartless sac (if present). In Trissexodontidae, the bifurcate mucous gland flows into the accessory sac; in *Suboestophora,* in which the mucous gland appears to be completely divided into two forked glands again, these flow independently into the base of the large accessory sac (unpublished observations).

The presence of a single or bifurcate mucous gland flowing into the accessory sac in some representatives of all Hygromioidea families suggests that this configuration is plesiomorphic respect to the insertion of the mucous glands into the vagina, which happens mostly in Hygromiidae. On the other hand, only Trissexodontidae and Hygromiidae have sacs with darts, and in both families there are some cases where the accessory sacs are attached to the dart sacs: this occurs in all Trissexodontidae genera with stimulatory apparatus and clearly in the hygromiid *Ponentina;* in the other hygromiids, whenever accessory and dart sacs are present, they are always closely attached and, in some cases, accessory sacs flowing into dart sacs can be seen (Schileyko, 1978). Again, an accessory sac flowing into the dart sac can be deduced as a plesiomorphic condition, rather than as a separate implantation of both on the vagina, which has been used as an argument to propose the existence of upper and lower stylophores.

(2) The chromosome number is unknown for many stylommatophores, but some numbers are clearly indicative: within the Helicoidea, the Ariantinae and Euparyphinae (Helicidae) have n = 29–30, whereas the Helicinae has n = 22, 25–27, 30, and the Elonidae has n ≥ 29 (M. T. Aparicio, personal communication); within the Xanthonychoidea, the Bradybaenidae has n = 28–29 and the Monadeniinae (Xanthonychidae) has n = 29. The most common number appears to be n =

29, a fact that agrees with the chromosome number of the related Camaenoidea and Mesodontiodea, in which n = 29 is the most common number (Patterson & Burch, 1978). Therefore, Nordsieck (1987) suggests that this number is plesiomorphic for Helicoidea and related superfamilies. Nevertheless, the chromosome number of Hygromiidae is lower, with n = 23–26 (Trichiinae and Euomphaliinae) and n = 21, 23–26 (Hygromiinae) (Patterson & Burch, 1978; Aparicio, 1983; Ramos & Aparicio, 1985), but surprisingly higher in *Oestophora,* n = 30 (Ramos & Aparicio, 1985). This suggests that the chromosome number of Hygromiidae is apomorphic in relation to that of Trissexodontidae. The chromosome number of *Helicodonta,* n = 27 (Rainer, 1967), is also unusual within Hygromioidea, but no conclusion about it is possible.

Therefore, the two discussed features of Trissexodontidae, mucous gland flowing into the accessory sac and high chromosome number, suggest that this family is a primitive group. Because all Trissexodontidae genera have a single stimulatory apparatus (except in *Gasulliella,* in which it is completely reduced; Gittenberger, 1980), we conclude that this condition is plesiomorphic for Hygromioidea.

There is another typical character of Trissexodontidae: the muscular ligament between the upper ends of both dart and accessory sacs and the spermoviduct. Nevertheless, this character seems to be plesiomorphic as well, because in addition to its presence in all Trissexodontidae genera (it can also be seen in *Gasulliella*—where dart and accessory sacs are absent—as a thin muscular line along the vagina wall; unpublished observations), it is also visible as a thin connective bridle in some Hygromiinae (Hygromiidae with single stimulatory apparatus) as, for example, *Cryptosaccus* (Prieto & Puente, in press-1), and in some Helicidae (Helicoidea) as, for example, *Iberus* Montfort, 1810 (García San Nicolás, 1957, described as a "duct" between the dart sac and the spermoviduct).

The function suggested by us for this muscular ligament is to maintain the stimulatory apparatus joined to the vagina to avoid a floating location in the haemocoel; the stimulatory apparatus would be primitively connected to the vaginal tract by the dart sac alone, because the accessory sac with the mucous gland flowing into it was attached to the dart sac. This structure would be related to an elongate asymmetric stimulatory apparatus.

In consequence, we cannot recognize any synapomorphic character in the genital system of Trissexodontidae; the only one synapomorphy that we suggest for this group is the regularly ribbed shell associated with the lack of hairs, which does not occur in any other group of Hygromioidea.

At present, a subfamiliar division of Trissexodontidae seems inappropriate to us, because its genital structure is rather conservative in spite of some modifications of the general pattern, for example, loss of flagellum (*Caracollina, Gittenbergeria, Oestophora*), loss of penial papilla (*Oestophora*), loss of the stimulatory apparatus (*Gasulliella*), or presence of two bifurcate mucous glands (*Suboestophora, Gasullia, Oestophorella, Mastigophallus*). These modifications could have happened several times during the evolution of this group. Therefore, analysis of possible evolutionary pathways into Trissexodontidae requires further research: a solid taxonomic revision based on accurate dissections and investigation of characters (e.g., chromosome number, enzymatic analysis, shell microsculpture, distribution patterns) overlooked previously.

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MELANISM IN THE LAND SNAIL *HELICELLA CANDICANS* (GASTROPODA, HELICIDAE) AND ITS POSSIBLE ADAPTIVE SIGNIFICANCE

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ABSTRACT

Shell banding polymorphism in 184 local populations of *Helicella candicans* (Pfeiffer) from western Czechoslovakia was investigated. The shells are white with up to nine dark brown bands, which may fuse. There was large within- and among-population variation in shell banding. An "index of melanisation," indicating proportion of shell surface covered with extended or fused bands, revealed geographic patterning of dark phenotypes. The frequency of dark forms was higher in some areas, due perhaps to decrease of incident sunshine by fog, clouds or industrial air pollution. High and dense vegetation cover were also associated with melanism. In the laboratory, temperature of irradiated dark shells increased more rapidly than that of light shells, and the thermal equilibrium of the former was higher. The differences were greatest on a white background and with low ambient temperature. In areas of reduced sunshine, dark individuals may be at an advantage, especially during the autumn breeding period. When exposed to sunshine during summer dormancy, light forms may also be able to maintain lower body temperature than dark forms.

INTRODUCTION

Helicella candicans (Pfeiffer) is a small helicid gastropod (shell diam. 9–20 mm). In Bohemia, western Czechoslovakia, it inhabits dry steppes on calcium-rich soils, particularly on the southern slopes of hills along the Ohře (Eger) and Labe (Elbe) rivers, in the Central Bohemian Karst, and in a few other sparsely distributed localities (Ložek, 1956). Oviposition was observed in late summer and early autumn. During dry periods in June to September, the animals aestivate attached to dry herbaceous vegetation.

The very diffuse nature of the variation is perhaps why the shell banding polymorphism of *H. candicans* has been little studied. Geographic variation in the proportions of different phenotypes is considerable. I have developed a system that enables the degree of melanism of the shell to be classified. I explored variation in melanism at a number of localities in Bohemia and attempted to establish the relationship between this variation and local microclimate.

MATERIALS AND METHODS

In 1987–1989, *H. candicans* was collected at 184 sites in central and western Bohemia. At each site, all shells were sampled from an area, the size of which varied according to snail abundance. This prevented collecting bias favouring certain morphs due to differences in relative crypsis to the collector. The minimum distance between the sites was 150 m. At each site, 50–150 living or well-preserved dead individuals were collected, and the density and height of vegetation cover was evaluated, specifically to estimate how it may shade the surface in late summer and early autumn, during the *H. candicans* breeding season. The vegetation was ranked into seven crude subjective categories that proved usable for quantification of plant cover effects on *H. candicans* melanism.

The dorso-ventrally compressed shell of *H. candicans* is white, with one to nine dark brown to black bands (Fig. 1). The single dorsal band is variable in width and may extend over the whole dorsal surface when the edges of the band become diffuse. There are zero to six lateral bands, the width of which vary less than that of the dorsal band. Adjacent bands may fuse to form a belt consisting of up to six original bands. There are zero to two narrow ventral bands. Individuals with diffuse dark coloration of the dorsum and with a lateral belt consisting of four or five fused bands were termed "dark" forms. Individuals having a thin dorsal band only were termed "light" forms.

Shell coloration was classified according to the degree of melanisation, i.e. the proportion

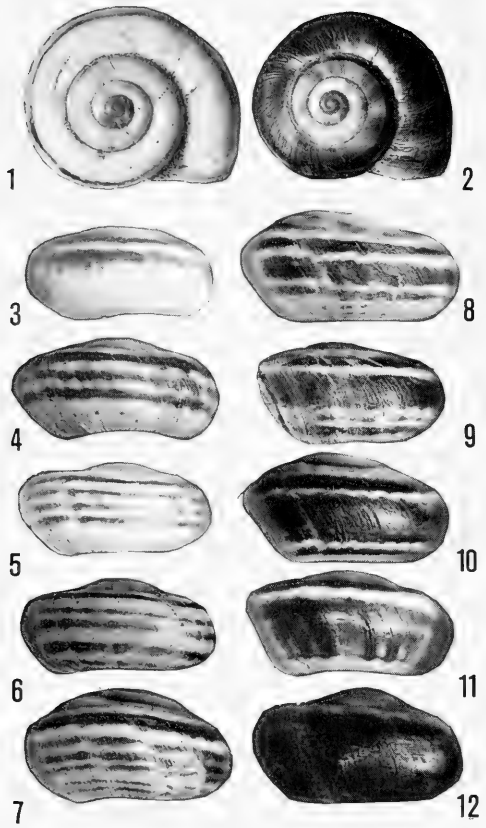

FIG. 1. Variation in shell banding pattern in *H. candicans*. 1–2, light and dark shells viewed dorsally. 3–7, shells with different numbers of lateral bands. 8–12, shells with 2–5 lateral bands fused into belts. Specimens 2 and 12 are examples of "dark" individuals.

of the shell surface colored dark, calculating an "index of melanisation." This index was calculated as follows. The dorsal band width was scored as: $<$ 0.15 mm, 0.15–0.39 mm, 0.40–0.69 mm, 0.70–1.00 mm, or $>$ 1.00 mm, these classes being given scores of 0.5, 1, 2, 3, 4, respectively. Lateral bands were split into three width classes: $<$ 0.15 mm, 0.15–0.30 mm, and $>$ 0.30 mm, with scores of 0.5, 1, and 2, respectively. Ventral bands, if present, were scored as 0.5 or 1. Every fusion of two adjacent bands was given a score of 2. The number of fused bands could be determined in most shells because one whorl back from the shell aperture the color of fusions is usually lighter than the color of bands. The index of melanisation for an individual shell was the sum of scores for all bands and all fusions. Individual indices varied between 0.5 (shells with traces of a dorsal band only) to 25 (dark individuals). The average index of melanisation for a population was the arithmetic mean of the individual indices for all shells in the sample from that population.

The temperature increase inside shells under incident radiation was measured using dead shells of 13–14 mm diameter (measured 1/4 whorl back from the shell aperture). A dark and a light shell were filled with petroleum jelly, thermocouples were inserted into the shell cavities, and the shells were placed simultaneously on a wooden block painted black or white, irradiated with a 60 W or a 200 W lamp from a distance of 25 cm. At the start of each experiment, the temperature in the shells was allowed to approach ambient. After switching on the light, the temperature in the shells was read (with 0.1°C accuracy) every 30 sec for 10 minutes. The experiments were made at low (average within shell temperature at the start 12.1°C) and high (average starting temperature 25.9°C) ambient temperatures. All measurements were repeated with two pairs of shells, twice with each pair.

Our explanation of the variation in banding (see Discussion) points to an influence of meteorological factors that decrease the amount of solar radiation reaching the earth's surface. No map indicating local variation of these factors with sufficient precision is available. Some relevant data (Fig. 2) were compiled from Veselý (1953) (number of overcast days per year, a map based on data from 270 meteorological stations in Czechoslovakia from 1926–1950) and Sládek (1977) (per cent days with fog per year, tabular data for nine meteorological stations within the study area from 1971–1975). The distribution of frequent autumn local fogs is based on the author's experience over several years and on consultation with local inhabitants.

RESULTS

There was a large inter-population variation in average shell melanisation. However, the distribution of dark populations (with average index of melanisation $>$ 11.0) was not completely random (Fig. 3). Many dark populations were found along the northwest section of Labe River, and several dark populations were also found further east along this river. Dark populations were found also near the cement

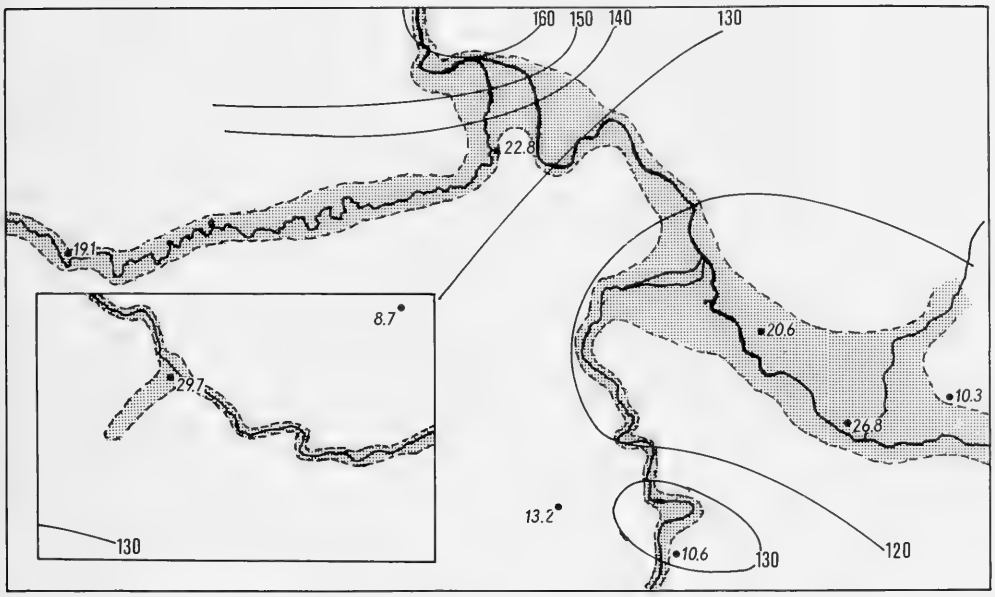

FIG. 2. Selected climatic data for the region of western Czechoslovakia shown in Fig. 3 (see right left upper insert in Fig. 3 for position of the region). The map indicates: (1) The iso-lines of the number of overcast days per year (an overcast day means 80–100% average cloud cover calculated from observations at 07.00, 14.00 and 21.00 h). (2) Per cent days with fog per year (italics) at nine meteorological stations (from left: Žatec, Doksany, Praha-Ruzyně, Praha-Karlov, Tišice, Brandýs nad Labem, Lysá. Insert: Beroun, Kladno). (3) The areas of frequent occurrence of fogs (shaded).

factory in Králův Dvůr in the Bohemian Karst (Fig. 3, asterisk on left insert). The populations with intermediate indices of melanisation were scattered over the whole area. Light populations (IOM < 9.0) prevailed in the hilly area of the Bohemian Karst (Fig. 3, insert). Despite this geographic pattern of distribution, there was a large local variation in IOM, and populations at sites closer than 0.5 km sometimes had quite different indices of melanisation.

Populations from habitats with dense and tall vegetation tended to be darker than populations of short grass steppes. I found a weak but significant relationship between index of melanisation and plant density (Fig. 4) or vegetation height ($r^2 = 2.7\%$, $p < 0.05$). Frequency of populations with high proportion of dark (IOM = 25) individuals also increased with vegetation density ($r^2 = 0.4\%$). These populations were more frequent at sites with tall vegetation than at short grass steppes (Fig. 4). However, the relationship between plant density or height and percent of dark shells was not significant. Low statistical significance was the consequence of many zero values for proportions of dark individuals in populations under each type of vegetation.

Dark and light shells differed in their rates of heating when exposed to radiation under experimental conditions. The rate of temperature increase and differences between dark and light shells depended on ambient temperature, intensity of radiation and color of the background (Fig. 5). The differences in within-shell temperature increased during the first six minutes of irradiation, when the temperature of dark shells increased faster than temperature of light ones. The highest differences were attained at low ambient temperature, with high intensity of radiation, on a white background. The maximum differences after the thermal equilibria were attained (approximately 10 minutes from the start of the irradiation) were about 2.5°C (Table 1). The thermal equilibria at low ambient temperature were highest on a black background, where the temperature excess over ambient was about 10°C.

DISCUSSION

Many factors including selection (by predators or climatic factors) and historical events

Bohemia
182–184
river Labe
river Vltava
river Berounka
river Jizera
river Dyje
10 KM
5 KM

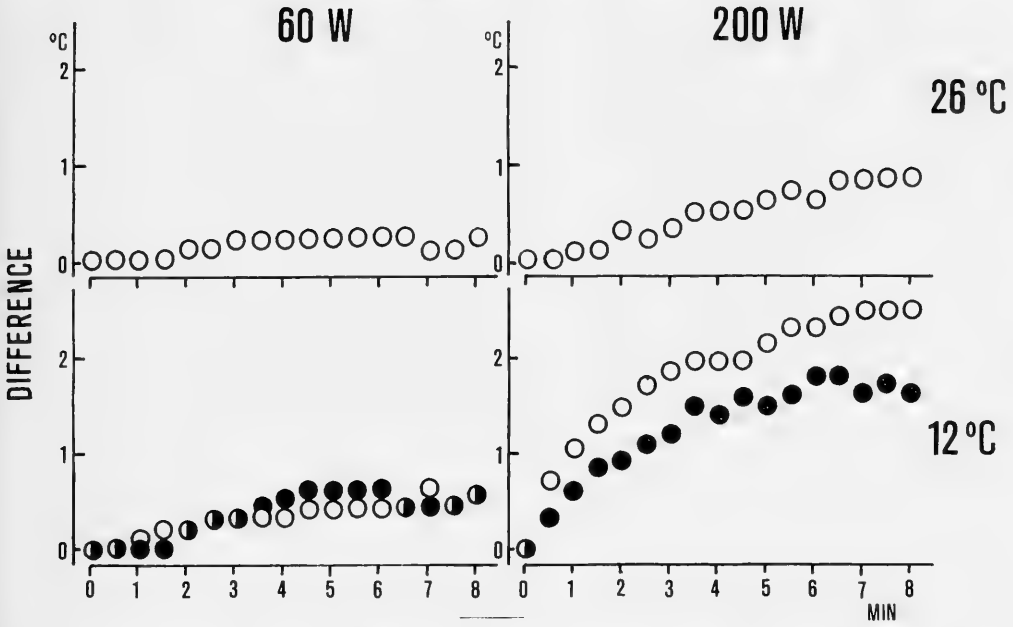

FIG. 4. Vegetation cover and shell melanisation. Top: Density of plant cover DEN and index of melanisation IOM, regression $y = 0.413\times + 7.84$, $t = 2.767$, $p < 0.01$, coefficient of determination $r^2 = 4.0\%$, $p<0.05$. Bottom: Average height of the plant stand and proportion of dark individuals MEL in populations, regression $y = 0.015\times + 0.807$, $t = 1.764$, coefficient of determination $r^2 = 1.7\%$, n.s. Symbols: 0 1–4 cases, and > 5 cases with similar proportion of dark individuals. Total number of investigated sites is 184.

(founder effect), and an extensive random variation (genetic drift) influence the composition of populations of polymorphic snail species. In addition, microhabitat choice of different morphs may also vary composition of populations. This plurality of evolutionary forces and behavioral effects also makes difficult the causal explanation of population structure in species with shell banding polymorphism (cf. Jones, 1973; Jones et al., 1977; Cain, 1983; Hazel & Johnson, 1990).

Helicella candicans is a typical example of species with variation that cannot be explained by a simple mechanism. There is a

FIG. 3. Geographic variability of the index of melanisation (IOM) in the valleys of Ohře and Labe rivers, and in the area of Central Bohemian Karst (left lower insert). The position of the areas shown on the territory of western Czechoslovakia is indicated in the right upper insert. Asterisks indicate major sources of industrial aerial pollution. Each circle represents one collecton site. Open: IOM <8.9, with central spot: 9.0 <IOM <10.9, solid: IOM >11.0. Localities included: 1. Přívlaky, 2–3. Stroupeč, 4. Žatec, 5. Lenešice, 6. Milá, 7–9. Raná, 10–11. Chraberce, 12. Chožov, 13–15. Dobroměřice, 16. Židovice, 17. Košetice, 18–21. Křesín, 22. Dubany, 23–25. Libochovice, 26–27. Klapý, 28. Radovesice, 29. Žabovřesky nad Ohří, 30. Břežany nad Ohří, 31–34. Doksany, 35–37. Libochovany, 38–39. Velké Žernoseky, 40. Žalhostice, 41–44. Litoměřice, 45. Velký Újezd, 46. Křešice, 47. Encovany, 48. Polepy, 49–51. Vrutice, 52. Hošťka, 53. Brzánky, 54. Kochovice, 55–59. Štěti, 60–61, Radouň, 62. Čakovice, 63. Stračí, 64–66. Počepice, 67. Ješovice, 68–69. Liběchov, 70. Vehlovice, 71. Mělnická Vrutice, 72. Malý Újezd, 73. Vavřineč, 74–75. Kelské Vinice, 76. Tuhaň, 77–80. Tuhaňské Větrušice, 81–83. Červená Píska, 84–86. Přívory, 87–88. Nedomice, 89–91. Dřísy, 92. Byšice, 93. Čečelice, 94. Konětopy, 95–97. Sudovo Hlavno, 98–100. Kostelní Hlavno, 101. Krpy, 102. Skorkov, 103. Tuřice, 104. Přerov nad Labem, 105–109. Semice, 110. Roudnice, 111. Ctíněves, 112. Kostomlaty pod Řípem, 113–115. Libkovice pod Řípem, 116–117. Nové Ouholice, 118. Mlčechvosty, 119. Úžice, 120. Veliká Ves, 121–122. Praha, 123. Slavíky, 124–128. Suchomasty, 129–132. Vinařice, 133–137. Všeradice, 138. Liteň, 139–140. Korno, 141–145. Měňany, 146–151. Tobolka, 152–155. Koledník, 156. Jarov, 157–159. Tetín, 160–167. Beroun, 168–174. Srbsko, 175. Karlštejn, 176–177. Hlásná Třebáň, 178. Mořinka, 179. Mořina, 180. Bubovice, 181. Loděnice, 182. Vrbice, 183. Vlkov pod Oškobrhem, 184. Hradčany. The localities are designated with names of the nearest village.

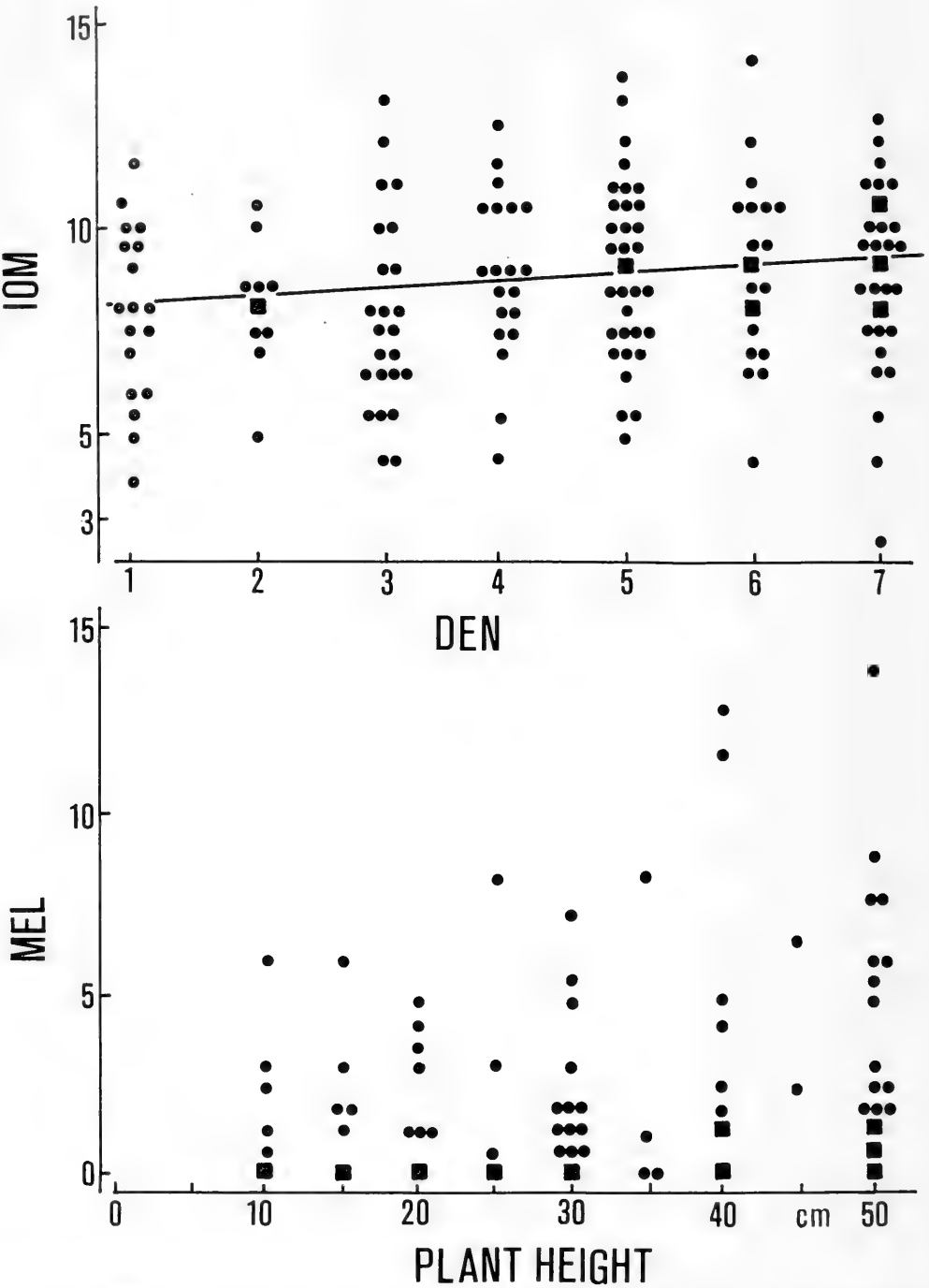

FIG. 5. The differences in warming up of the light and dark shells of H. candicans, under 60 W (left) and 200 W (right) lamp, at 26°C (above) and 12°C (below) ambient temperatures. The circles indicate differences in within-shell temperature read every 30 s from the start of the experiment. Open circles, white ground surface, solid circles, black ground surface. Each circle represents the mean of three measurements; standard errors for all means were between 0.20°C and 0.29°C.

TABLE 1. Average temperature (°C) excess (± SE) over ambient after 10 minutes of irradiation of dark (D) and light (L) shells, at two ambient temperatures. Starting temperature is an average of temperatures established within the shells left to cool to ambient temperature, at the start of the irradiation.

	Light source			
	200 W		60 W	
Starting temperature	D	L	D	L
White background surface				
12.1°C	7.9	5.3	2.1	1.5
	±0.5	±0.4	±0.1	±0.2
25.9°C	9.8	8.6	4.1	3.9
	±0.6	±0.2	± 0.2	±0.4
Black background surface				
12.1°C	11.0	9.6	3.5	2.8
	±0.9	±1.1	±0.7	±0.3

large within- and among-population variation in shell banding, and a weak association between environment factors and melanism. The genetic basis of polymorphism in *H. candicans* is unknown, but a genetic component in shell banding polymorphism may be inferred from analogy with other helicids (e.g. Wolda, 1969), and here I assume that a genetic control of shell banding polymorphism does exist. The large individual variation at all localities studied indicates an important indeterministic component affecting the variation of shell banding forms (cf. Cameron et al., 1980; Cameron & Dillon, 1984; Ratel et al., 1989). Although a large proportion of variation may be random, a part of variation may have adaptive significance.

The only significant factor of shell melanisation that could be demonstrated from this study is climatic selection. I suppose that the reduced incident solar radiation may favour dark populations. This is indicated by increased frequency of dark populations in areas with frequent fogs and increased cloudiness. This particularly applies to area around the northwest section of Labe River (Fig. 3). This river crosses the České Středohoří Mountains through a narrow valley. In this region, there are several chemical factories and electric plants using lignite (Fig. 3, asterisks) that are sources of air pollution. These factors favour the origin of local fogs, which often appear in the autumn, decreasing solar radiation reaching the earth's surface. The greater cloudiness in this area also decreases solar radiation reaching the earth's surface (Fig. 2). Several dark populations were found further east along the Labe River where local fogs are also frequent. Local fogs and aerial pollution may affect the occurrence of dark populations near the cement factory in Králův Dvůr (Fig. 3, insert), whereas the light populations prevailed in the rest of the hilly area of Bohemian Karst with relatively clean air, low cloudiness and low fog frequency (Fig. 2, insert). Plant cover may also reduce the intensity of incident solar radiation, and several examples of increased melanisation under dense and tall plant stands were found.

The shell banding polymorphism in *H. candicans* may have adaptive significance related to different thermoregulation properties of dark and light morphs (cf. Tilling, 1983; Etter, 1988). High index of melanisation and incidence of dark shells were associated with environments where sunshine was reduced. Variation in other snail species provides parallel examples of association between shell color and microclimate (cf. Heller & Volokita, 1981a; Livshits, 1981; Nevo et al., 1981; Emberton, 1982; Nevo et al., 1982; Heller & Gadot, 1984; Ramos, 1984, 1985; Sacchi, 1984; Vicario et al., 1988; Hazel & Johnson, 1990). I suggest that dark shell coloration may help to maintain increased body temperature on cool and overcast days. Such conditions are frequent in the autumn, the breeding season of *H. candicans,* particularly at localities near rivers and sources of air pollution, which both contribute to frequent fog. Then, a quicker increase of body temperature during the short spells of sunshine may confer some advantage on darks (cf. Heller & Volokita, 1981b).

On the other hand, being dark may also have negative consequences. The snails are particularly sensitive to overheating and des-

iccation when active, and there is a selection for pale body color in warm areas (Cowie & Jones, 1985; Cowie, 1990). Light individuals may maintain lower thermal equilibria than dark individuals, the coloration which may then become a disadvantage. I have no data on mortality, but I suppose that at the steppe localities, e.g. on the southern slopes of hills in the Bohemian Karst, heat stress from solar radiation may affect survival.

Although the advantage that arises from different thermoregulation properties of dark and light morphs probably contributes to differentiation of phenotype frequencies among the populations, climatic selection explains only a very small fraction of among-population variation in shell melanisation. Further study may reveal other selection forces, and I suppose that a great proportion of variation is random.

ACKNOWLEDGMENTS

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DAILY MOVEMENT PATTERNS AND DISPERSAL IN THE LAND SNAIL *ARIANTA ARBUSTORUM*

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ABSTRACT

The relationship between daily movements of individuals and their dispersal over longer periods was studied in two natural populations of the land snail *Arianta arbustorum* in Switzerland. In a forest clearing, daily movements of individually marked snails ranged from 0 to 4.44 m (median 0.58 m); the frequency distribution of the distances traveled fitted a function with exponential decay. The snails showed no preference in direction of movement. Further, the directions chosen by an individual on consecutive days were independent from each other. These findings agree with the assumptions of a random movement model. In a 1-m wide belt of tall grass and forbs along a ditch, daily movements of *A. arbustorum* were exponentially distributed and ranged from 0 to 1.57 m (median 0.40 m). The snails' movements were confined to favourable vegetation; individuals that reached the edge of the belt did not enter the drier surroundings (a mown meadow); instead they continued to move in a new direction within the belt.

Using characteristics of the movement pattern of the *A. arbustorum* population in the forest clearing, we simulated snail dispersal in habitats of different shape over longer periods. The simulations showed that snails dispersed significantly longer distances in a two-dimensional habitat than in linear habitats of 1 and 8 m width. A comparison with literature data on helicid snails dispersing in two-dimensional habitats (meadows, pastures) and linear habitats (roadside verges, river embankments, hedges) supports this result.

Key words: *Arianta arbustorum,* Gastropoda, dispersal, gene flow, movement pattern, habitat.

INTRODUCTION

The distances moved by organisms between locations where they are born and where they mate and reproduce are important determinants of population structure. From a population genetics perspective, vagility can strongly influence effective population size and the rate of gene flow, especially when populations are spatially structured by discontinuities of suitable habitats or resources. Restricted gene flow, in turn, can lead to genetic differentiation of local populations as a result of locally differing selection pressures or genetic drift.

Dispersal in non-flying animals is often confined to suitable habitat. Type and heterogeneity of habitat, local population density and such individual characteristics as body size, age, nutritional condition and homing tendency have been assumed to influence dispersal in terrestrial gastropods (e.g. Cain & Currey, 1968; Greenwood, 1974; Pollard, 1975; Oosterhoff, 1977; Dan, 1978; Cook, 1979, 1980; Lind, 1988, 1989; Baker & Hawke, 1990). The purpose of this study is twofold. First, we quantify the relationship between daily movement patterns of individuals of the land snail *Arianta arbustorum* (L.) and the distances dispersed during periods of different lengths. Second, we examine the effect of habitat form (either two-dimensional or linear) on distances dispersed.

Dispersal is defined here as the distance travelled by a snail in its daily activity during periods longer than one day (Endler, 1977). Daily movement, or distance covered per day, is defined as the straight line between the positions of an individual on two successive days. We assume that the snails live in relatively homogeneous habitats, and consequently in the present context ignore directed seasonal migrations between hibernation, aestivation and oviposition sites as described for *Helix pomatia* (Edelstam & Palmer, 1950; Pollard, 1975; Tischler, 1973; Lind, 1989), *Theba pisana* (Johnson & Black, 1979; Johnson, 1981; Lebel, 1991) and *Cernuella virgata* (Baker, 1988a, b).

MATERIALS AND METHODS

The Species

Arianta arbustorum is a simultaneously hermaphroditic helicid gastropod that is common

in moist habitats in northwestern and central Europe (Kerney & Cameron, 1979). Shell growth is restricted to spring and summer and is completed after one or several hibernations with the formation of a shell lip at the edge of the shell aperture, with adult snails measuring 16–20 mm in shell diameter (Baur & Raboud, 1988; Baur, 1990). The mean adult life span of *A. arbustorum* is 3–4 years, but a maximum longevity of 14 years after reaching sexual maturity has been recorded (Baur & Raboud, 1988).

Locomotory activity occurs only under particular physical conditions, temperature, photoperiod and air humidity being the important determinants (Cameron, 1970a, b). During periods of drought and heat, *A. arbustorum* aestivates either buried in the soil or attached to leaves and stems of plants (Frömming, 1954; B. Baur, 1984, 1986). During winter the animals hibernate in the soil (Frömming, 1954; Terhivuo, 1978).

Recording of Movement Patterns

Daily movements of *A. arbustorum* were recorded in a grass-covered clearing, 20×30 m in size, in a coniferous forest 10 km south of Basel, Switzerland (47°28′N, 7°34′E; altitude 360 m a.s.l.). A grid of 25 units, each 4 m^2 in area, was set up in the central part of the clearing by marking the corners of each unit with a stake. Sixteen subadult (individuals with a shell diameter $>$ 8 mm but without a reflected lip at the shell aperture) and 51 adult (individuals with a reflected lip) *A. arbustorum* were collected within the clearing and individually marked on their shells with numbers written in permanent felt pen on a spot of correction fluid (Tipp-Ex). The shell diameter of each snail was measured to the nearest 0.1 mm with vernier callipers. Marking and measuring were carried out in the field, and the snails were released immediately at their original positions. On 11 consecutive days in April and five days in May 1990 the grid and the adjacent area within 5–8 m were carefully searched for marked *A. arbustorum.* The position of each marked snail was recorded by measuring the distances to the nearest two stakes of the grid; based on these data, coordinates were calculated. Field work was always done in the late afternoon; therefore the snails' positions usually represent their daytime resting sites.

Using the coordinates of the position of each snail, we calculated: (1) the distance between the positions on two successive days (to the nearest cm), (2) the angle of each daily displacement relative to the grid system (= orientation of movement), and (3) the angle (measured in a counter-clockwise direction) between two successive daily displacements.

To test the accuracy of the method, the daily positions of 32 snails were marked with numbered flags. The distances between successive positions were measured directly and compared with those calculated from coordinates using correlation analysis. The direct measurement of displacements was simple, but did not allow any estimate of angles between successive movements. The calculated distances covered were highly correlated with those measured directly ($r = 0.998$, d.f. $= 60$, $p < 0.001$), indicating a high accuracy of the coordinate method.

To estimate dispersal over a longer period, the clearing was carefully searched for *A. arbustorum* 30 days after initiation of the study. Later observations (after two and three months) indicated that some snails had reached the clearing's edge, which consisted of stands of blackberry (*Rubus corylifolius*). However, no snails were found in blackberry stands and in the adjacent pine forest, indicating that this type of habitat was repellent to the snails and thus influenced their movements.

Daily minimum and maximum air temperatures were obtained from a minimum-maximum thermometer placed 10 cm above ground in the clearing. Data on precipitation and duration of sunshine were recorded at Aesch and Schönenbuch, situated 3 and 8 km away from the clearing. During the study, the weather was favourable for snail activity: daily minimum temperatures ranged from 2.5 to 14.0°C and maximum temperatures from 10.5 to 21.0°C. Precipitation was distributed fairly evenly over the period and occurred on 10 of the 16 days.

Daily movements of *A. arbustorum* were also monitored in a 1-m-wide and 50-m-long belt of forbs and grass in a subalpine pasture at Potersalp, 1290 m a.s.l., in the eastern Swiss Alps (47°17′N, 9°20′E). Snail densities of up to 6.8 adults per m^2 were recorded (B. Baur, 1986). The height of the vegetation in the belt was 30–50 cm. A partly overgrown ditch (5–20 cm wide) ran down the middle of the belt. The meadows adjacent to both sides of the belt were cut to a height of 7–10 cm. For detailed description of the habitat and local climate, see B. Baur (1986, site A).

In September 1981, 60 *A. arbustorum* were individually marked with numbers in India ink on 1 mm × 2 mm pieces of paper glued onto their shells. Shell size was measured as above. Marking was carried out in the field, and the snails were immediately released at their original positions. A grid of $1m^2$ units (11 squares in a line) was set up to enable recording of the positions of marked snails. Daily displacements of snails were recorded as above during five successive days.

Air temperature and relative humidity were recorded by a thermohygrograph 10 cm above ground in the belt of tall vegetation. During this study, minimum air temperature ranged from 0.8 to 2.4°C, and maximum air temperature from 3.2 to 10.5°C. Humidity in the vegetation belt averaged 86.5% (range 79.4–94.8%).

In the vegetation belt, a second experiment was conducted to examine dispersal of *A. arbustorum* over a longer period using the same grid. On 16 August 1981, 92 *A. arbustorum* were marked with dots of car-lacquer; individuals from each grid unit were marked with a different coloured lacquer. Snails were marked in the field and released as described above. After ten months, the grid and the adjacent area within 10–20 m were carefully searched. The positions of marked individuals were recorded. Dispersal of snails was determined by calculating the distances between the grid units where the snails were marked and recovered (distance between neighbouring units = 1 m).

Simulation Model

A model of random movement was used in computer simulations to examine dispersal of *A. arbustorum* over longer periods. Random movement can be assumed if (1) traveling animals do not prefer any direction, (2) the direction of movement does not depend on the direction of preceding movements, and (3) the distance moved by each animal is an exponential random variate (Pielou, 1969). The pattern of distances covered per day by *A. arbustorum* in the clearing indicates that these assumptions were fulfilled as long as the snails did not reach its edge (see Results).

To simulate dispersal in a two-dimensional habitat, we assumed a uniform distribution of angles of orientation (no preference for any direction). For each snail, x (= number of days) random variates generated from the exponential distribution of daily distances covered (Fig.1a) were assigned to a random direction (derived with an accuracy of 1° from a uniform distribution in the interval from 0° to 360°). Daily movements were summed by vector addition of Cartesian coordinates resulting in a final distance moved from the origin. The entire simulation procedure was repeated for 1,000 "snails," each of them "moving" x days from a common starting point (x = 10, 20, 30, . . . 110, 120 days). We assume that 120 days correspond approximately to one year of activity in *A. arbustorum* living in lowland populations in Central Europe (c.f. B. Baur & Raboud, 1988).

To simulate dispersal in linear habitats of 1 and 8 m width, for each "snail" random variates were generated from the exponential distribution of daily distances moved in the clearing (Fig. 1a), and a random direction from a uniform distribution was assigned to each variate. If a "snail" reached one of the edges of the linear habitat, a new random direction among the angles possible within the favourable habitat was generated, and the "snail" moved from its position at the edge the remaining part of the daily distance in this new direction. Daily net movements were summed as described above.

Dispersal in linear habitats (river embankments, roadside verges) is often measured in one dimension (i.e. distances dispersed along the x-axis only are considered) (Goodhart, 1962; B. Baur, 1984, 1986; A. Baur & B. Baur, 1990). To compare simulated dispersal in two-dimensional and linear habitats with literature data, we also calculated the distances dispersed along one axis in our simulations for both habitat forms.

RESULTS

Movement Patterns in Natural Populations

In the clearing, the recovery rate of marked *A. arbustorum* averaged 47.5% (range 20.0 – 71.4%) after 24 h. A total of 119 daily distances moved by 50 *A. arbustorum* were recorded. The distances covered within a day ranged from 0 to 4.44 m (median value: 0.58 m), and their frequency distribution fitted a function with exponential decay (Fig. 1a). A proportion of the snails (28.6%, Fig. 1a) remained inactive or moved very short distances (< 25 cm), even in 24-h intervals with favourable weather conditions (rainy nights).

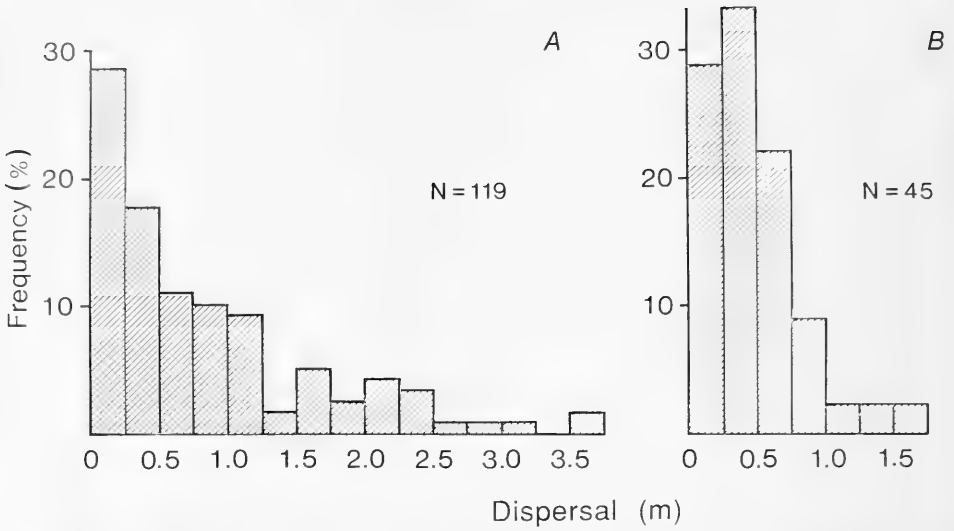

FIG. 1. Frequency distribution of distances moved per day by *A. arbustorum* in (a) a forest clearing and (b) a belt of grass and forbs (1 m wide). Exponential functions were fitted to the distributions: (a) $y = 21.510\ e^{-.010x}$, $r^2 = 0.79$, $t = 6.74$, d.f. = 12, $p < 0.001$; (b) $y = 55.060\ e^{-.022x}$, $r^2 = 0.88$, $t = 6.00$, d.f. = 5, $p < 0.01$; x = distance in cm and y = frequency (%).

The mean distance covered per day (all snails considered) was positively correlated with daily minimum temperature ($r = 0.59$, $n = 16$, $p = 0.016$), and negatively correlated with the number of sunshine hours ($r = -0.76$, $n = 16$, $p < 0.001$). Thus, snails moved larger distances during relatively warm nights, whereas sunny days restricted their movements. The distances moved per day were not influenced by the age-class of the snails (0.88 m in subadults vs. 0.92 m in adults; Mann-Whitney U-test, $n = 119$, $p > 0.4$). We cannot exclude that data about the most- and the least-mobile snails are underrepresented, because snails moving long distances are less likely to be recovered than those moving less far and individuals remaining inactive for several days are often buried in the soil. However, these sources of bias may balance to some extent.

Representative movement tracks of *A. arbustorum* recorded in the clearing are illustrated in Figure 2a. Overall, the snails showed no preference in direction of movement (Rayleigh test, $n = 119$, $p > 0.1$). Furthermore, the direction chosen by a traveling snail was independent of that of the preceding day (Rayleigh test, $n = 45$, $p > 0.2$). Finally, the snails moved equal distances in all directions (Kruskal-Wallis test, d.f. = 5, $p > 0.6$, analysis based on sectors of 60°). Six *A. arbustorum* were recovered 30 days after marking. The distances dispersed averaged 3.43 m (range 0.77–6.28 m).

In the vegetation belt, the recovery rate of marked *A. arbustorum* averaged 42.0% (range 33.3–50.0%) after 24 h. A total of 45 daily distances covered by 25 *A. arbustorum* were recorded. The distances covered were exponentially distributed and ranged from 0 to 1.57 m (median = 0.40 m) (Fig. 1b). As in the clearing, a proportion of the snails (28.9%, Fig. 1b) were inactive or moved distances <25 cm even in 24-h intervals with favourable weather conditions. Subadult and adult *A. arbustorum* did not differ in the distances covered (0.26 m vs. 0.48 m, Mann-Whitney U-test, $n = 45$, $p > 0.05$).

Representative movement tracks of *A. arbustorum* living in the vegetation belt along the ditch are illustrated in Figure 2b. The snails showed no preferred direction of movement (Rayleigh test, $n = 45$, $p > 0.8$). Likewise, the direction chosen by a moving snail was independent of that of the preceding day (Rayleigh test, $n = 18$, $p > 0.8$). Repeated observations during the day revealed that the snails did not enter the drier surroundings (a mown meadow); individuals that reached the edge of the vegetation belt continued their movements in a new direction within the favourable habitat. The repeated returning at

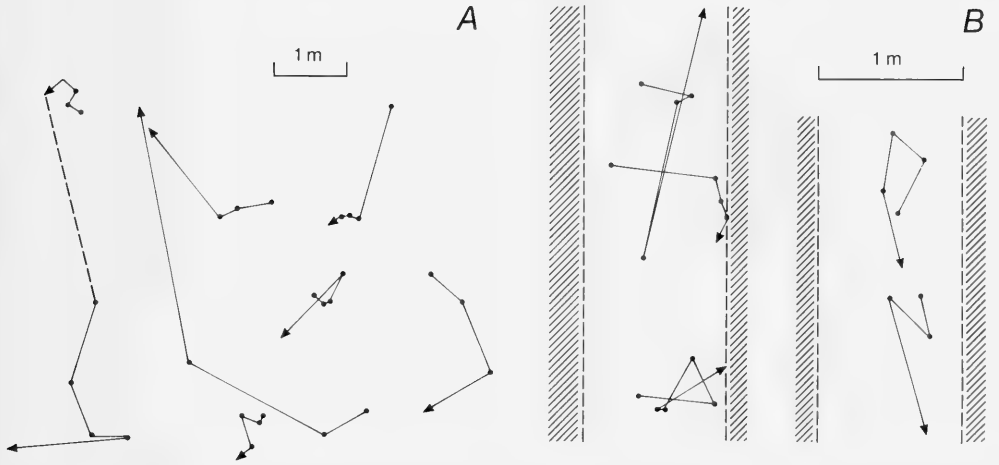

FIG. 2. Representative movement tracks of individuals of *A. arbustorum* in (a) a clearing and (b) a vegetation belt (1 m wide). Dots indicate the snails' positions on consecutive days and arrows the directions of movement. Dashed line indicates movement in two days.

the edges may result in shorter distances dispersed in a linear than in a two-dimensional habitat. This suggests that the pattern of dispersal of *A. arbustorum* is influenced by the form of the habitat.

In the second experiment performed in the vegetation belt, 13 out of the 92 marked *A. arbustorum* were recovered after ten months. The distances dispersed along the ditch averaged 6.2 m (range: 0–15 m).

Simulated Dispersal

Simulated mean dispersal for 1,000 snails in a two-dimensional habitat increased from 4.0 m in 10 days to 14.5 m in 120 days (dispersal in two dimensions considered: Fig. 3a), the maximum distances dispersed being 15.1 m and 39.6 m, respectively.

The form of the habitat had a significant effect on snail dispersal: in linear habitats the animals dispersed shorter distances per time unit than in a two-dimensional habitat (Fig. 3a). Furthermore, the width of the linear habitat influenced snail dispersal (Fig. 3a). When dispersal along one axis was considered, the distances dispersed per time unit decreased, but the difference between habitat forms remained (Fig. 3b).

Literature data suggest that helicid snails disperse larger distances in two-dimensional habitats than in linear habitats, supporting the results of our simulation (Table 1). For example, mean dispersal of *Cepaea nemoralis* was found to be 10 m in one year in a grassland in England and 4.7 m along a slope of a river bank (a linear habitat). Dispersal of *A. arbustorum* averaged 4.9 m in three months in a clearing in central Sweden. Corresponding figures for roadside verges of 2 and 2.5 m width with similar vegetation were 2.2 m and 2.9 m, respectively.

DISCUSSION

This study indicates that long-term dispersal of land snails can be estimated on the basis of daily movements. Our simulation model incorporates several assumptions: (1) the distribution of daily distances moved does not change during the activity season, (2) the length of the activity season is fixed (in our case 120 days), (3) the structure of the habitat is homogeneous, and (4) the snails show no homing behaviour.

Our simulations may accurately estimate snail dispersal, presupposing that the assumptions are fulfilled. In the field, the daily activity of snails and the distance moved in a day are mainly determined by abiotic factors (e.g. humidity, changes in temperature, light), time of the year, and endogenous rhythms (Dainton, 1954; Bailey, 1975; Rollo, 1982; Dainton & Wright, 1985; Ford & Cook, 1987; Munden & Bailey, 1989). The length of the activity period (time from arousal in spring until hibernation in late autumn) of snails in nat-

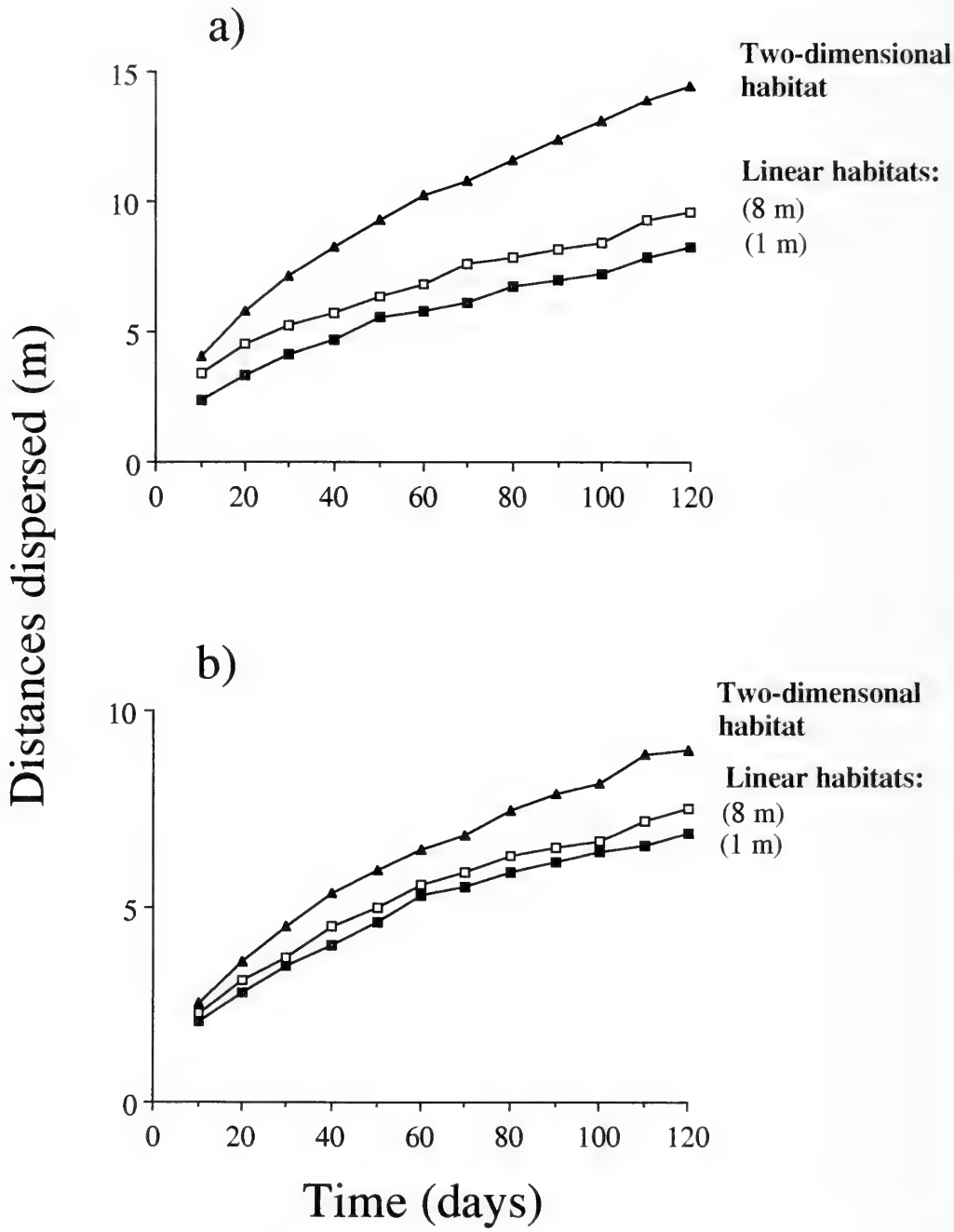

FIG. 3. Simulated dispersal of snails in habitats of different form for periods of 10, 20, ... , 110, 120 days. Each point represents the mean dispersal for 1,000 snails. For details of the simulation model, see Material and methods. Dispersal is calculated in two dimensions (a) and in one dimension (b).

TABLE 1. Summary of dispersal in three species of helicid snails in two-dimensional and linear habitats.

Species	Locality	Habitat vegetation	Habitat width (m)	Time after release	Dispersal (m) mean [maximum]	Number (%) of snails recaptured	Density (no. of adults/m^2)	Type of release*	Source
Two-dimensional habitats:									
Cepaea nemoralis	France	garden	—	2 years	9.7 [25]	8(4.0)	2.0	C	Lamotte (1951)
C. nemoralis	France	herb meadow	—	5 months	8.1 [20]	30(15.0)	—	C	Lamotte (1951)
C. nemoralis	Germany	uncultivated	—	6 months	23.8 [46]	13(13.0)	<1	C	Schnetter (1951)
		meadow,	—	2 years	32.1 [67]	13(13.0)			
		scattered bushes							
C. nemoralis	England	area of long grass and nettle	—	1 year	10	—	1.4	O	Murray (1962), cited by Greenwood (1974)
C. hortensis	Iceland	herb meadow	—	2 months	2.1[7.5]	48(19.0)	—	C	Bengtson et al. (1976)
Arianta arbustorum	Switzerland	alpine grassland, with scree material	—	1 year	12.0 [23]	18(18.2)	2.4	O	Baur (1984, 1986)
A. arbustorum	Sweden	clearing,	—	1 month	3.3 [11]	14(16.7)	21.3	O	Baur & Baur (1990)
		rough herbage		3 months	4.9 [11]	24(28.6)			
A. arbustorum	Switzerland	clearing, rough herbage	—	1 month	3.4 [6]	6(25.0)	~3	O	present study
Linear habitats:									
C. nemoralis	England	slope of a bank, grazed meadow	8	4 weeks	2.0 [7]	133(66.5)	10–20	L	Goodhart (1962)
				13 weeks	3.3 [11]	108(54.0)			
				1 year	4.7 [17]	83(41.5)			
A. arbustorum	Switzerland	belt of nettle along a scree band	1	1 year	7.0 [16]	28(14.5)	5.9	O	Baur (1984, 1986)
A. arbustorum	Sweden	roadside verge,	2	1 month	1.3 [8]	199(37.6)	26.1	O	Baur & Baur (1990)
		rough herbage		3 months	2.2 [14]	169(31.9)			
A. arbustorum	Sweden	roadside verge,	2.5	1 month	2.3 [10]	66(34.0)	5.5	O	Baur & Baur (1990)
		rough herbage		3 months	2.9 [12]	49(25.3)			
A. arbustorum	Switzerland	subalpine pasture, along a ditch	1	10 months	6.2 [15]	13(14.1)	6.8	O	present study

*C = released at a central point, O = individually released at original site, L = released in a line.

ural populations is relatively well known (e.g. Dan, 1978; B. Baur & Raboud, 1988). However, at present no data are available about the number of days the snails actually show locomotory activity in natural populations (but see Bailey, 1989a, for activity under experimental conditions). This represents a major problem for any simulation of dispersal.

Dispersal in land snails has been shown to be affected by type and height of vegetation (Cain & Currey, 1968; Cowie, 1980, 1984; Baker & Hawke, 1990), local population density (Greenwood, 1974), snail size (Szlavecz, 1986; A. Baur & B. Baur, 1988), homing tendency (Cook, 1979, 1980; Bailey, 1989b), and time of the year (Cameron & Williamson, 1977; B. Baur, 1984, 1986). Possible effects of habitat structure, type of vegetation and local population density on daily distances moved and thus on dispersal were beyond the scope of this study. Furthermore, we considered exclusively fully grown and almost fully grown individuals of *A. arbustorum* which did not differ in movement behaviour. The distribution of daily distances moved may change in the course of the activity season. Helicid snails have been observed to move farther during the reproductive season than in autumn shortly before hibernation (Cameron & Williamson, 1977; B. Baur, 1984, 1986; A. Baur & B. Baur 1990). Detailed data on seasonal variation of daily distances moved are so far lacking.

The marking procedure, type of release (crowded at a central point or individually at original positions) and searching procedure significantly influence snail dispersal over shorter periods (Oosterhoff, 1977; Cowie, 1980). We tried to minimise the latter effects by marking the snails in the field and releasing them immediately at the positions where they were found. However, monitoring of snail movements in natural habitats needs repeated recoveries of individually marked snails. Intense and repeated searching procedures damage the vegetation and change the microclimate, which in turn may alter the snails' behaviour (Cameron & Williamson, 1977). Consequently, to record daily movements, the search intensity should be moderate, and reduced recovery of marked snails must be accepted. Recovery of marked individuals is further reduced by the snails' resting behaviour. During the activity season, *A. arbustorum* frequently rests for periods of up to several days buried in the soil. A proportion of snails remain inactive in the soil even under conditions favourable for activity (Peake, 1978). For example, *Helix aspersa* was active in a test arena during 67% of nights with favourable conditions (Bailey, 1989a).

In the vegetation belt, we observed during the day that individuals reaching the edge of the belt generally did not enter the suboptimal surroundings, but rather continued their movement in a new direction within the favourable habitat. The adjoining mown meadow may constitute an unsuitable habitat to *A. arbustorum* for several reasons. The short vegetation of the meadow retains less humidity and hence, curtails the snails' activity. Daily fluctuations in temperature may be more extreme and insolation more intense in short grass than in the tall vegetation of the belt. Furthermore, the short vegetation makes snails more vulnerable to visually hunting predators (the song thrush, *Turdus philomelos,* is an important predator of *A. arbustorum* in that area; B. Baur, 1984). Finally, due to repeated cutting, different species of grass dominated the meadow (grass is not a major constituent of the diet of *A. arbustorum;* Frömming, 1954; Speiser & Rowell-Rahier, 1991).

Literature data revealed that snails dispersed shorter distances in linear habitats than in unlimited two-dimensional habitats supporting the results of our simulation study. The fact that dispersal is reduced in linear habitats may be of importance for estimates of effective population size and rate of gene flow.

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GEOGRAPHIC VARIATION IN REPRODUCTIVE TRAITS OF *HELIX ASPERSA* MÜLLER STUDIED UNDER LABORATORY CONDITIONS

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ABSTRACT

The reproductive characteristics of the land snail *Helix aspersa* were investigated under artificial conditions in ten populations exposed to contrasting selective pressures in their natural environments. Two of them were studied for two different years.

Significant geographic variation was detected not only in fecundity (clutch number, clutch size significantly related to shell size) but also in the timing of mating and egglaying. Thus, seasonal adjustments (breeding season and duration), related to the geographic location of populations, seemed to be partially preserved under uniform laboratory conditions.

In order to assess the extent of genetic or environmental determination of variation in these characters, three successive generations of snails from four ecologically distinct regions were reared under the same artificial conditions. This experiment revealed that a large proportion of the initially observed variation in natural populations from Lorient and Toulouse, France, and in snails from St. Denis, La Réunion, was environmentally induced. Animals born and reared in the laboratory exhibit similar traits: they mate two or three times, lay a mean of 1.3 clutches corresponding to between 120 and 130 eggs per snail. On the other hand, snails from Algeria retain their natural characteristics (larger shell size, larger clutches with larger eggs) under artificial conditions.

In the context of intraspecific life-history variation of *Helix aspersa,* observed combinations of traits might illustrate two tactics: (i) Snails from Algeria have a large size (*H. a. maxima*), which allows them to have a higher egg production in comparison with "norms" of the species (i.e. all other known populations), but not with respect to their shell volume (smaller than possible clutch volume). This production could compensate for a high mortality, which would affect all age categories in the field. (ii) Life-history patterns of populations from more or less recently colonized habitats, always dependant on human activities, would be considered as the second tactic of the species: stable populations of smaller adults with a smaller egg production and considerable plasticity in life-history traits.

Key words: *Helix aspersa,* reproduction, geographic variation, phenotypic plasticity.

INTRODUCTION

The helicid land snail *Helix aspersa* Müller, native to the western Mediterranean area, is now very abundant in human-modified habitats of northwestern Europe. This wide distribution leads to geographic variation in annual activity rhythms. Thus, the breeding season is restricted to spring and summer in northern localities, to autumn or even winter in the Mediterranean area (Chevallier, 1983). Periods of activity are followed in northern latitudes by hibernation, which has a diapause value (Bailey, 1983; Lorvelec & Daguzan, 1990), in southern ones by estivation, which, in some cases, is only a warm torpor. Sacchi (1971) suggested that reproduction is potentially continuous and might occur during all sufficiently wet and warm periods of the year. Thus, the annual activity rhythm and life cycle of this species present a high degree of flexibility, of which an important part can be observed in the same population. Previous studies have also documented variation in the seasonality of reproductive activity (Potts, 1975; Crook, 1980; Madec & Daguzan, 1991) and geographic variation in egg production per snail (Guemene & Daguzan, 1982).

In other pulmonate landsnails, several life-history traits (growth rate, age at maturity, adult size, and life span) often covary with reproductive characters (Peake, 1978; Calow, 1983; Cowie, 1984). Some combinations clearly adapt the populations to local climatic conditions (Baur & Raboud, 1988). However, such covariation need not be adaptative, and it is therefore necessary to determine the genetic component of the variation. Quantitative genetic methods should permit this determination (heritabilities and

genetic correlations), but their use often presents many technical difficulties. Another approach consists of transplant experiments to artificial conditions to observe if natural contrasts remain constant through several generations of laboratory culture or if the progenies converge to a common form (Clarke et al., 1978; Brown, 1985).

The first approach has yielded estimates of heritability for shell characters, including a significant genetic component of shell size variation among populations (Clarke et al., 1978; Goodfriend, 1986). The inheritance of variation in *Helix aspersa* shell size, which is very extensive in natural conditions and strongly correlated with fecundity, has been studied using both the first (Crook, 1980; Panella, 1982) and second approaches (Madec, 1989a). In this way, laboratory colonies of four natural populations characterized by large differences in adult shell size showed the strong influence of the environment (climate, population density) in determining small size (dwarfs from the island of La Réunion) and a primary role played by the genetic component in the determination of the giant size of individuals from Algeria (*Helix aspersa maxima* Taylor). However, the great phenotypic plasticity shown by the other snails (*Helix aspersa aspersa* Müller) could be itself under genetic control.

The present study reports on: (i) natural variability in reproductive traits of *Helix aspersa* examined in samples from ten localities covering its whole ecological range. (Because the experiments took place under uniform laboratory conditions, this comparative study was designed primarily to obtain information on variation in reproductive potential of the species, but can also be used to discuss the disturbances in activity rhythms of transplanted snails from contrasting habitats.) (ii) examination of the persistence of variation under the same conditions, following the continuous rearing of three generations of snails from four source populations with different life histories.

MATERIAL AND METHODS

Relevant reproductive behaviour of *Helix aspersa* has been described by Tompa (1984) and Adamo & Chase (1988).

Origin and Maintainance of Animals

Random samples were collected from colonies covering the whole range of the species. Snails were taken as adults from their natural environments from April to May 1983 or/and 1985, just after the natural hibernation for samples from France and Balearics, and after the winter activity for snails from Algeria; the annual activity rhythm of snails from La Réunion is not known, but animals were active or just attached with strong mucus to various hard surfaces when they were collected. French populations sampled included (Fig. 1): Lorient (northwest), Surgères (central-west), Toulouse (southwest), Belmont (east), Lyon (central-east), Avignon (southeast), and Bastia (Corsica). Colonies from Lorient, Belmont and St. Denis de La Réunion were sampled twice. A comparative study of colonies from Lorient and other Breton populations had already shown that the only significant variation between samples concerned the start of the breeding season (Madec & Daguzan, 1991); in the present study, we used only the sample from Lorient to represent this region and referred, if necessary, to the others. In addition, we also studied a sample from a population recently introduced by man from Brittany (Madec, 1991) to St. Denis de La Réunion, a volcanic island of the Mascarene Archipelago (Indian Ocean), a sample from Palma de Mallorca (Balearics), and another from Alger (Algeria). Snails from this last sample belong to a different subspecies, namely *Helix aspersa maxima,* initially described by Taylor in 1883, more recently studied by Chevallier (1983). Climatic data for each locality are illustrated in Figure 1.

From the natural populations, two from France (Lorient, Toulouse) and those from St. Denis and Algeria were selected to represent the most important variations of reproduction in this species. However, the breeding of the Algerian stock could not be maintained and consequently, only the results from the sample of snails collected in the natural population and a sample of the F6 generation of an experimental population obtained from collaborating researchers[1] are presented here. For the others, four generations were identified as follows:

—AS generation: snails collected as adults in their natural environment;

[1]J. C. Bonnet, Institut National de la Recherche Agronomique, Domaine du Magneraud, Surgères.

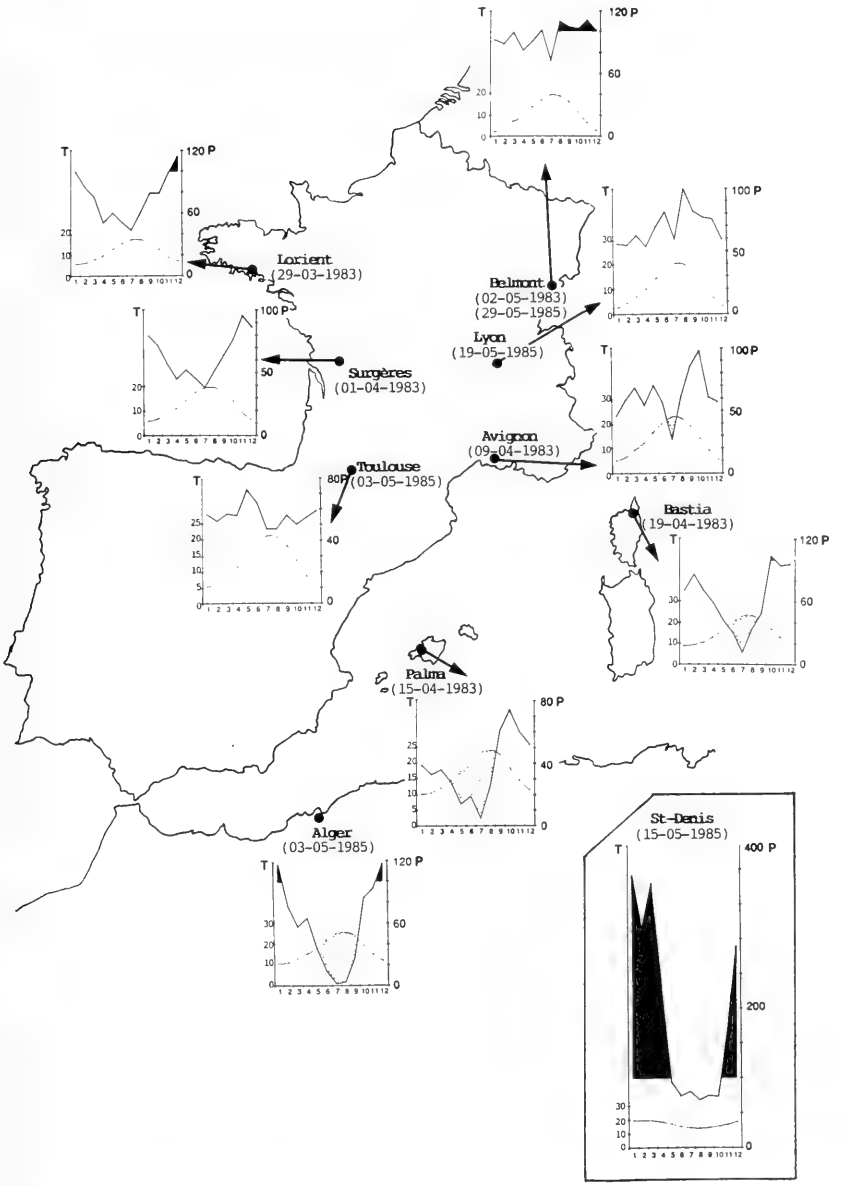

FIG. 1. Location of the ten sampled sites (except St. Denis de la Réunion), sampling dates, and diagrams of relation during one year between rainfall (P: mean monthly rainfall, mm) and temperature (T: mean monthly temperature, °C).

—JS generation: snails, collected as juveniles in their natural environment, which became mature in artificial conditions;

—F1 generation: offspring of random crosses between individuals of the AS generation;

—F2 generation: offspring of random crosses between individuals of the F1 generation.

In the laboratory, snails of the AS generation remained into an artificial hibernation (5±1°C; 60±5% R.H.; 0L:24D light cycle) for one week,

except for samples from La Réunion and Algeria, which were kept directly in the breeding conditions. For the others, revival was triggered in a room at 12°C, 80% R.H. and a 12L:12D light cycle, in which snails were fed again. For the reproduction experiment, snails were reared in controlled temperature and relative humidity rooms maintained at 20±1°C, 80±5% R.H. and a 16:8 light:dark cycle. They were housed in polythene containers (50 × 30 × 10 cm; 29 × 18 × 7 cm) with a biomass density per cage of approximatively 18 kg/m^3 (13–15 individuals in small boxes and 35 in the others). These values were selected as optimal for breeding activity of snails living in western France, e.g. Surgères or Lorient (Daguzan, 1981; Le Guhennec & Daguzan, 1983). For snails from Algeria, which are larger, the density was 30 kg/m^3 (8–10 individuals in small boxes). At least two replicate cages were used per population to take possible "cage effects" into account. Furthermore, the location of boxes in the rearing room was changed each day, and adjoining boxes always contained snails from different populations.

All individuals were fed with the same composite food supplied *ad libitum* and renewed at least twice a week. Water was available in a watering place, and the synthetic foam covering the cage bottom was kept moist and washed every day. Laying jars containing a moist and light soil (sterilized compost) were placed in the cages, two in small cages and four in large ones. A jar was replaced by another as soon as a snail laid in it. Afterwards, jars with clutches were transferred to an incubator (T = 20±1°C; R.H. = 100%; 12L:12D).

For the JS, F1, and F2 samples, growth and reproduction occurred under the same conditions of temperature (20°C), photoperiod (16L:8D), and humidity (80% R.H.), and with the same diet. However, during growth, snails were sorted, and densities modified according to snail size to avoid the effects of crowding (Madec, 1989a). After the growth period, which finished approximatively three months after birth in F1-F2 generations, snails were induced into artificial hibernation for three months (5°C; 60% R.H.; 0L:24D light cycle). Revival was triggered in a room at 12°C, 80% R.H. and a 12L:12D light cycle, in which snails were fed again.

Methods

Adult Measures and Monitoring: Adult shell height and maximum breadth were measured to the nearest 0.1 mm using a vernier calliper; each animal was numbered with an adhesive stamp. Mating and egg-laying in *Helix aspersa* have durations of about eight hours and 18 hours respectively, so two daily observations (08:00 hr; 18:00 hr) permitted monitoring of all layings and 97% of the matings (percentage based on dart presence in a cage without mating observation). Dates when individuals resumed activity and dates of death were also recorded. The length of the reproductive season was different for each population because it was based on the end of layings, which generally coincided with the start of a higher mortality.

Egg Collection and Measures: Each clutch was identified by its parentage and its position (1st, 2nd, 3rd clutch of the same snail), date of laying, its size (number of eggs), and hatching date. Of each clutch from AS, JS, F1, and F6 populations, 30 eggs chosen at random were weighed (±0.01 g) and their diameter (diameters when ovoïd) measured with a dial calliper (±0.01 mm). After that, all the eggs were replaced in a soil cavity, and the laying-jar was covered by a plexiglass plate before being placed in the incubator. Newly hatched juveniles emerging from the soil were counted, removed and the durations of incubation and hatching noted. From each hatching, 30 individuals chosen at random were weighed.

Statistical Methodology

Data analysis was performed using the STAT-ITCF (1988) programs. Where possible, contingency tables were studied with the help of χ^2 tests; samples with quantitative data were compared with analysis of variance followed by S.N.K. multiple comparisons tests, if the F was significant. The t-test was previously used to compare the means of the different cages of the same sample. When differences were not significant ($P > 0.05$), we used one set of data per sample. When non-normality or heterogeneity in variances were detected or could not be tested, non-parametric statistics were adopted (see Results).

RESULTS

Variation Between Samples in Reproductive Activity Under Artificial Conditions

Timing Fluctuations: Significant variations between AS snail samples were observed not only in the dates of resumption or termination

of mating and laying activities, but also in the rhythm of these activities during the breeding period (Fig. 2). Thus, mean numbers of days between revival and the mating and laying activities measured for the ten first reproducing individuals for each sample were significantly different (Kruskal-Wallis tests; $P < 0.001$). According to the non-parametric test of multiple comparisons with a level of significance $P = 0.01$ (Scherrer, 1984), snails from northern France formed two homogeneous groups (Lorient/Surgères; Lyon/Belmont), in which snails started to reproduce after one week, significantly earlier than snails from Toulouse and Avignon, which started to mate more than two weeks after revival, from Bastia and Palma (on average eight weeks during which many snails had reformed an epiphragm), and from Algeria, which were not sexually active before October (24 weeks), as they were in their natural environment. The level of sexual activity of snails from St. Denis was always low, but this sample was relatively close to the group Lorient/Surgères. Groups constituted according to first ovipositions gave similar indications, but northern ones were dissociated and the sample from St. Denis was close to Belmont (Lyon < Belmont ≤ St. Denis < Lorient < Surgères, with $P < 0.05$). In addition, there was no significant variation between samples of the same populations sampled for two years (Belmont 1983/1985; St. Denis 1985/1986), either for distributions of matings numbers per week, or for ovipositions (Kolmogorov-Smirnov tests; $P > 0.05$). Thus, snails seemed to reproduce gradually later from northern to southern populations.

The phase of reproductive activity increase up to a peak (first mode of distributions of mating numbers per week and, to a lesser degree, oviposition numbers) confirmed the distinctions between AS samples. Snails from Belmont and Lyon reached a high level of reproductive activity in only one week and then remained at it for several weeks (Fig. 2). On the other hand, we observed a slow progression to a single peak for both mating and laying activities in the Bastia and Palma samples; peaks were followed by a fast decrease of reproductive activity, which stopped completely three weeks after these maxima. In between, other distributions were not very different, but the sample from Lorient was close to those from Belmont and Lyon, and the sample from Avignon was close to those from Bastia and Palma.

The most contrasting curves of seasonal activity are shown in Figure 3. In addition to the differences between eastern and southern populations (accentuated by high degrees of skewness of the distributions), we noted that effective lengths of the breeding period in these two contrasting samples (12–13 weeks) were shorter than in others (14–16 weeks).

Over three generations in the laboratory (JS, F1, F2, only F6 for Algeria because of the small size of the JS sample), the timing of both mating (mainly due to a shift in the Toulouse population) and oviposition converged among all four populations (Fig. 4). These snails tended to produce clutches earlier than their conspecifics from the field (Kolmogorov-Smirnov tests; Toulouse and Alger, $P < 0.001$; Lorient, $0.07 > P > 0.01$; La Réunion AS-F2, $P = 0.05$, N.S. for the other comparisons). Frequency distributions of matings and layings per week in the F1, F2, and (F6) generations were not significantly different in the four populations (χ^2 tests: matings, $P = 0.08$; layings, $P = 0.65$).

Variation in Number of Matings and Clutches: AS populations differed significantly in terms of mean rates of mating and egglaying (χ^2 tests; $P < 0.001$); total numbers of matings or clutches per sample varied approximately between ten (Alger) to 100 (Belmont) (Table 1). However, the numbers of matings and clutches produced per individual were also variable in the same population (Fig. 5). Distributions of snails according to their total number of matings were significantly different between AS populations (χ^2 test; $P < 0.001$); these variations in level of reproductive activity led us to distinguish three significantly different groups (Simultaneous Test Procedure with a significance level $P = 0.05$): a first group of samples with a high level of individual activity (Belmont, Lyon, Toulouse, Avignon; distributions with a mode of three matings per snail), a second with moderate activity (Lorient, Surgères; 20% of the snails did not mate), and a third group (Bastia, Palma, St. Denis) with a low level of activity (samples with at least 55% of snails with at most one mating). The comparison of distributions of snails according to their total number of clutches led to the distinction of only two groups with significantly different levels of egglaying activity. Thus, there was sharp contrast between AS samples from mainland France and insular ones.

When distributions of AS and JS individuals

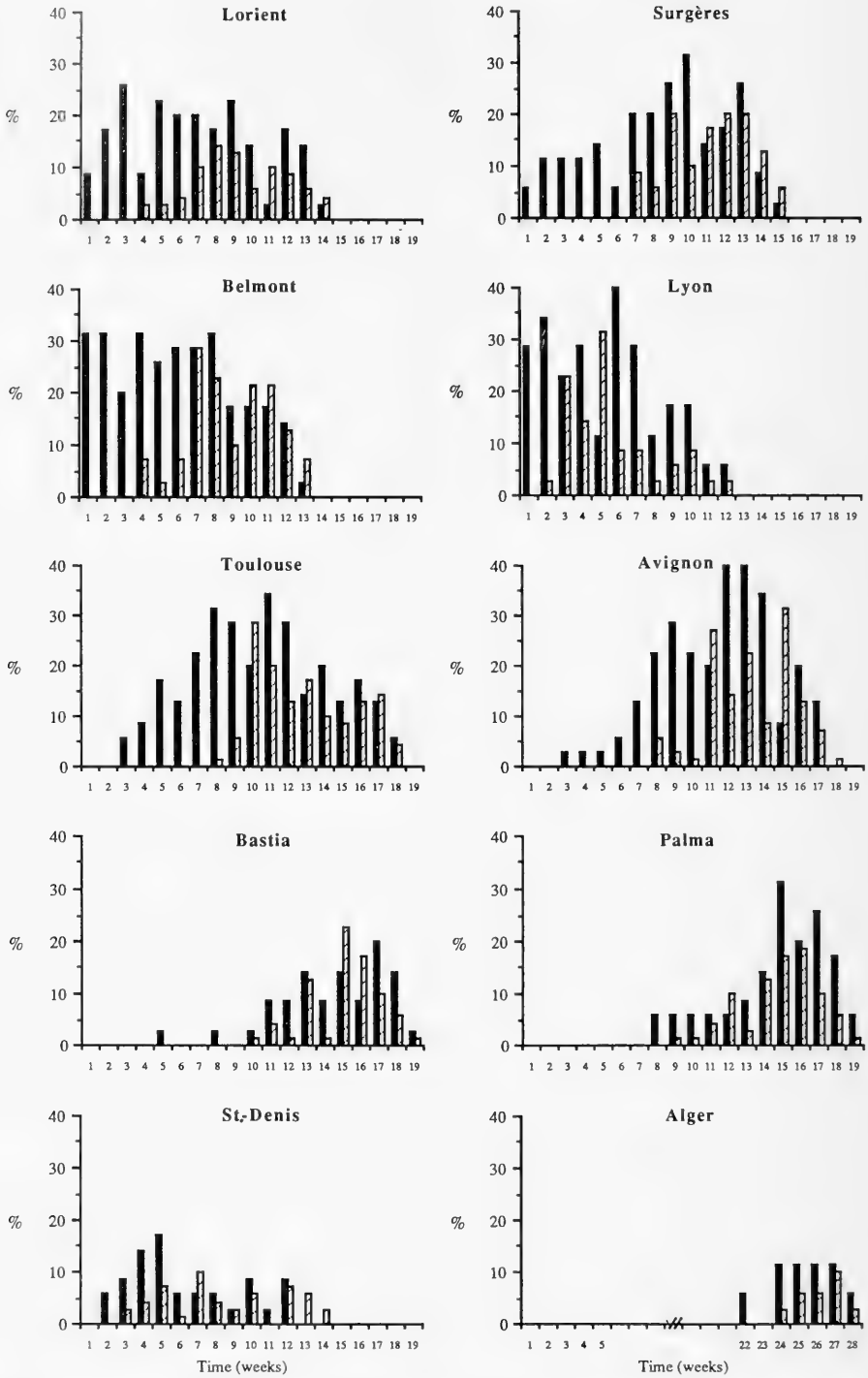

FIG. 2. Weekly variations of mating (solid) and oviposition (crosshatched) numbers, according to the origin of snails (expressed as % of the total number of individuals per sample).

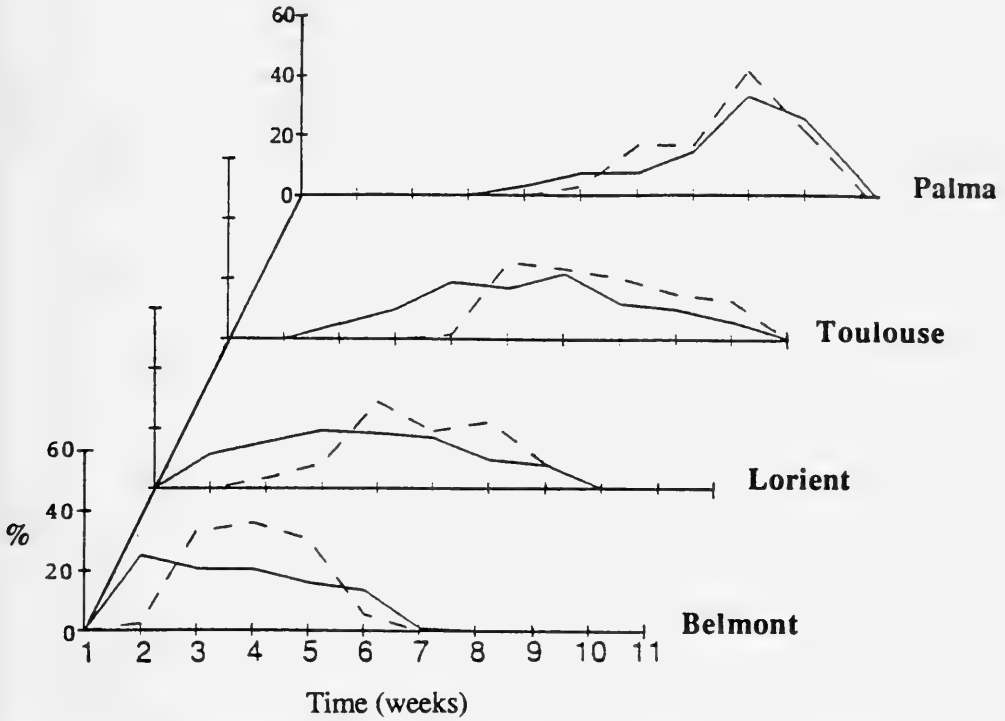

FIG. 3. Evolution in fortnights of matings (solid line) and clutches (stippled line), expressed as % of their respective total numbers within four natural populations of *Helix aspersa*.

according to their total number of matings were compared, we observed that among all the populations (Lorient, Toulouse, St. Denis), only the AS sample from St. Denis was unique because 40% of snails had no mating activity. In addition, the mode for populations raised in the laboratory from field-collected juveniles was a single mating (Fig. 6). Distributions of individuals according to their clutch production were also significantly different. For the same origin, the total number of clutches laid by snails from JS generation was always higher than the one of AS generation. Moreover, snails from Toulouse (AS, JS) were characterized by the highest individual clutch production (Table 2). The multiple comparisons between all AS and JS populations led to three homogeneous groups (Simultaneous Test Procedure with $P < 0.01$; [1]: population JS Toulouse; [2]: populations AS-JS Lorient/AS Toulouse/JS St. Denis; [3]: populations AS St. Denis/Algeria).

With the exception of one sample (St. Denis, F2), all F1, F2, (and F6) populations presented a mating rate of 100%, snails often mating twice during the period of reproduction. Distributions of individuals according to their total number of matings were not significantly different (χ^2 test; $P = 0.32$). Even if the total number of matings in the F2 population of La Réunion was very low, only one snail did not mate during the breeding season. Distributions of F1 and F2 individuals according to their total ovipositions were remarkably homogeneous (χ^2 test; $P = 0.68$). Snails from the Algerian-F6 sample gave a very different result: 50% of them produced at least four clutches and, on average, twice as many as the others (Fig. 7).

Finally, with the exclusion of these F6 snails, all animals born and reared in laboratory conditions behaved in the same way: the total number of matings by sample was low, but their distribution among individuals was equal; snails had a similar oviposition activity, which was expressed, after nearly 12 weeks of reproduction, by about 60 clutches for 45 individuals, corresponding to 1.3 clutches per snail.

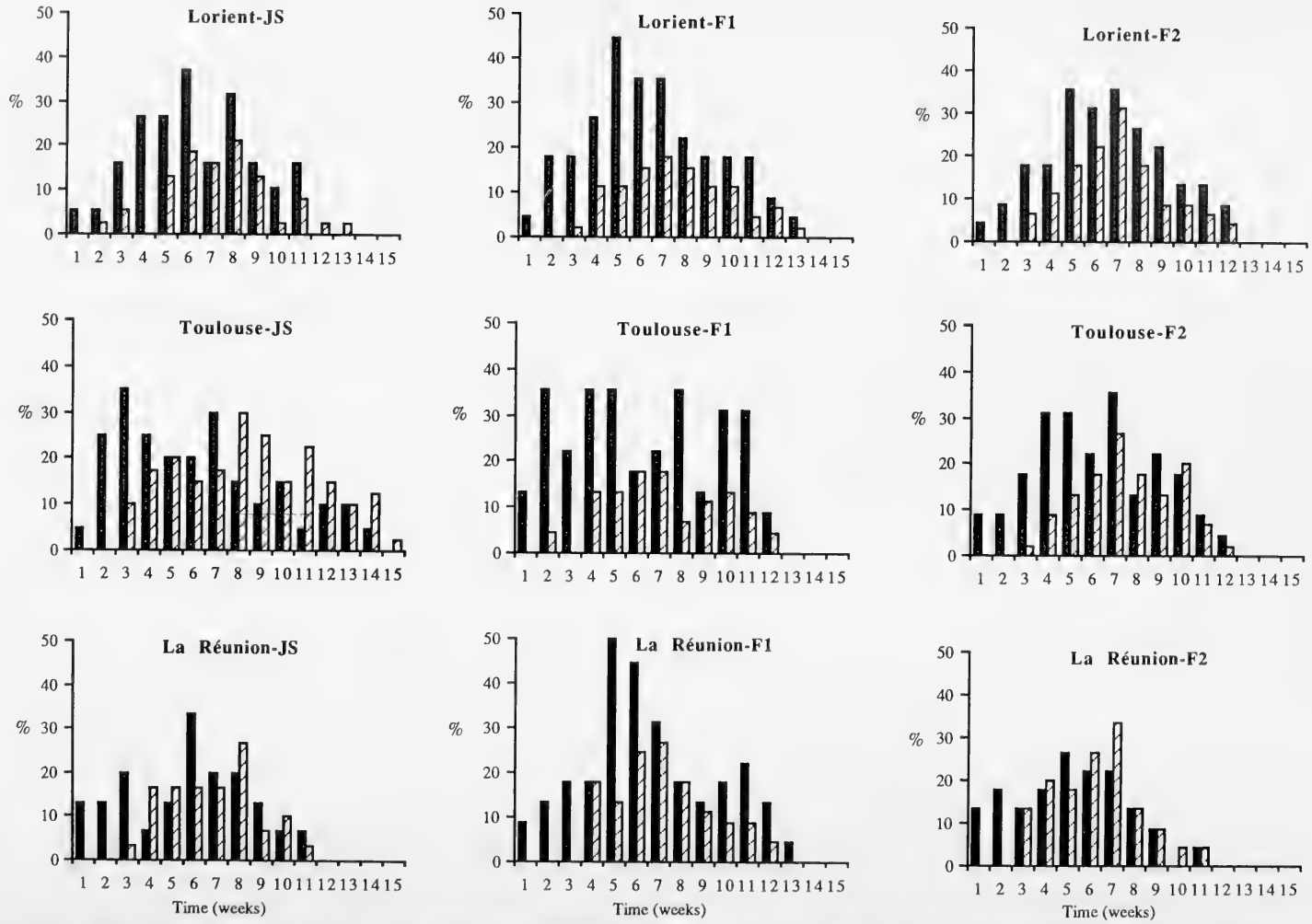

FIG. 4. Weekly variations of mating (solid) and oviposition (crosshatched) in JS, F1, and F2 generations, according to the origin of snails (expressed as % of the total numbers of snails within each generation).

TABLE 1. Reproductive characters, shell size and mortality of *Helix aspersa* from nine natural populations studied under uniform laboratory conditions ($\bar{x} \pm$ standard error).

Origin (sampling year)	Lorient (1983)	Surgères (1983)	Toulouse (1985)	Avignon (1983)	Belmont (1983)	Belmont (1985)	Lyon (1985)	Bastia (1983)	Palma (1983)	St. Denis (1985)	St. Denis (1986)
Sample size	70	70	70	70	70	70	35	70	70	70	35
Shell breadth (mm)	30.5 ± 0.2	32.9 ± 0.2	33.6 ± 0.2	33.4 ± 0.2	31.0 ± 0.2	30.8 ± 0.2	29.3 ± 0.2	28.4 ± 0.2	29.3 ± 0.2	26.2 ± 0.2	27.0 ± 0.1
Mean rate of matings (%)	80.0	80.0	95.7	90.0	98.6	98.6	97.1	68.6	74.3	60.0	62.9
Mean number of matings per ind.	2.1 ± 0.2	2.3 ± 0.2	2.7 ± 0.2	2.6 ± 0.1	2.7 ± 0.1	2.9 ± 0.1	2.5 ± 0.1	0.9 ± 0.1	1.4 ± 0.1	0.8 ± 0.1	1.1 ± 0.1
Mean rate of layings (%)	60.0	74.3	78.6	80.0	88.6	85.7	77.1	60.0	62.9	41.4	42.9
Mean number of clutches per ind.	0.9 ± 0.1	1.2 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	1.4 ± 0.1	1.5 ± 0.1	1.1 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	0.6 ± 0.2	0.6 ± 0.1
Mean number of eggs per ind.	82.3 ± 9.7	137.2 ± 13.4	175.5 ± 14.8	157.2 ± 14.6	130.3 ± 10.2	122.8 ± 9.5	96.6 ± 13.6	61.0 ± 8.2	76.7 ± 8.1	38.6 ± 5.8	36.8 ± 6.7
Clutch size	99.3 ± 4.3	116.0 ± 5.8	132.1 ± 5.9	124.7 ± 5.1	92.1 ± 5.2	85.1 ± 5.1	86.8 ± 5.2	80.6 ± 4.0	89.6 ± 4.3	69.1 ± 3.9	71.4 ± 3.8
Hatching success (%)	90.8	86.5	90.4	86.8	87.3	79.5	93.2	88.8	89.2	86.1	89.7
Adult mortality (%)	27.1	30.0	4.3	27.1	24.3	5.8	11.4	25.7	15.7	8.6	22.9

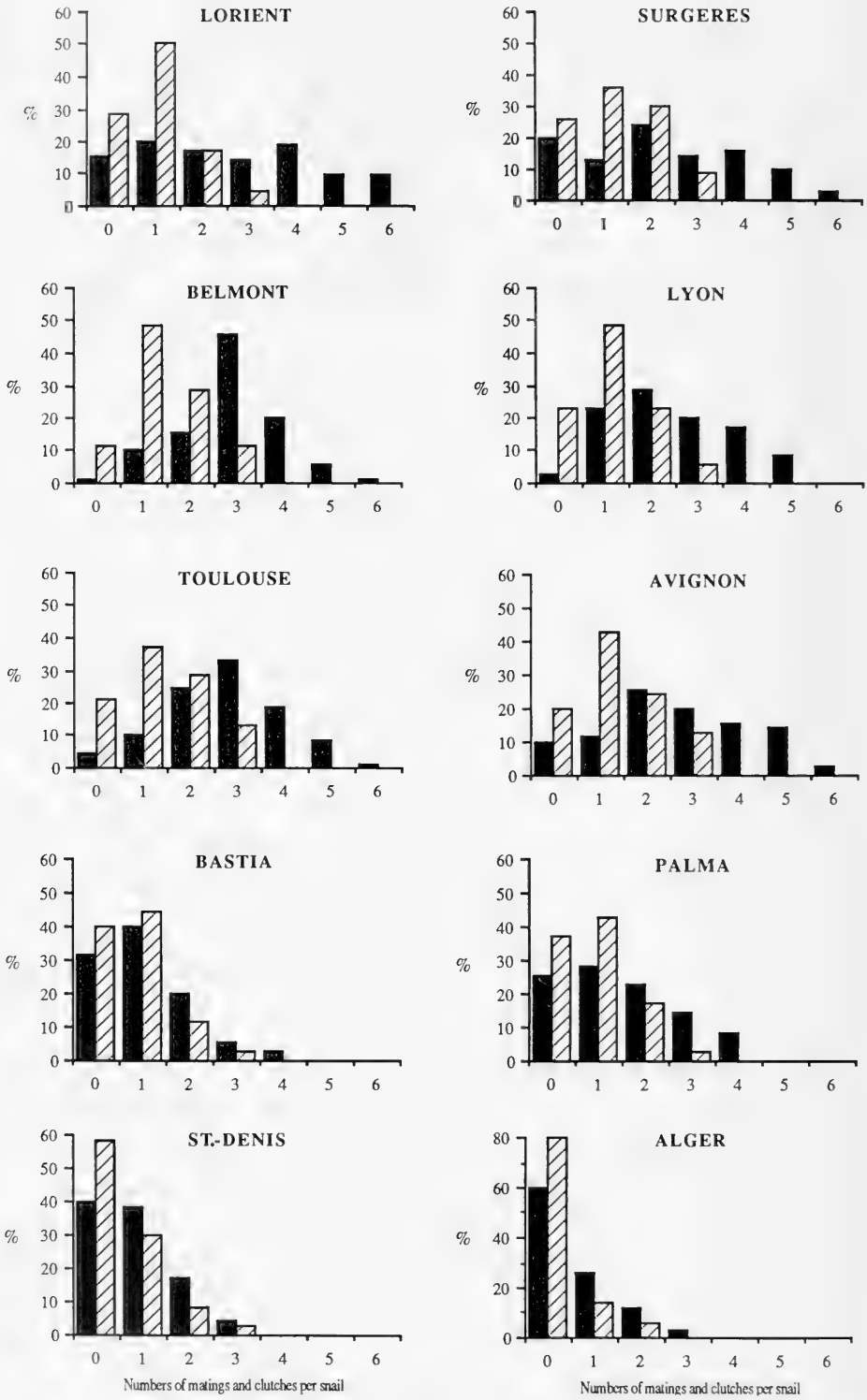

FIG. 5. Distributions of the snails (in %) according to their total number of matings (solid) and clutches (crosshatched) in the ten natural populations studied.

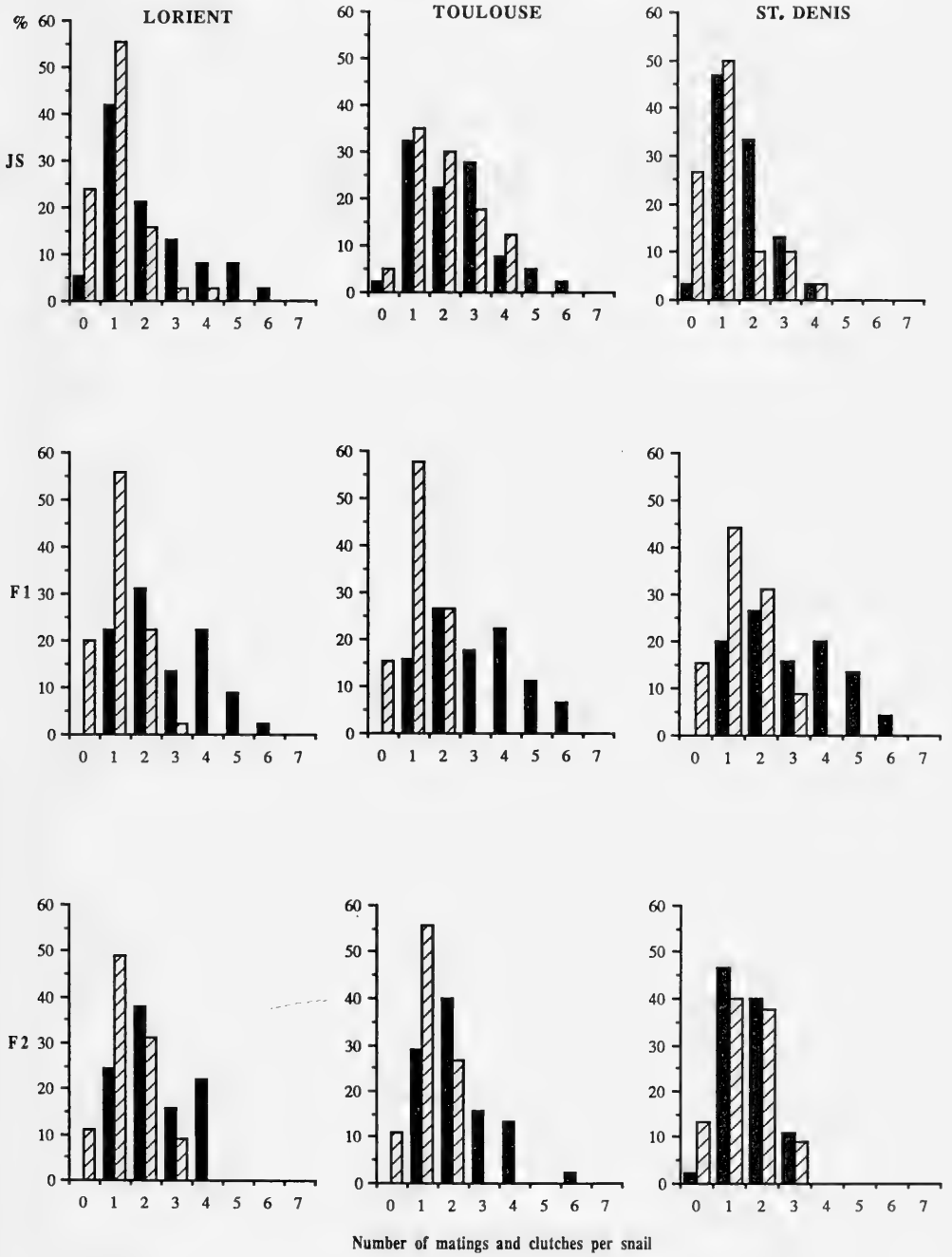

FIG. 6. Distributions of the snails (in %) according to their total number of matings (solid) and clutches (crosshatched) in different generations of the three populations considered.

TABLE 2. Reproductive characters, shell size and mortality of *Helix aspersa* under artificial conditions, according to origin and generation of the snails ($\bar{x} \pm$ standard error).

Origin	Lorient			Toulouse			St. Denis		
Generation	JS	F1	F2	JS	F1	F2	JS	F1	F2
Sample size	38	45	45	40	45	45	30	45	45
Shell breadth (mm)	30.8 ± 0.3	31.2 ± 0.3	32.0 ± 0.2	31.6 ± 0.2	31.4 ± 0.2	32.6 ± 0.2	27.6 ± 0.4	30.7 ± 0.2	32.0 ± 0.3
Mean rate of matings (%)	94.7	100	100	97.5	100	100	96.7	100	97.8
Mean number of matings per ind.	2.2 ± 0.2	2.7 ± 0.2	2.3 ± 0.2	2.5 ± 0.2	3.1 ± 0.2	2.2 ± 0.2	1.6 ± 0.2	2.9 ± 0.2	1.6 ± 0.1
Mean rate of layings (%)	76.3	80.0	88.9	95.0	84.5	88.9	73.3	84.5	86.7
Mean number of clutches per ind.	1.1 ± 0.1	1.1 ± 0.1	1.4 ± 0.1	2.0 ± 0.2	1.1 ± 0.1	1.3 ± 0.1	1.1 ± 0.2	1.3 ± 0.1	1.4 ± 0.1
Mean number of eggs per ind.	102.8 ± 10.6	92.4 ± 10.1	127.8 ± 11.2	201.9 ± 19.5	96.7 ± 8.9	123.8 ± 10.9	87.6 ± 9.1	125.6 ± 11.5	130.4 ± 12.8
Clutch size	97.7 ± 3.8	86.6 ± 3.9	92.8 ± 3.7	96.8 ± 3.1	87.0 ± 3.4	96.1 ± 3.5	77.3 ± 3.6	94.2 ± 3.1	92.2 ± 4.1
Hatching success (%)	89.0	91.2	83.7	86.9	86.8	88.3	88.1	90.4	87.4
Adult mortality (%)	18.4	15.5	13.5	10.0	8.9	11.1	30.0	13.3	11.1

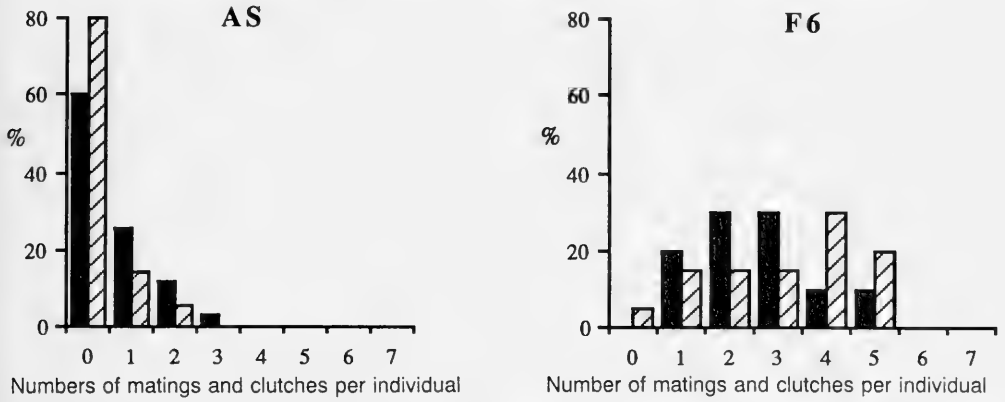

FIG. 7. Distributions of the snails (in %) according to their total number of matings (solid) and clutches (crosshatched) in two generations of Algerian snails.

Changes in Number of Eggs and Young

In AS populations, the number of eggs of the first clutch (N1) was significantly higher than the next ones for snails that laid at least two clutches (t-test; $P < 0.001$), and linearly related to shell size, with a highly significant correlation coefficient, except in the Algerian sample in which only seven clutches have been considered (Table 3). In addition, the nine regression lines compared were significantly different (ANCOVA; $P < 0.001$). Thus, for a given shell size, snails from a population with on average larger individuals were inclined to lay larger clutches.

Differences between samples (without the Algerian one) in mean first clutch size and mean shell size were also highly significant (ANOVA; $P < 0.001$), and there was, as might be expected, the same differences between samples for the two characters after multiple comparisons tests (Table 4): snails from southern populations seemed to be larger and to lay larger clutches, whereas insular snails size was reduced, as was their mean clutch size, especially for the sample from St. Denis.

In addition, samples with the lower mean clutch size were also those with the lower mean number of clutches laid per snail. As AS populations did not differ in hatching success for "healthy" clutches (Table 1), mean numbers of young produced per snail presented the same differences or homogeneities between them as those observed for mean numbers of eggs. However, some clutches were infected by various parasites, mainly nematodes, to different degrees according to their origin (from a maximum of 28.9% in Belmont 1985 to a minimum of 5.1% in St. Denis 1985 with, respectively, hatching success of 27.7% and 53.9%; no apparent infection in samples from St. Denis 1986 and Algeria).

For the populations studied through four generations, individual shell breadth and first clutch size were introduced in a two-way (generation, origin) ANOVA with replication. Each factor and their interaction have highly significant effects ($P < 0.001$) and therefore, the population classification according to N_1 led to the following conclusions (Table 5):

—Significant differences were observed only between AS populations. The homogeneity of all the other populations for this character was the result of a decrease of the mean value in JS, F1, and F2 samples from Toulouse with respect to the AS generation and, in contrast, an increase of the mean clutch size in successive experimental generations from La Réunion. Differences between snails from Lorient were not significant, whatever the generation was.

—The F1 samples from Lorient and Toulouse were characterized by small clutches, which could be associated with a relatively low number of clutches produced per snail. Thus, snails born and reared in the laboratory laid clutches with a number of eggs independent of parental origin and between 90 and 100.

The mean numbers of eggs deposited per AS-JS snail during the season (total fecundity) showed differences between populations in accordance with the preceding compari-

TABLE 3. Relationship between first clutch size N1 (dependent variable) and shell breadth (in mm × 10) in *Helix aspersa* from ten natural populations. P: level of significance of r.

Origin	N	Slope	Intercept	r	P
Lorient	40	0.88	−164.6	0.60	***
Surgères	51	0.74	−115.5	0.44	**
Toulouse	55	0.84	−131.2	0.51	***
Avignon	56	0.82	−141.5	0.46	**
Lyon	27	1.30	−291.2	0.68	***
Belmont	60	0.90	−179.9	0.66	***
Bastia	41	0.82	−149.3	0.60	***
Palma	44	0.65	−95.3	0.63	***
St. Denis	29	0.98	−182.4	0.74	***
Alger	7	0.15	+121.5	0.10	NS

TABLE 4. Classification of natural populations according to shell breadth and first clutch size N1 (S.N.K. test; $P < 0.05$)

Shell breadth classification						Clutch size classification					
Terms used	Means	SNK test				Terms used	Means	SNK test			
Toulouse	33.5	A				Toulouse	150.2	A			
Avignon	33.3	A				Avignon	132.8	A			
Surgères	32.4	A				Surgères	124.3	A			
Belmont	30.8		B			Lorient	104.9		B		
Lorient	30.5		B			Belmont	97.3		B	C	
Lyon	29.4		B	C		Palma	95.1		B	C	D
Palma	29.3		B	C		Lyon	91.1		B	C	D
Bastia	28.4			C		Bastia	83.8			C	D
La Réunion	26.3				D	La Réunion	74.1				D

TABLE 5. Classification of AS, JS, F1 and F2 samples according to shell breadth and first clutch size (S.N.K. test; $P < 0.05$)

Shell breadth classification						Clutch size classification					
Terms used	Means	SNK test				Terms used	Means	SNK test			
AS-Toulouse	33.3	A				AS-Toulouse	145.9	A			
F2-Toulouse	32.6	A	B			F2-La Réunion	102.8		B		
F2-Lorient	32.0	A	B	C		F1-La Réunion	101.2		B		
F2-La Réunion	31.9	A	B	C		F2-Lorient	100.5		B		
JS-Toulouse	31.5		B	C		JS-Toulouse	100.3		B		
F1-Toulouse	31.3		B	C		F2-Toulouse	100.1		B		
F1-Lorient	31.1		B	C		AS-Lorient	100.1		B		
F1-La Réunion	30.8		B	C		JS-Lorient	99.7		B		
JS-Lorient	30.6		B	C		F1-Toulouse	91.2		B	C	
AS-Lorient	30.4			C		F1-Lorient	90.7		B	C	
JS-La Réunion	27.5				D	JS-La Réunion	80.8			C	D
AS-La Réunion	26.4				D	AS-La Réunion	74.1				D

sons of clutch size. However, we noticed that all JS snails have laid more eggs than the corresponding AS populations (Tables 1, 2). In spite of the results relative to F1 generations from Lorient and Toulouse, it did appear that eggs numbers produced per snail born and reared under artificial conditions converged among the three populations.

For snails from Algeria, there was no significant relationship between clutch size (N1) and shell breadth, but the mean numbers of eggs of clutches of both AS, JS and F6 snails,

TABLE 6. Reproductive characters, shell size and mortality of Algerian *Helix aspersa* from three generations under artificial conditions (x ± standard error).

Generation	AS	JS	F6
Sample size	35	10	20
Shell breadth (mm)	44.2 ± 0.3	42.5 ± 0.1	44.2 ± 0.2
Mean rate of matings (%)	40.1	100.0	100.0
Mean number of matings per individual	0.6 ± 0.1	3.2 ± 0.4	3.4 ± 0.1
Mean rate of layings (%)	20.0	80.0	95.0
Mean number of clutches per individual	0.3 ± 0.1	3.0 ± 0.6	3.1 ± 0.1
Mean number of eggs per individual	42.1 ± 15.3	443.8 ± 104.9	608.3 ± 59.1
Clutch size	163.7 ± 28.5	160.6 ± 17.6	186.6 ± 12.0
Mean weight of eggs (mg)	39.2 ± 4.3	41.6 ± 3.8	41.0 ± 3.2
Hatching success (%)	94.8	78.7	82.4
Adult mortality (%)	31.4	20.0	20.0

which seemed to have preserved characteristics of snails from the field (shell and clutch sizes), were higher than all the others (Table 6). The only important difference between generations (total fecundity) was a consequence of the number of clutches produced per snail and could be attributable to physiological disturbance of AS snails, as the JS results suggested. Because the populations did not differ significantly in hatching success, the mean number of young produced per Algerian snail that had laid eggs was by far the highest.

Mortality During the Breeding Season

There was no significant difference between AS populations in total number of dead snails during the same breeding period (Table 1). However, in 1985, the majority of snails survived, except in the sample from Algeria; on average, only 7.5% of the snails collected in 1985 died, versus 25% in 1983 (χ^2 test; $P < 0.001$).

The numbers of snails dead in F1 and especially F2 generations were comparable from one population to the other (Table 2). Differences among AS or JS generations could be attributable to acclimatization problems, especially for the JS sample from St. Denis, which had been subjected to an artificial hibernation.

DISCUSSION

In the present study, snails were reared under uniform artificial conditions, whatever their origin. For AS and JS samples, variation in reproductive characters may consequently be genetically determined or induced by environmental factors prior to the snails' capture. This prior conditioning could include many factors, such as time of year, duration of activity suspension, or the reserves carried over winter which are able to contribute to modification of fecundity (Brown et al., 1985; Baur & Raboud, 1988). Furthermore, variation in egg production of *Helix aspersa* cannot be dissociated from shell size, itself dependent on several proximate factors that act on growth rate and age at maturity. One may also suspect interactions between genotypes and laboratory conditions and differences in acclimatization ability, which lead to a change of reproductive activity for snails adapted to other proximal conditions, in comparison with their real potential expressed in the field. For example, we can assume that reproductive characteristics of snails from La Réunion and Algeria, for which spring and summer are not (or not necessarily) the breeding season, are affected not only by the starting date of the experiment, but also by the 16L:8D cycle selected in the laboratory as an optimal combination for reproduction of snails from western France (Daguzan, 1981; Le Guhennec & Daguzan, 1983). Therefore, total egg production of snails from Breton samples during the rearing period is not different from the annual egg production of snails of the same populations living in the field. However, the length of their breeding period and the timing of mating and oviposition may be notably shorter, according to a variation in proximate factors (Madec & Daguzan, 1991). In natural environments, the time of year of breeding takes gradually place from spring (Brittany) to winter (Algeria), with possibly two breeding seasons (spring and autumn) or, in contrast, a short and single period in the late spring for mountain popula-

tions (Belmont). Even if the present work gives no precise evaluations, it seems that seasonal adjustments are partially retained under laboratory conditions and may lead, when local conditions are very different (late autumn or winter reproduction), to important disturbances (snails from Algeria). Under climatic conditions of La Réunion, it is possible that reproduction of *Helix aspersa* occurs throughout the year (Fig. 1), and then eggs deposited by a snail during this experiment would represent just a little part of its annual egg production in natural conditions.

The continuous rearing of three generations of snails from four populations with contrasting reproductive characteristics (Lorient, Toulouse, St. Denis, Algeria) demonstrates that the major proportion of phenotypic variation observed in *H. a. aspersa* (all populations except the Algerian one) is environmentally induced. Thus, differences between AS samples, for the most part, disappear when snails are reared for two generations in the same environment, whatever the initial degree of variation and the characters concerned. The phenomenon is already perceptible among individuals that in the beginning of their lives had very different ecological constraints (JS generation). *Helix a. aspersa* seems to be characterized by the ability to respond to environmental changes with a large range of phenotypes, which suggests an important plasticity. However, this experiment does not allow us to explain the specific differences observed in AS populations or to give precise estimates of the respective effects of environmental and genetic components. In addition, other factors could interfere before the initiation of reproduction in the laboratory. Thus, we have to consider the age of snails when reproduction occurs (six-seven months for JS, F1, and F2 individuals; unknown for AS snails from La Réunion; at least two years for the others). In this regard, Le Calve (1988) emphasizes that an older snail has a tendency to mate more often but seldom to lay. Their clutch size is higher and correlated with smaller eggs. Young adults (JS) produce clutches at a rate higher than that of adults from the corresponding AS generation which are, on average, older. On the other hand, when shell-size effects are removed, clutch size of young adults seems to be smaller. These results are different from those of Wolda (1963) for *Cepaea nemoralis* but, in each case, it seems that a balance finds its expression in an egg production per snail for one breeding season not very different from one age class to the other.

Snails from Algeria (*H. a. maxima*) seem to have developed a specific combination of reproductive traits. Egg weight (or size; $r_{w/s}$ = 0.94), clutch size, and number of eggs produced per snail in one season indicate a higher reproductive investment for an Algerian snail and, at the species level, lead to surprising relationships as, for example, the positive one between egg size and egg numbers. However, we should have weighted these values by the size of animals, and in addition, results of this experiment should be considered with caution because of the small size of the samples. Furthermore, we are not able to know if the extent of reproductive investment affects the survivorship of snails, only one breeding season being studied in laboratory conditions. Nevertheless, variation in these large snails may have a specific genetic basis and thus, is not a part of the plasticity that characterizes *H. a. aspersa.*

In order to discuss these combinations of traits and to compare them with other Helicidae, we have to integrate the variation in reproductive characters in the species' life history and in the context of its natural environment. Unfortunately, relevant field data on other life-history traits, their genetic components, and local ecological constraints are unavailable or are imprecise. Nevertheless, the two opposite trends, illustrated in the extremes by populations from St. Denis (recently introduced) and Alger (natural distribution area), can be useful for the understanding of the life-history variability of *Helix aspersa.* Additional data (Chevallier, 1983; Madec, 1988, 1989b) are used to specify the identity of the two forms in Table 7.

Differences between these two patterns are obviously related to their respective habitats. Our purpose is then to compare two contrasting habitats and possible life-history solutions adopted by the species, with the help of predictions of theoretical life-history models. In this respect, the general demographic classification of habitats (Begon et al., 1987) allows consistent hypotheses about interpretation of observed patterns by looking at the mortality factors affecting infra-populations of juveniles and adults.

At St. Denis de La Réunion, ameliorating effects of altitude (900 m., decrease of temperature) and proximity of the ocean (increase of humidity) lead to a climatic regime favourable to a long growing period (annual

TABLE 7. Summary of life-history traits observed in *Helix aspersa* from La Ŕeunion and Algeria.

Population from Algeria	Population from St. Denis
•Thicker shells	•Thinner shells
•Adult size larger	•Adult size smaller
•Later maturity	•Earlier maturity
•Longer length of life	•Shorter length of life
•More offspring, smaller/parent size	•Fewer offspring, larger/parent size

cycle) and an extended breeding season, which allows, if necessary (calcium not easily available at this basaltic site), egglaying of several small clutches per snail. In addition, large size of eggs in comparison to shell size of adults (Madec, 1988) seems to be obtained at the expense of the number per clutch, and, if not only a phylogenetic constraint, this would have an explanation in a high population density, because favourable climatic conditions avoid a high mortality of eggs and young; juveniles may be advantaged by large size because of strong intraspecific competition. The small size of adults could also be related to high population density, which acts on growth rate via the mucus secreted for locomotion, as demonstrated for *Helix aspersa* (Dan & Bailey, 1982; Lucarz & Gomot, 1985) and other Helicidae (Oosterhoff, 1977; Cameron & Carter, 1979). Moreover, snails from La Réunion are characterized by their thinner shells, perhaps related to the calcium deficiency and the high rainfall (Goodfriend, 1986). This low resource (calcium) allocation for growth and maintenance, which probably does not affect snail survival, would lead to a higher (and earlier) egg production. In other habitats colonized by *H. a. aspersa* (western Europe, USA), populations exhibit notably different features (larger adult size, larger clutches); this variability could be partially explained by high egg and juvenile mortality by desiccation, frost and predation (Potts, 1975; Daguzan, 1982), which is also a characteristic of numerous other Helicidae in Europe (Wolda & Kreulen 1973; Pollard, 1975; Cowie, 1984). Thus, lower population density (growth rate increase) and longer length of growth lead to an increase of adult size, consequently larger clutches, which counterbalance higher juvenile mortality (Peake, 1978). On a smaller scale, Potts (1972) noticed that two neighbouring colonies of *Helix aspersa* in California (one living on waste ground, another in a garden) produce such different demographic traits as, in this experiment, populations from La Réunion and Surgères, only by reason of daily watering. Finally, this first trend seems to be the result of a considerable flexibility in life-history traits, which allows *H. a. aspersa* to successfully colonize a large range of unstable habitats.

By contrast, snails from Algeria (*H. a. maxima*) have larger shells, which are twice as thick as those from La Réunion, obtained after a growth period of, at least, three years, including long suspensions of activity during summer. This greater shell volume allows the production of larger clutches with significantly larger eggs (Madec, 1988). The present study gives no pertinent information on egg production per breeding season for Algerian AS snails because the experiment began when they were preparing to aestivate in the field. However, data on JS and F6 generations, which confirm larger clutch and egg sizes, indicate that sexually active snails lay on average three clutches during the breeding period under laboratory conditions, that is to say a mean number of eggs per snail between 450 and 600. Moreover, because these characteristics are genetically determined, an allometric relationship seems to exist, which leads in *H. a. maxima* to a decrease of the proportion of shell volume allocated to clutch volume in comparison to *H. a. aspersa* "norms," despite their higher mean egg and clutch sizes. With reference to the theory, an efficient protection against abiotic mortality (and perhaps such other factors as predators) represented by a larger shell in adults as in juveniles is related to other features: delayed maturity, smaller reproductive allocation, and investment in a large size (protection) leading to an increase of residual reproductive value. In this respect, *H. a. maxima* differs from other Mediterranean *Helix,* which seem to fit this model better, because of a small clutch size with larger eggs (*Helix lucorum:* Staikou & Lazaridou-Dimitriadou, 1988; *Helix texta:* Heller & Ittiel, 1990). In addition, our hypothesis remains speculative because not only is nothing known about residual reproduction but also a proportion of the observed variation has no

genetic basis. Thus, the life-cycle length variability is essentially environmentally induced, because snails from all populations, including Algerian ones, reach maturity from three to six months after birth under laboratory conditions (Madec, 1989b). This observation raises the problem of the precise localization of natural populations of this form, and the necessity of studying several of them in order to define the degree of variation of its life cycle in particular ecological conditions. Similarly, Heller & Ittiel (1990) show that in unstable populations of *Helix texta,* a low population density, caused by a massive predation of adults, allows a very rapid growth of young. An other density-dependent mechanism, also related to predation and climate (semi-arid environment), pressures on two slopes of a wadi, leads to an important variation of fecundity in nearby populations of *Trochoidea seetzeni* (Yom-Tov, 1972).

Finally, a valid comparison with the predictions of life-history models requires a field study on tactics used by *Helix aspersa* to respond to various selection pressures, i.e. to test: (i) the hypothesis based on an adaptative plasticity in life-cycle traits in *H. a. aspersa,* which lives in "favourable" but often human perturbed environments and which could explain its widespread geographic and ecological distribution; (ii) the hypothesis of a specific combination adopted by *H. a. maxima* as a response to harsh conditions of its reduced distribution area.

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ANATOMY AND FUNCTIONAL MORPHOLOGY OF THE FEEDING STRUCTURES OF THE ECTOPARASITIC GASTROPOD *BOONEA IMPRESSA* (PYRAMIDELLIDAE)

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ABSTRACT

The ectoparasitic snail *Boonea impressa* (Say, 1822) feeds on a variety of invertebrates. In the laboratory, *Boonea impressa* parasitized both *Crassostrea virginica* (Gmelin, 1791) and *Geukensia demissa* (Dillwyn, 1817), positioning itself on the edge of the host's shell, thus providing access to the host's mantle tissue exposed when the bivalve is open. Feeding structures of *Boonea impressa* include: (1) an acrembolic or completely invaginable proboscis, (2) a buccal sac comprised of sucker, mouth, stylet with separate buccal opening, and stylet bulb, (3) a muscular buccal pump, (4) a pair of salivary glands, and (5) a coiled esophagus. These enable the snail to feed once the extended proboscis locates the host's soft tissue, which is penetrated by the stylet. Subsequently, the muscular action of the buccal pump removes host hemolymph. Retraction of the everted proboscis and the muscles involved in this process are examined and discussed. Scanning electron microscopy and transmission electron microscopy revealed details of the feeding structures (e.g., tufts of cilia apically located on the papillae of the proboscis) previously unknown for this genus. When *B. impressa*'s feeding structures were compared to those of selected European pyramidellids described in the literature, morphological and ultrastructural differences became apparent. These differences further support the retention of this species in *Boonea.*

Key words: *Boonea impressa,* Pyramidellidae, ectoparasite, feeding structures, histology, functional morphology.

INTRODUCTION

Boonea impressa (Say, 1822), commonly cited as (*Odostomia impressa*), is an ectoparasite within the large gastropod family Pyramidellidae, which feeds on the body fluids of invertebrates (Hopkins, 1956; Wells, 1959; Allen, 1958; Robertson & Orr, 1961; Scheltema, 1965; Cheng, 1967; Abbott, 1974; Robertson, 1978; Robertson & Mau-Lastovicka, 1979). It commonly inhabits the littoral and sublittoral zones of the western Atlantic from New Jersey, USA, to Quintana Roo, Mexico (Robertson, 1978).

Recent studies have examined aspects of this ectoparasite's population dynamics, behavior, and its effects on *Crassostrea virginica* (Gmelin, 1791) (White et al., 1984, 1985; Ward & Langdon, 1986; Powell et al., 1987a, 1987b; White et al., 1988a, 1988b). *Boonea impressa* can be deleterious to oysters by reducing growth, net productivity, and survival rates, while also effectively altering valve movement and lowering filtration rates (White et al., 1984; Ward & Langdon, 1986). In addition, White et al. (1987) have suggested that *B. impressa* may be a vector for the oyster pathogen *Perkinsus marinus.*

To date, no detailed anatomical studies have been conducted on species within the genus *Boonea* (formerly included in *Odostomia* Fleming, 1817; Robertson, 1978). Although White et al. (1985) cursorily examined a portion of *B. impressa*'s alimentary system in a comparison of Texas and North Carolina specimens and European pyramidellids, an understanding of the structural and functional morphology of *Boonea impressa* is lacking. The objectives of this investigation were: (1) to describe the morphology and function of feeding structures and (2) to compare these structures with those of selected European pyramidellids described in the literature.

MATERIALS AND METHODS

Boonea impressa was collected from the Folly River and Inlet Creek oyster reefs near Charleston, South Carolina, from 1984 to 1986. Each collection yielded approximately 200 snails, which were maintained in an aquarium of filtered sea water.

Snails (3–6 mm shell length) were removed from their shells with a vise or pliers. Snails were dissected under a dissecting mi-

croscope equipped with an ocular micrometer. Photographs were taken with a camera mounted on a Nikon Labophot microscope or a Zeiss Tessavar.

Snails were decalcified using a commercial agent (Decal) to prepare serial sections of the entire snail. In order to section the proboscis in its extended condition, snails were relaxed in a sea water and Sevin-acetone solution (Carriker & Blake, 1959) prior to decalcification. Tissue was fixed in 10% seawater formalin, effectively dehydrated in alcohol, cleared in xylene, and embedded in paraffin. Sections were cut at 2–5 μm and stained with hematoxylin (Ehrlich acid alum or Gills) and with eosin-Y. Photographs were taken with a photomicrographic system (model PM-10AK) mounted on an Olympus BH2-DO microscope.

Snails for histochemical studies were decalcified prior to fixation in B-4 (consisting of 0.1% glutaraldehyde, 6% HgC_{12}, and 1% sodium acetate) for 5 h. Tissue was treated as described above. Once sections were cut (3–5 μm) they were deparaffinized, dezinkarized with Lugol's iodine, hydrated, and placed in a solution of HID (high iron diamine) overnight (Sheenan & Hrapchak, 1980). They were then thoroughly rinsed with distilled water and counter-stained with alcian blue (Ph 2.5) for 30 min. After rinsing, the tissue was dehydrated, cleared in xylene, and mounted.

Scanning electron microscopy was used to examine the gross and ultrastructural morphology of the alimentary structures. Specimens were relaxed in Sevin-acetone, removed from their shells and fixed in 2.5% glutaraldehyde, in a sodium cacodylate buffer and sea water solution. Following fixation, tissue was rinsed in cacodylate buffer, effectively dehydrated in ethanol, critical point dried, coated with gold-palladium, and examined with a JEOL JSM-35C scanning microscope operating at 20 kev.

For transmission electron microscopy, snails were treated with Sevin-acetone and seawater solution, decalcified, and rinsed thoroughly in sea water. Denuded snails were fixed for 24 h in a 2.5% glutaraldehyde-cacodylate solution, washed in cacodylate buffer and post-fixed in osmium tetroxide (Shennan & Hrapchak, 1980). Following osmication, snails were rinsed in distilled water, effectively dehydrated in a series of graded ethanol, and placed in propylene oxide. Specimens were transferred to a 1:1 solution of propylene oxide and 812 embedding resin and agitated overnight with an Adam's nutator. Next, specimens were placed in a 2:1 solution of embedding resin and propylene oxide for 7 h. Once the snails had been placed in pure embedding resin, infiltration by the supporting medium was again facilitated by agitation for 24 h. The specimens were vacuum infiltrated for 4 h and then placed in a mold and oriented. Thin sections were cut with a Sorvall M22 ultramicrotome, stained with UALC (uranyl acetate and lead citrate), and examined with a JEOL 100 Selectron microscope.

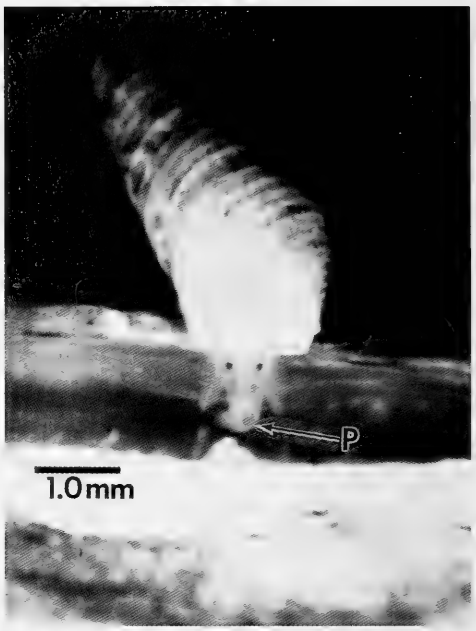

FIG. 1. *Boonea impressa* at the edge of valve of *Crassostrea virginica,* with proboscis (P) extended, feeding suctorially on the bivalve's mantle.

DESCRIPTIVE MORPHOLOGY

The external anatomy of *Boonea impressa* is typical of the Pyramidellidae. This species has a well-developed, tentaculate head, a pair of eyes located beneath the epithelium medial to the tentacles, and a large operculated foot tapered posteriorly (Fig. 1). The mentum located just ventral to the head extends as a shelf over the propodium. A capacious mantle cavity narrows posteriorly, extending to the most anterior position of the

visceral mass. The right anterior portion of the mantle edge forms a short canal or siphon. Other mantle cavity features characteristic of the family include opposing dorsal and ventral ciliated strips (responsible for the transport of water into and out of the mantle cavity), a pallial kidney, a simple apectinate osphradium, and a pigmented mantle organ (Fig. 2A).

The epidermis of the anterior region (tentacled head, foot, and mantle) is composed of one layer of cuboidal or columnar cells (Fig. 3A) that are usually ciliated and have basal nuclei. The head-foot and mantle have large subepidermal gland cells that are basophilic. These cells contain granulated droplets (spheroids), which discharge between the epidermal cells; no ducts are present. Preliminary tests utilizing HID/AB (high iron diamine-alician blue) show that a majority of these cells stain purple-black, indicating the presence of sulfated mucins. A few (inside the dorsum of the mentum) stain pale blue by alician blue, indicating the presence of nonsulfated acidic mucins. The pedal gland lies in a medial position just above and parallel to the ventral surface of the foot (Fig. 3A). This gland is an invaginated thin layer of ciliated epithelial tissue that surrounds a lumen. The epithelia are encircled by an aggregate of gland cells, staining dark purple by hematoxylin and eosin and also containing sulfated mucins. The opening of the pedal gland is located midline on the underside of the posterior portion of the foot.

The pedal sinus complex traverses the length of the lower foot and is comprised of numerous sinuses surrounded by nucleated connective tissue (Fig. 3A). The columellar muscle, located behind the foot and extending posteriorly to the visceral mass, is composed of smooth muscle. Numerous muscle fibers radiate from the columellar muscle into the head-foot, including those interspersed throughout the gland cells and hemolymph sinuses.

The cephalic hemocoel is visible without dissection once the shell has been removed. The hemocoel is bordered by the columellar muscle ventrally and by the floor of the mantle cavity dorsally (Figs. 2B, 3A). It terminates posteriorly at the visceral mass, and anteriorly it extends to just behind the head. The majority of the alimentary structures are located within the cephalic hemocoel.

When retracted (Fig. 2B), the proboscis, referred to as the introvert, is completely inverted, and largely within the cephalic hemocoel. This inversion results in the looping of the introvert into three consecutive upright u's. The introvert extends posteriorly from its opening or aperture, passes through the nerve ring, and joins the buccal sac (comprised of sucker, mouth, stylet with separate buccal opening and stylet bulb) located well within the cephalic hemocoel (Fig. 2B). The temporary lumen created by this inversion is mainly bordered by the papillae of the proboscis. Beneath the papillae and extending the length of the proboscis is a layer containing both circular and longitudinal muscles (Fig. 3B, C). A basal lamina extends between the papillae and this layer of muscle, which appears mesh-like in light microscopy. Internal to this is a layer of connective tissue bordering the lumen, which is present when the proboscis is protracted (Fig. 3B; see Fig. 2C for the position of the proboscis and other feeding structures when the proboscis is extending). It is through this connective tissue that secondary retractor muscles of varying length pass to insert at points along the proboscis (Fig. 3C).

The everted proboscis appears rough and pustulose, with the greatest concentration of papillae anterior to the tips of the tentacles (Figs. 2C, 4A). The proximal portion of the proboscis within the boundaries of the tentacles, although tuberculate with scattered clusters of cilia, is non-papillate (Fig. 4A). The papillae are flattened and compressed when first everted from the temporary lumen; however, once in position on the external surface of the protracted proboscis, these papillae become tumescent (Fig. 4B). Cilia extend from the center of each papilla as apical tufts. Each papilla is composed of several elongate cells containing organelles and darkly colored secretory granules, the number of which varies among papillae. Each papilla contains a central cell from which the cilia (possessing a $9+2$ microtubule arrangement) originate (Fig. 4C, D). The papillae are bordered apically by fusiform microvilli covered by a glycocalyx.

The introvert joins the buccal sac at two locations. Just outside the sucker, the papillae are replaced by simple cuboidal cells that attach directly to the sucker (Fig. 5A). These have numerous cilia, presumably of a tactile nature, that extend well into the temporary lumen. Beneath the cells are the aforementioned layers of muscle and connective tissue extending posteriorly to insert at the base of the sucker beside the primary retractor mus-

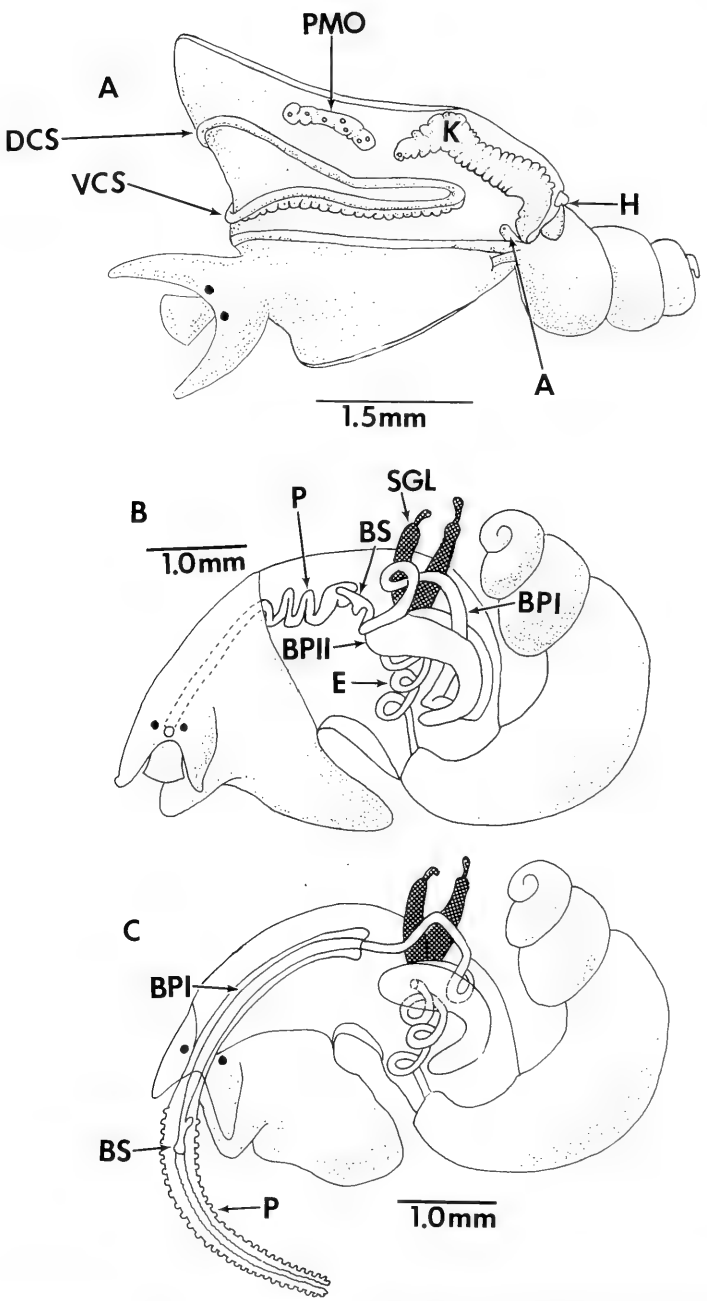

FIG. 2. A. Generalized representation of pallial complex. Mantle skirt cut on left side and reflected to the right. B. Schematic of *Boonea impressa* in the non-feeding posture, with proboscis retracted. Mantle removed and cephalic hemocoel opened to expose alimentary structures in "natural position," with exception of salivary glands. Salivary glands shown upright to reveal location to right of buccal pump II. C. Schematic of partially protracted proboscis, with buccal pump I uncoiling as it is pulled forward. Note new position of the buccal sac, now lying just anterior to head. A = anus; BpI = buccal pump I; BpII = buccal pump II; BS = buccal sac; DCS = dorsal ciliated strip; H = heart; K = kidney; MO = mouth; P = proboscis; E = esophagus; PMO = pigment mantle organ; SGL = salivary gland; VCS = ventral ciliated strip.

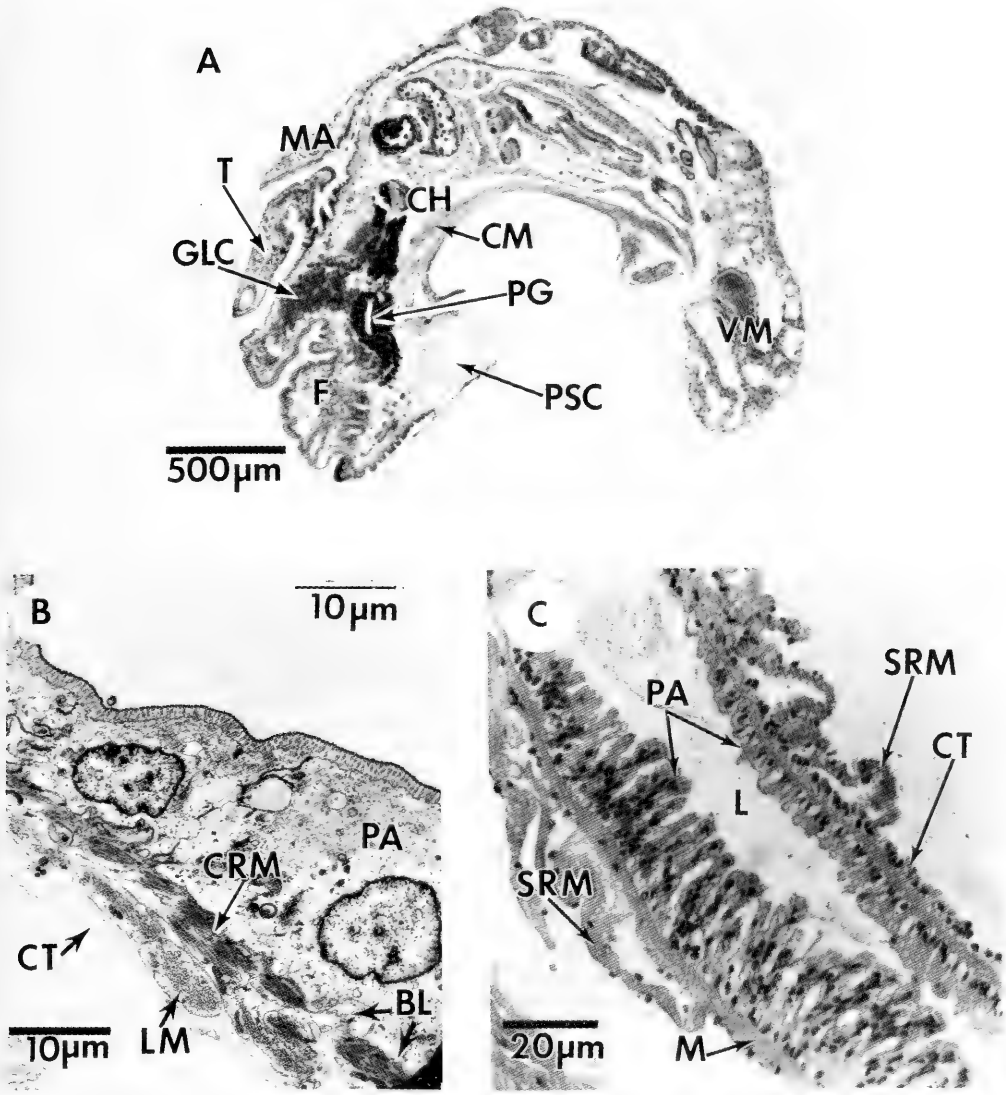

FIG. 3. A. Section through head-foot, mantle, and cephalic hemocoel. B. Transmission electron microphotograph of internal proboscis morphology. Note lamina between papillae, layer of circular and longitudinal muscle and thin layer of connective tissue beneath muscle layers. C. Longitudinal section of inverted proboscis. BL = basal lamina; CH = cephalic hemocoel; CM = columella muscle; CRM = circular muscle; CT = connective tissue; F = foot; GLC = gland cell(s); LM = longitudinal muscle; MA = mantle; M = muscle; PA = papilla(e); PG = pedal gland; L = temporary lumen; PSC = pedal sinus complex; SRM = secondary retractor muscle(s); T = tentacle; VM = visceral mass.

cle. The primary retractor muscle, the base of which is attached to the columellar muscle, extends into the cephalic hemocoel to insert on ether side of the sucker (Fig. 5A).

The buccal sac has two major components: the stylet bulb and the buccal sucker (Fig. 5B, C). The stylet bulb, extending posteriorly, curves dorsally to lie beneath the most anterior portion of the buccal pump. Within the posterior portion of the stylet bulb is a crescent-shaped lumen, surrounded by the muscles of the stylet bulb (Fig. 5A). The stylet

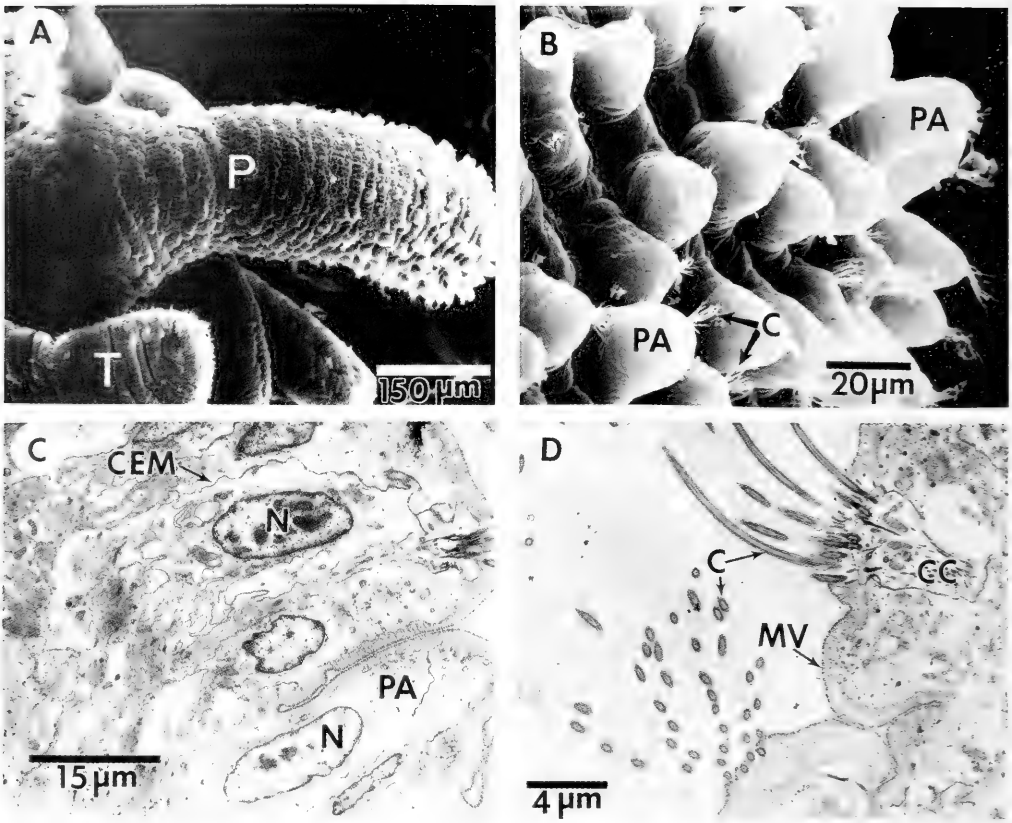

FIG. 4. A. Scanning electron microphotograph of partially extended proboscis. B. Tumid papillae on external surface of the proboscis, each with apical tuft of cilia. C. Transmission electron microphotograph of individual papillae; each papilla comprised of several elongate cells, delineated by distinct cell membranes. D. Central cell from which papillary cilia originate. Cilia possess a 9 + 2 microtubule arrangement. C = cilia; CC = central cell; CEM = cell membrane; MV = microvilli; N = nucleus; P = proboscis; PA = papilla; T = tentacle.

bulb's shape varies from round to oblong. The globe-shaped buccal sucker is comprised of a thick muscular wall comprised of numerous columnar cells arranged in a stack-like manner that surrounds the elevated inner labium (Fig. 5A). Within, the sucker the labium appears smooth and corpulent. The center of the labium contains an aperture through which the stylet emerges. Dorsal to this opening is the true mouth, located at the junction between the inside sucker wall and the base of the labium (Fig. 5A, C). The oral tube extends posteriorly from this opening, to join the buccal pump at the buccal pump-buccal sac junction. The oral tube is bordered ventrally by simple cuboidal cells and lined dorsally by a thin layer of flattened epithelium (Fig. 5A). The stylet, which lies within a cavity behind the sucker, is surrounded by a cuticular sheath. This cuticular sheath opens anteriorly to extend as a hood over the stylet's apex (Fig. 5B, D). The sheath, indented ventro-medially, has a prominent longitudinal dorsal ridge (Fig. 5D). The stylet is broad at its base and tapers distally, with the apex emerging through the opening in the sheath. Dorsally, the surface of the stylet, distal to its base, is notched by a series of parallel grooves that terminate prior to its apex. The medial indentation is bordered on either side by uneven, laterally grooved ridges (Fig. 5E). Retractor muscles within the base of the stylet insert at the buccal sac wall (Fig. 5A). The two salivary ducts, after entering the buccal sac from the buccal pump, unite to form a common duct, which enters the lower portion of the stylet

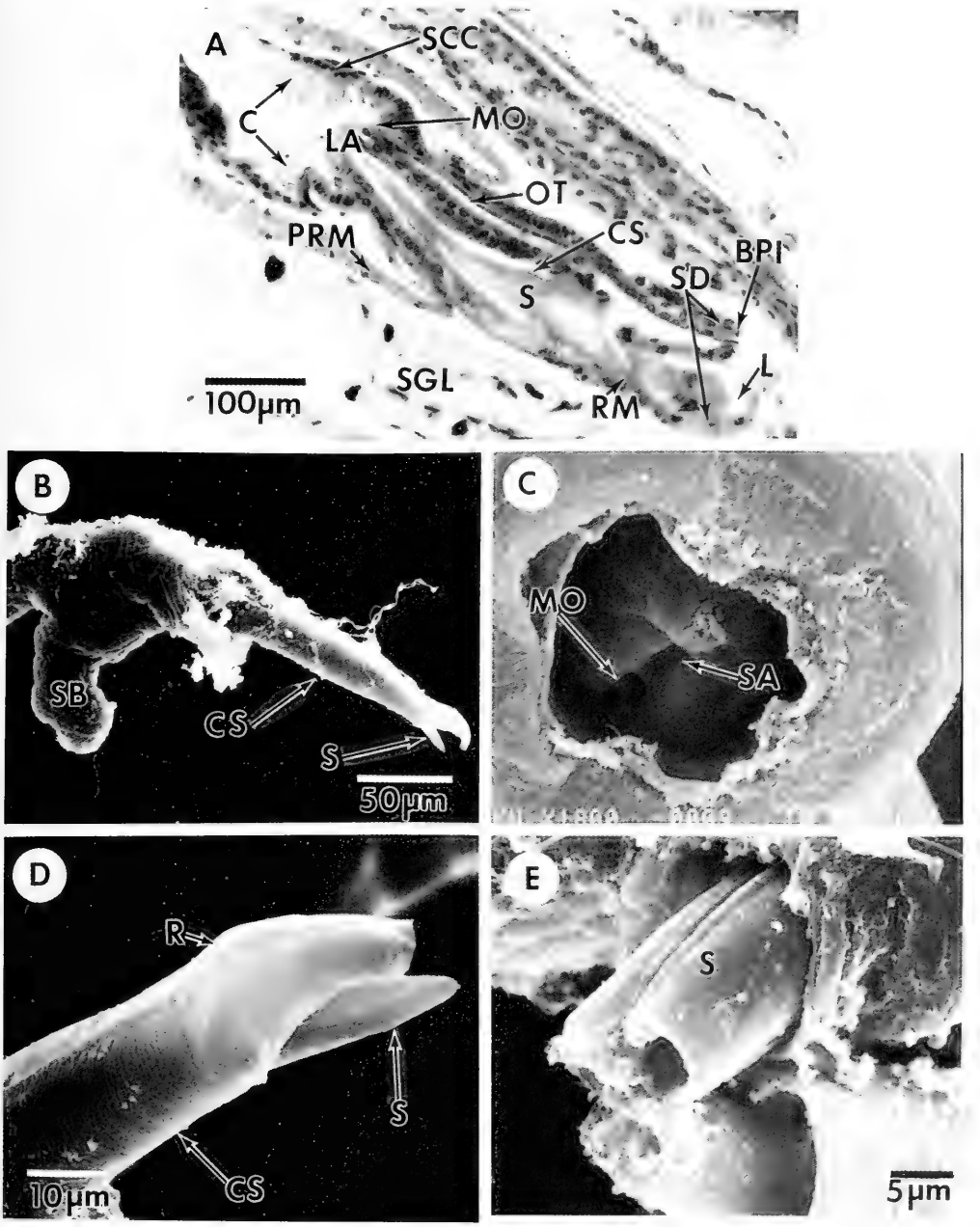

FIG. 5. A. Histological section through buccal sac. B. Scanning electron microphotograph of buccal sac; portion of buccal sac surrounding stylet and cuticular enclosure removed. Stylet bulb intact. C. Globe-shaped sucker; within sucker is true mouth and stylet aperture. D. Scanning microphotograph of anterior part of cuticular sheath enclosing stylet (note prominent ridge). E. Cross-sectional view of stylet. BpI = buccal pump I; C = cilia; CS = cuticular sheath; L = lumen; LA = labium; MO = mouth; OT = oral tube; PRM = primary retractor muscle; R = ridge; RM = retractor muscle; S = stylet; SA = stylet aperture; SB = stylet bulb; SCC = simple cuboidal cell; SD = salivary duct; SGL = salivary gland.

and continues internally along its length (Fig. 5A).

The buccal pump can be divided into two distinct regions (Fig. 2B); the anterior portion of the buccal pump (termed buccal pump I) is an elongate cylindrical structure that possesses an outer covering of very thin epithelium enclosing a layer of circular muscle (Fig. 6A, B). Internal to this layer is a matrix of cells and muscle fibers that extends to the triangular lumen. A large part of this organ is composed of tightly packed elongate muscle cells (Fig. 6C), which radiate outward from the lumen to lie adjacent to the layer of circular muscle encircling this structure. Distinct bands of muscle fibers, anchored within a layer of connective tissue internal to the cuticular layer lining the lumen, pass between the muscle cells to insert just beneath the external epithelium. Buccal pump I increases in diameter along the last quarter of its length prior to uniting with the remainder of the buccal pump. The large posterior portion of the buccal pump (termed buccal pump II) curves downward and then bends anteriorly, allowing accommodation within the confines of the cephalic hemocoel (Fig. 2B). This portion of the buccal pump (with the exception of its central lumen) is composed almost solely of muscle tissue (Fig. 6A). This segment of the buccal pump, elliptical in cross section, is covered by a thin layer of furrowed epithelium, not unlike that covering buccal pump I (Fig. 6D). Buccal pump II is similar to the buccal pump I in wall composition, but lacks buccal ducts and has a greater overall diameter and larger elliptical lumen. It is composed primarily of muscle fibers that radiate from the lumen and extend to a layer of circular muscle located just underneath the peripheral layer of epithelium of the pump. The same kind of myofilament bands present in buccal pump I intermittently traverse the width of buccal pump II to anchor within a cuticularized layer lining the lumen (Fig. 6E). At the junction of buccal pump I and buccal II is a ring of muscle.

The esophagus originates at a point below and just posterior to where the buccal pump is divided into two distinct sections (Fig. 2C). Elongate cilia are present at the junction of the buccal pump II and esophagus. This section of the esophagus coils repeatedly as it extends downward and then posteriorly to join the stomach, located within the visceral mass. The esophagus is very irregular and uneven along its length, surrounded by a thin layer of epithelium and muscle (Fig. 7A). The lining of the central lumen has numerous folds covered with uniformly distributed cilia (Fig. 7B).

Connecting the salivary glands to the alimentary canal are the salivary gland ducts (Fig. 6A, B). The ducts enter the ventral side of the buccal pump I, just anterior of the buccal pump I\buccal pump II juncture, and extend the length of this section of the alimentary canal. The salivary ducts are comprised of a lumen encircled by multiple layers of circular and longitudinal muscle. Epithelial tissue lining these ducts can occlude the lumen (Fig. 7C). The salivary glands lie together on the right side of buccal pump II within the cephalic hemocoel and are composed of variably sized cells located along a central canaliculus, which extends to the vesicle-like structure distally (Fig. 7A). The cells are tightly packed with a fine granular substance. The glands show differential staining along their lengths. This varies among individual snails, with no discernable pattern. The vesicle-like structure at the distal portion of the buccal gland is apparently a lumen lined with epithelium that extends the length of the gland to line the canaliculus. No cilia project from the epithelium lining the lumen of this distal portion, although the lining of the canaliculus is ciliated. Scanning electron microscopy confirmed the presence of numerous secretory granules within the gland (Fig. 7D). With the exception of the striated outer surface, the ciliated canaliculus, and the distal sac-like portion of this structure, this organ is composed solely of acinar secretory packets.

DISCUSSION

Anatomical studies of *Boonea impressa* shows that its external anatomy is very similar to the European pyramidellid species described by Fretter & Graham (1949), Maas (1965), and Ankel (1949) (Table 1 lists the taxa they examined). There are, however, both configurational and ultrastructural differences, particularly concerning feeding structures. These are discussed below, as is the generic assignment of *Boonea impressa.*

Large gland cells that stain differentially by hematoxylin and eosin lie beneath the epithelial layer in *B. impressa,* and are scattered throughout the head-foot and mantle. These cells produce and release granulated spheres that transude the intercellular matrix, migrate between the epithelial cells, and eventually

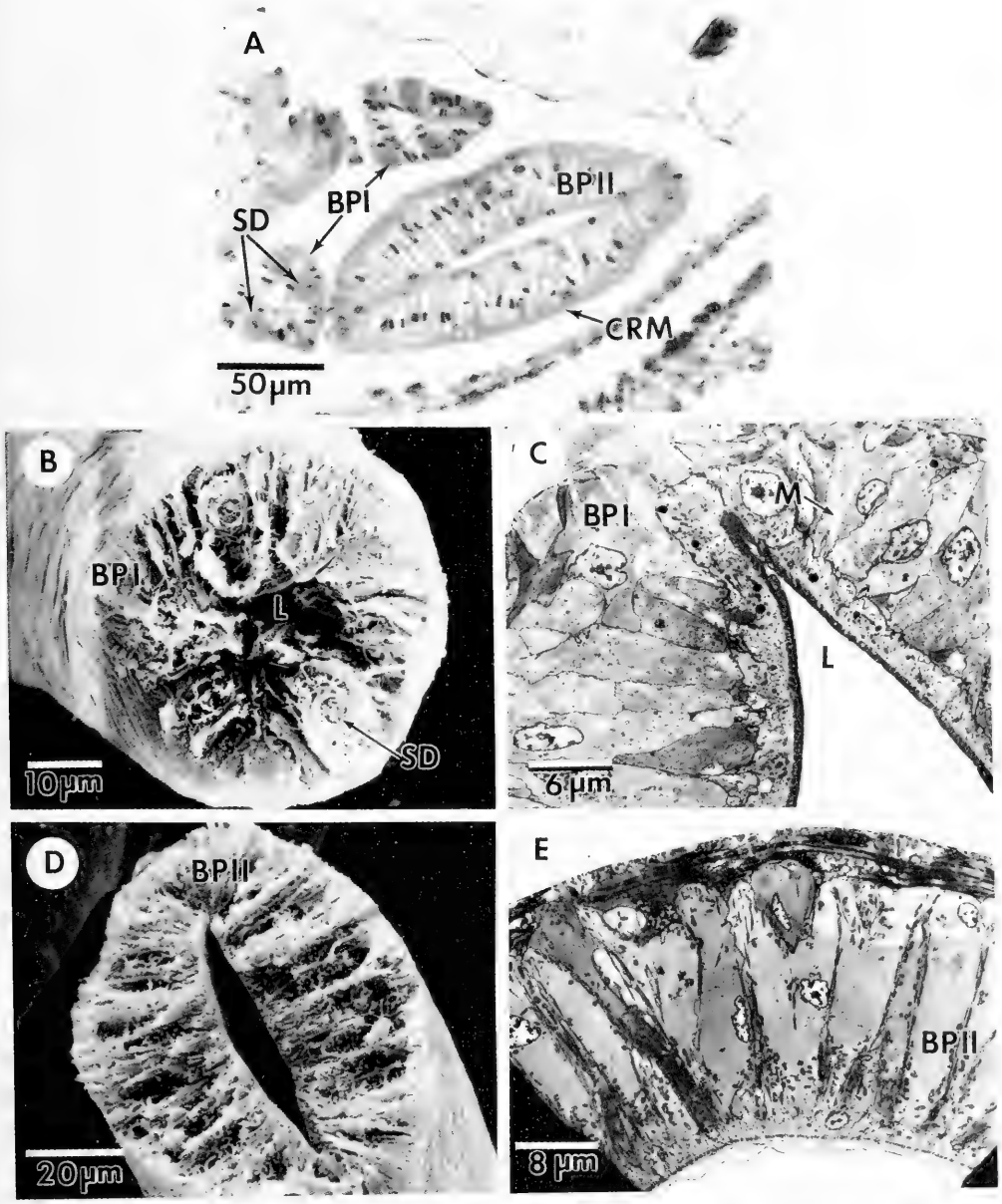

FIG. 6. Feeding structures. A. Cross sections of buccal pump I lying to one side of larger buccal pump II. B. Scanning electron microphotograph of buccal pump I in cross section. Etched outer covering encloses internal layer of muscle fibers extending to the lumen. C. Transmission electron microphotograph of buccal pump I in oblique section; numerous cells radiate from lumen to lie adjacent to layer of circular muscle encircling esophagus. D. Scanning electron microphotograph of buccal pump II covered by a thin layer of epithelium, comprised of myofibrils. E. Transmission electron microphotograph of buccal pump II in cross section. Note circular muscle, longitudinal muscle, and muscle perpendicular to the organ's axis. BpI = buccal pump I; BpII = buccal pump II; CRM = circular muscle; L = lumen; M = muscle; SD = salivary ducts.

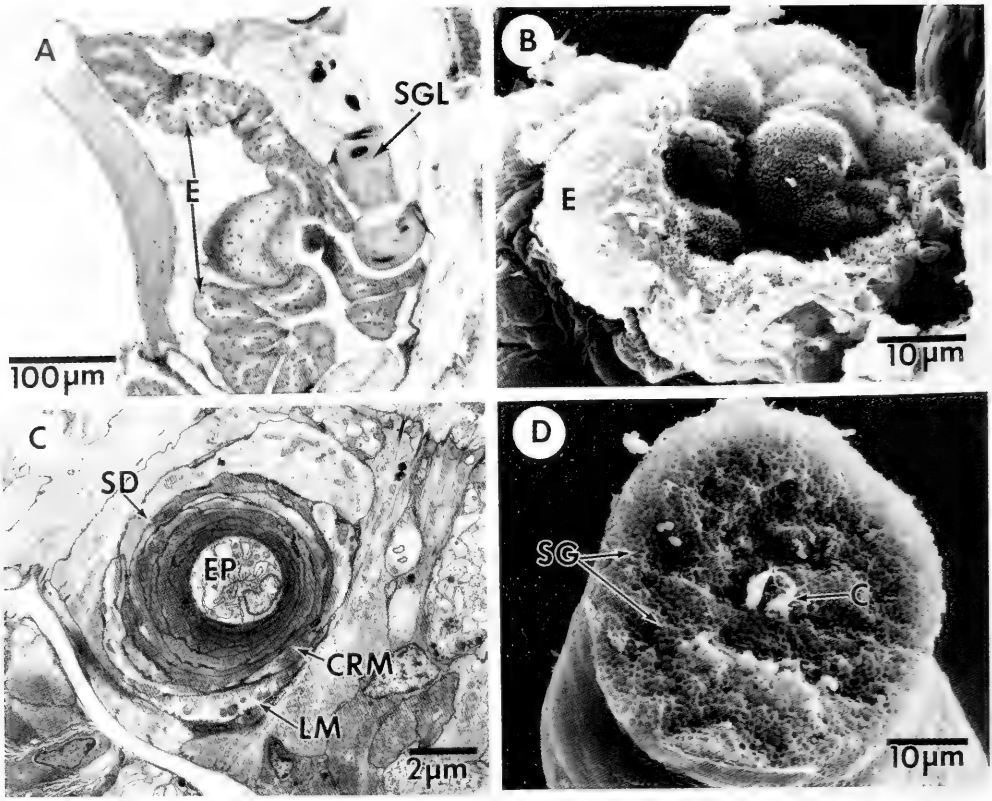

FIG. 7. A. Histological section of the esophagus and a single salivary gland. B. Scanning electron microphotograph of interior of the esophagus. C. Transmission electron microphotograph of single salivary duct in transverse section. Salivary duct enclosed by multiple layers of circular and longitudinal muscle. D. Scanning electron microphotograph of a cross-section of a salivary gland, composed of innumerable secretory granules with the exception of striated outer surface, ciliated lumen, and distal sac-like portion. C = cilia; CRM = circular muscle; EP = epithelium; LM = longitudinal muscle; E = esophagus; SG = secretory granules; SD = salivary duct; SGL = salivary gland.

coat the ciliated exterior. No ducts lead from these gland cells to the external surface of the gastropod. This is contrary to observations of Fretter & Graham (1949), who found that in European pyramidellids they examined, the large gland cells of the head-foot had well-defined ducts, with non-mucoidal products. For *B. impressa,* a majority of these cells possessed sulfated mucins (a major constituent of mucus), whereas a small number, located just inside the dorsal surface of the mentum, contained nonsulfated acidic mucins. Therefore, these ductless cells function in the production of the mucus that coats the external surface of the mantle and head.

The pedal gland of *Boonea impressa* contains sulfated mucins. Based on the arrangement of the gland cells, the presence of ciliated epithelium, and its position within the foot, this structure is similar to the lateral streak or aggregate of cells, located on either side of the foot and dorsal to the sole, described by Fretter & Graham (1949) in *Odostomia unidentata* and other species they examined (Table 1). On the basis of bundles of long cilia, associated with the lateral streak, these authors thought that it might function as a sensory organ. I did not observe the bundles of cilia in *Boonea impressa,* and my findings suggest that these same cells comprise the pedal gland in *B. impressa* (Fig. 2A). In *B. impressa,* the pedal gland is responsible for the formation of the suspensory thread with which this snail fastens itself to its surroundings. An attachment thread has also been observed in other pyramidellids (Ponder, 1973;

Hoffman, 1979; J. E. Ward, 1985, pers. comm.).

FEEDING STRUCTURES AND THEIR FUNCTIONAL MORPHOLOGY

The feeding structures of *Boonea impressa* enable this gastropod to feed suctorially on a number of hosts. The proboscis is capable of extending to a length equal to or greater than the snail's shell, enabling it to reach its host's soft tissues. The stylet perforates the host's tissue, presumably once the muscular sucker is firmly attached to the host. The forward movement of the stylet is accomplished by the compression of the stylet bulb's crescent-shaped lumen. Retractor muscles ensure the return of the stylet to its original position within the stylet cavity (Figs. 5A). The dorsal surface of the stylet possesses a combination of grooves and ridges enabling the stylet to penetrate the host's tissue readily (Fig. 5E). The opening of the true mouth, through which host hemolymph and perhaps torn tissue fragments enter the alimentary canal, is connected to buccal pump I by the oral tube (Fig. 5A, C). Contractions of only buccal pump II draw host hemolymph into the alimentary canal. Located at the junction of buccal pump I and buccal pump II is a ring of muscle that closes this passageway when contracted, thereby forcing host hemolymph into the esophagus once the lumen of buccal pump II is compressed. Elongate cilia, present at the junction of the buccal pump II and esophagus, facilitate movement. Cilia within the esophagus (Fig. 7B), in conjunction with possible peristaltic movement, convey host hemolymph to the stomach.

Movement of the proboscis involves a complex series of events. Protraction of the proboscis is presumably hydraulic, a consequence of the compression of the cephalic hemocoel and the redistribution of hemolymph. Retraction of the proboscis is accomplished by the contraction of specific muscles. The most obvious of these, and possibly the most important, is the primary retractor muscle. Figure 8A shows the muscle's position when the proboscis is retracted; however, once the proboscis is extended (Fig. 8B), this muscle is brought forward as the mouth moves to its most anterior position at the tip of the completely protracted proboscis. Contraction of the primary retractor muscle initiates the often rapid invagination of the proboscis. In concurrence with the contraction of the primary retractor muscle, the secondary retractor muscles contract sequentially, starting with those at the most anterior portion of the extended proboscis. The secondary retractor muscle arrangement in the right anterior portion of the snail is shown (simplified) in Figure 8C. Only three of the approximately 24 secondary retractor muscles are illustrated. The axis or pivot point for the secondary retractor muscles is located in the head just behind the eye. From this point, two of the muscles extend anteriorly into the proboscis, and the third muscle extends posteriorly to attach to a portion of the proboscis that is still within the cephalic hemocoel. If the proboscis were fully protracted, the most posterior secondary retractor muscle would eventually lie anterior to the other two secondary retractor muscles. If, however, the proboscis is retracted, the most anterior secondary retractor muscle would contract, resulting in the inversion of the most anterior portion of the proboscis.

SYSTEMATIC CONCLUSIONS

In the process of resolving some of this family's taxonomic problems, Robertson (1978) excluded three Western Atlantic American pyramidellids from the genus *Odostomia* Fleming, 1813, where they were originally assigned and proposed a new genus, *Boonea,* to accommodate them. His actions were based on differences (e.g., in protoconch shape, operculum configuration, excurrent siphon, penial complex, pigmented mantle organ coloration, and in the location of the common gonoduct opening) between these species and European species once considered congeneric. As additional substantiation of Robertson's decision, this study compared the feeding structures of *B. impressa* to literature accounts of the feeding structures of the European odostomians (including the type species of *Odostomia, Odostomia plicata*) described by Ankel (1949), Fretter & Graham (1949), and Maas (1965).

The feeding structures of *Boonea impressa* follow the general anatomical scheme described for other odostomians, with some important exceptions. Structurally, the proboscis of *B. impressa* is unlike those of the odostomian species described by Fretter & Graham (1949) and Maas (1965) (Table 1). The European species examined by Fretter & Graham

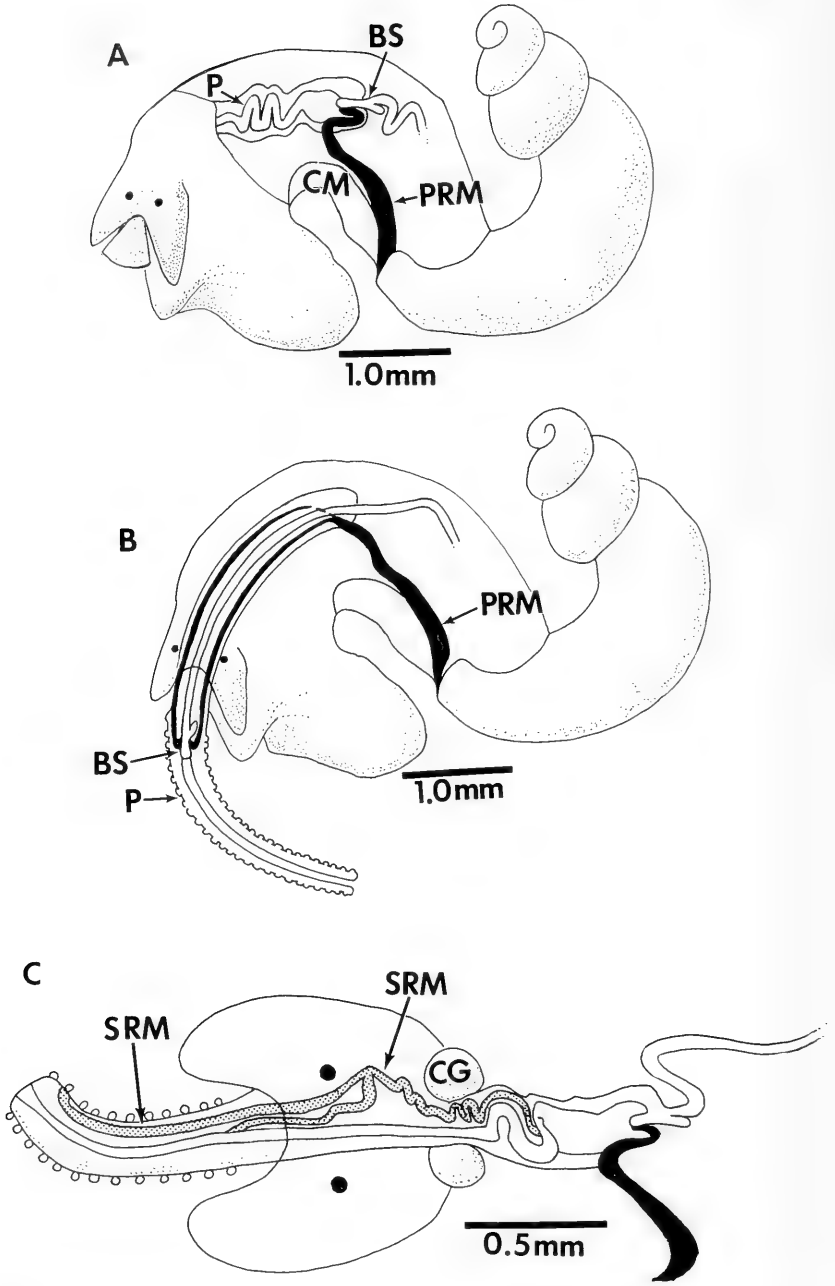

FIG. 8. Retractor muscles of the proboscis. A. Schematic representation of primary retractor when proboscis completely inverted. Primary retractor muscle originating at columella muscle, extends into cephalic hemocoel to pass through the sheath of the proboscis and insert on either side of buccal sucker's base. B. Primary retractor when proboscis partially protracted. Primary retractor muscle carried forward during extension, lying posterior to proboscial tip. C. Schematic of secondary retractor muscle arrangement (right lateral view of head region). Only three of approximately 24 secondary retractor muscles illustrated. BS = buccal sac; CG = cerebral ganglion; CM = columella muscle; P = proboscis; PRM = primary retractor muscle; SRM = secondary retractor muscle.

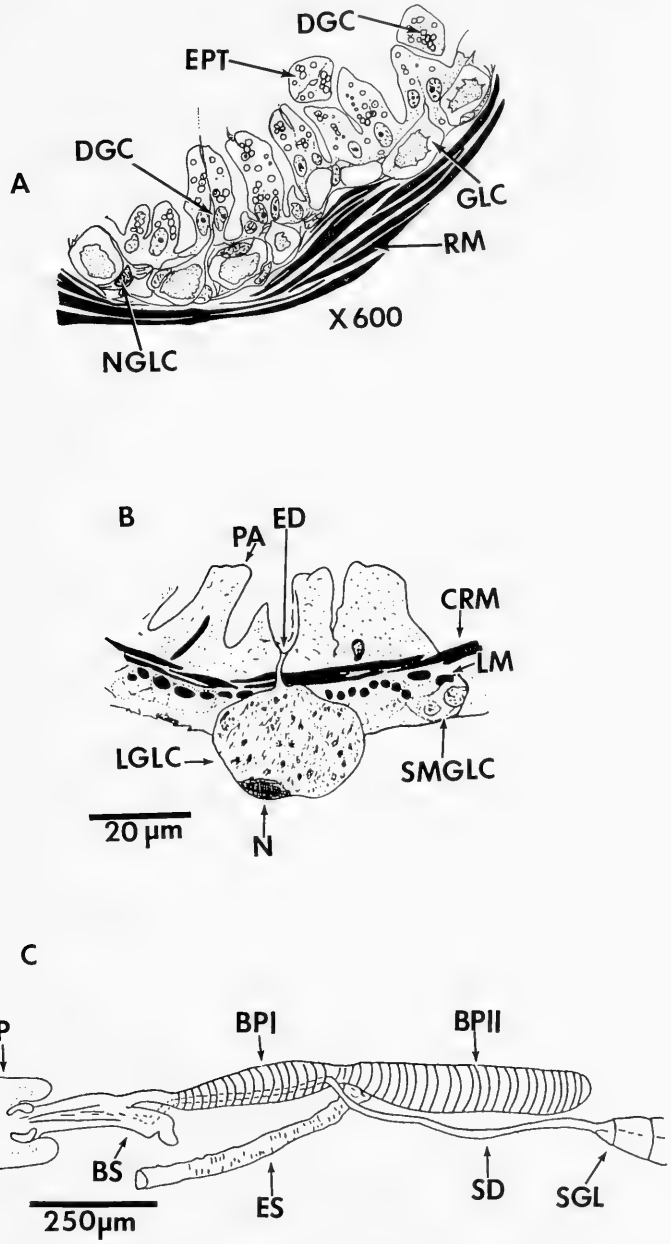

FIG. 9. European odostomians. A. Longitudinal section of proboscis of *Odostomia unidentata.* Papillae consist of three to four cells. Extending from subepithelial cells located within the layer beneath papillae are ducts that pass through center of papillae to open apically (redrawn from Fretter & Graham, 1949). B. Schematic of internal proboscial arrangement of *Odostomia eulimoides.* Papillae comprised of large-celled epithelium; note large gland cell duct extending between papillae to open externally (redrawn from Maas, 1965). C. Schematic of feeding structures of *O. eulimoides* (redrawn from Maas, 1965). BS = buccal sac; BPI = buccal pump I; BPII = buccal pump II; CRM = circular muscle; DGC = gland cell duct; ED = excretory duct; EPT = papilla (tran. sec.); ES = esophagus; GLC = gland cell(s); LGLC = large gland cell; LM = longitudinal muscle; N = nucleus; NGLC = nucleus of gland cell; P = proboscis; PA = papilla; RM = retractor muscle; SD = salivary duct; SGL = salivary gland; SMGLC = small gland cell.

TABLE 1 Morphological and ultrastructural differences between feeding structures of *Boonea impressa* and those of selected European odostomians (listed below).

This Study	*Maas; Ankel	**Fretter & Graham
(1) Proboscis:		
(a) papillae composed of numerous, elongate cells.	(a) papillae composed of large-celled epithelium.	(a) papillae composed of only 3 or 4 cells.
(b) beneath papillae a layer of circular & longitudinal muscle enclosed by connective tissue.	(b) internal to papillae a layer of circular muscle, above a layer of longitudinal muscle.	(b) beneath papillae a of layer gland cells with ducts that extend to exterior via the center of the papillae.
(c) no gland cells or ducts.	(c) beneath the layers of muscle an aggregate of large & small gland cells, the larger with ducts that terminate between the papillae externally.	(c) internal to the glandular layer, a layer of longitudinal muscle.
(2) Buccal pump: divided into two regions, with BpI twice the length of BpII.	divisible into approximately equal length sections.	not divisible, uniform.
(3) Salivary ducts: enter buccal sac & then stylet bulb, without exiting alimentary canal.	exit alimentary canal just behind buccal sac and then enter stylet bulb.	exit alimentary canal posterior to buccal sac & then enter stylet bulb.

*Examined in detail *Odostomia eulimoides, O. plicata,* and *Liostomia clavula,* with cursory attention given to *Odostomia rissoides, Chrysallida spiralis,* and *C. obtusa.*
**Examined in detail *Odostomia unidentata, O. plicata,* and *O. lukisii,* with some attention given to *O. scalaris,* (= *O. rissoides*), *O. trifida,* and *Chrysallida spiralis.*

(1949) (e.g., *Odostomia unidentata*), possessed papillae comprised of only three to four cells, containing large basal nuclei, side by side within the neck of the papillae, and arranged so that they formed a narrow base, widened medially and then tapered to a blunt apex (Fig. 9A). Present within each papilla (along its longitudinal axis) was a duct that extended from a subepithelial gland cell located within the connective tissue of the wall of the proboscis. Fretter & Graham (1949) also determined that beneath the layer of gland cells, and underneath the epithelium of the buccal region, was an array of muscle fibers that comprised part of the mechanism for the retraction of the proboscis. Maas (1965) investigated several other odostomian species (e.g., *Odostomia eulimoides;* Table 1) and found the papillae of the proboscis to be comprised of large-celled epithelium (Fig. 9B). Internal to the papillae is a layer of circular muscle that lies above longitudinally oriented band of muscle. Beneath the muscle, a glandular layer contains a mixture of small and large (30μm) gland cells. According to Maas (1965), the larger gland cells have ducts that pass through the layer of muscle, terminating between the papillae.

Boonea impressa differs from the described European snails in several ways, the most noteworthy being in the histology of the proboscis (Table 1). Papilla are each composed of numerous elongate cells bordered internally by a layer of both circular and longitudinal muscle (Figs. 3B, C, 4B-D). This layer of muscle is enclosed by a thin layer of connective tissue. No gland cells or ducts are present within the papillae or the proboscis. Each papilla has a central cell from which cilia protrude as an apical tuft. Only a single species, *Liostomia clavula,* examined by Maas (1965) possessed papillary cilia.

All the European odostomian species investigated by Ankel (1949) and Maas (1965) have two well-developed buccal pumps that are delineated in part by a narrowing at their junction (Fig. 9C). Fretter & Graham (1949) examined some of the same species but did not consider the buccal pump as two separate entities: they treated the structure as a single pump and stated that it was histologically uniform along its length (Table 1). Maas (1965) disagreed with Fretter & Graham's (1949) description of the buccal pump, although Maas did not examine *O. lukisii,* one of the species Fretter & Graham (1949) used as an example. According to Mass (1965), *O. pilicata* (a species examined by Fretter & Graham), has

two buccal pumps (Bp I and Bp II respectively) that are histologically discrete (Fig. 9C). The first buccal pump (like the buccal pump I of *B. impressa*) has a trifid lumen (divided into three lobes with narrow sinuses), and the second buccal pump is flattened laterally, not dorso-ventrally as described by Fretter & Graham (1949). My investigations indicate that *B. impressa* possesses a buccal pump divided into anterior and posterior regions, similar to that for the species described by Maas (1965). However, the BpI of *Boonea impressa* is very elongate and twice the length of the BpII, whereas in all examined European odostomians, the buccal pump is divided into approximately equal sections (Fig. 9C). The BpI of *Boonea impressa* is a well-developed structure comprised chiefly of muscle cells that surround a triangularly shaped lumen (Fig. 6A, 6C). This is contrary to White et al. (1985), who determined that this portion of the feeding apparatus of *B. impressa* was a poorly developed tube.

The other major difference between *B. impressa* and the European pyramidellids is the way in which the salivary ducts traverse the alimentary canal and enter the buccal sac (Table 1). Both Fretter & Graham (1949) and Maas (1965) described the salivary ducts as entering the first buccal pump just anterior to the junction between the two buccal pumps (Fig. 9C). Prior to entering the buccal sac, they exit the buccal pump (i.e., the alimentary tract) to then enter the stylet bulb. My study demonstrates that the salivary ducts of *B. impressa* pass into the ventral surface of the BpI, traverse the length of this portion of the buccal pump, and eventually extend into the buccal sac. However, at *no* point do the salivary ducts leave the buccal pump, and within the buccal sac they unite to form a single duct that enters the base of the hollow stylet and extends to the stylet's apex. These differences provide further evidence that Robertson (1978) was correct in excluding *B. impressa* and other eastern American "odostomians" from the genus *Odostomia.*

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INFLUENCIA AMBIENTAL SOBRE EL CRECIMIENTO ALOMÉTRICO DE LA VALVA EN *NACELLA (PATINIGERA) DEAURATA* (GMELIN, 1791) DEL CANAL BEAGLE, ARGENTINA

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ABSTRACT

Environmental influence on shell allometric growth in *Nacella (Patinigera) deaurata* (Gmelin, 1791) from the Beagle Channel, Argentina.

The allometric relationships among a variety of shell characters were studied in *P. deaurata,* which inhabits the lower intertidal zone in Beagle Channel. Shell height and weight as well as inner volume were significantly higher in specimens living on coasts exposed to strong wave action. It is suggested that individuals inhabiting exposed surfaces are obliged to have a stronger grip, and consequently the mantle does not extend past the edge, resulting in shell height increase. The variations observed are related to the different exposures to wave action. Desiccation is not an important factor in the habitat of this species.

Key words: morphology, allometry, environmental influence, intertidal zone, limpets, *Nacella,* Prosobranchia. Palabras clave: morfología, alometría, influencia ambiental, intermareal, lapas, *Nacella,* prosobranquios.

INTRODUCCION

Los gasterópodos presentan valvas que varían su morfometría general y las proporciones entre los distintos parámetros estructurales de la valva en relación con las variaciones del ambiente, generando alometras en el crecimiento. Los factores ambientales que producirían cambios más marcados sobre la morfometría valvar serían el oleaje o corrientes intensas y la exposición a la desecación (Balaparameswara Rao & Ganapati, 1971; Vermeij, 1973, 1980; Branch, 1975; Bannister, 1975; Branch & Marsh, 1978; Lowell, 1984; Simpson, 1985). Debido a que las lapas se encuentran en habitats muy variados, desde el intertidal superior al inferior, en zonas expuestas y protegidas, resultan un adecuado material para analizar las influencias ambientales en la morfología valvar.

Nacella (Patinigera) deaurata (Gmelin, 1791) habita el intertidal inferior quedando expuesta a la desecación solamente en las mareas de sicigia. Por ello las variaciones morfológicas que presenta pueden correlacionarse fundamentalmente con el grado de exposición al oleaje. El propósito de esta investigación fue comparar los diferentes parámetros estructurales en *Nacella (P.) deaurata,* colectada en dos localidades con diferente grado de exposición.

MATERIAL Y METODOS

Los muestreos se realizaron en dos localidades (Fig. 1): (a) Punta Occidental (PO) (54°50′S., 68°20′W.: área expuesta a los vientos dominantes del SO, fuerte oleaje, declive suave, con abundancia de coralináceas incrustantes como *Pseudolitophillum* sp. y *Synartrophitum* sp. (Mendoza, 1988) y ejemplares aislados de *Macrocystis pirifera.* (b) Bahía Lapataia (BL) (54°52′S., 68°35′W.): costa orientada hacia el norte, protegida de los vientos dominantes, con fuerte pendiente y denso cinturón de *Macrocystis pirifera.* Las lapas fueron extraídas por buceo autónomo. Se separaron las partes blandas de las valvas, las que se secaron al aire durante varios días hasta que el peso no varió.

Las caracteristicas de las valvas que se consideraron fueron las siguientes (Fig. 2): Largo Total (LT), desde el extremo anterior al posterior, altura total (AT), desde el apex perpendicularmente a la base, ancho (A), diámetro máximo tomado perpendicularmente a LT, perímetro (P) y área basal (AB). Estas medidas fueron tomadas al milímetro inferior con un calibre vernier. Además se determinaron el peso de la valva (PV) con una precisión de 0.01 gramo y el volumen interno (VI). Este fue obtenido llenando las valvas con arena fina tamizada a 600 micras determinándose el

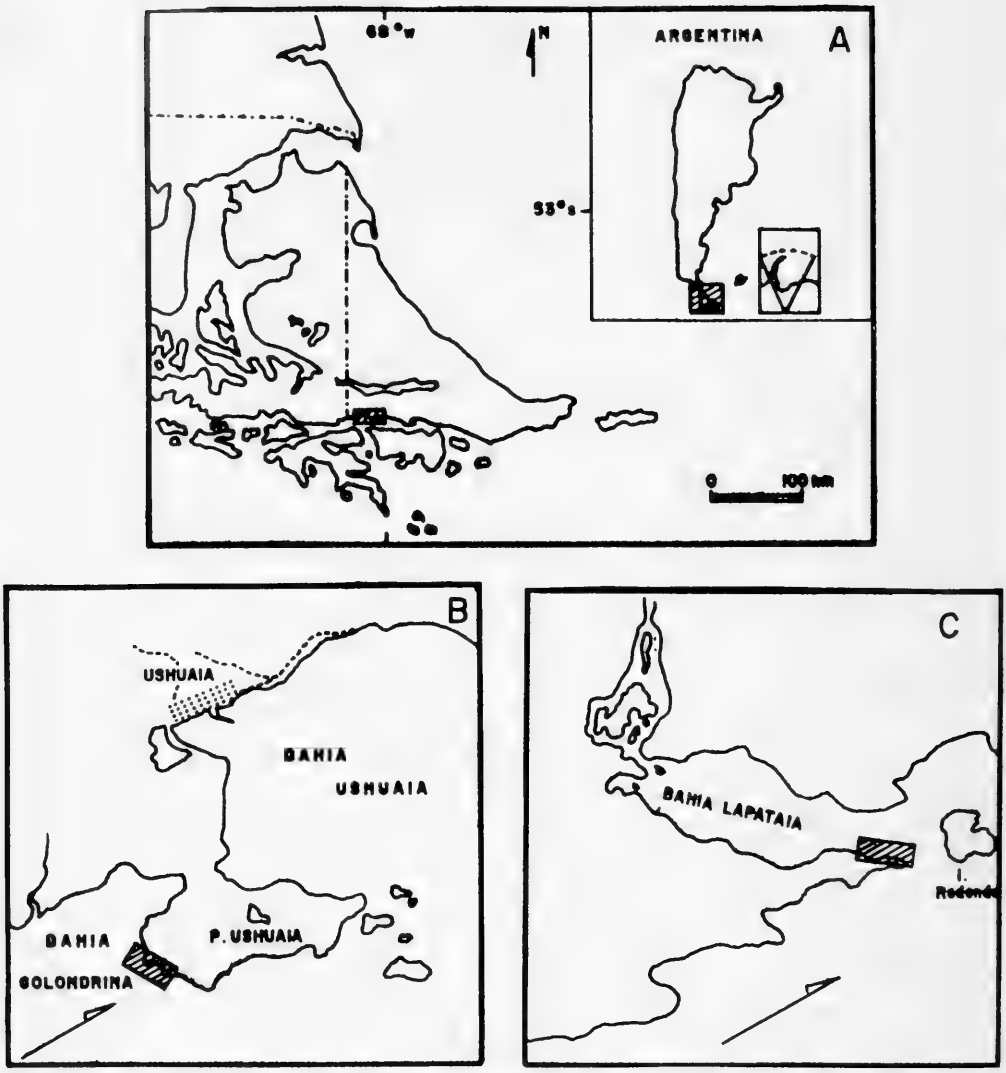

FIG. 1: Ubicación de las localidades de muestreo. A: Punta Occidental (54°50′S, 68°20′W) y Bahía Lapataia (54°52′S, 68°35′W) área sombreada. B: Punta Occidental, zona expuesta (área sombreada). La flecha señala los vientos dominantes. C: Bahía Lapataia, zona protegida (área sombreada). La flecha señala los vientos dominantes.

peso de la misma. Luego se pesó 1 cm^3 de arena, calculándose el volumen correspondiente a cada valva. La transformación peso de arena a volumen se realizó promediando el peso de diez réplicas de 1 cm^3 de arena.

Las valvas utilizadas fueron seleccionadas empleando números al azar de la colección total de valvas (PO: 662 ejemplares; BL: 628 ejemplares). Las valvas dañadas o con epibiontes fueron descartadas del muestreo.

El rango de LT considerado comprendió valvas de 13 a 65 mm estableciéndose clases de 5 mm. En una primera selección se tomaron diez valvas para cada clase en ambas localidades; posteriormente y a los efectos de disminuir la dispersión de las variables dependientes se aumentó a 20 por clase el número de valvas de las clases mayores de 36 mm. Las variables (AT, PV y VI) fueron tomadas como dependientes del LT, calcu-

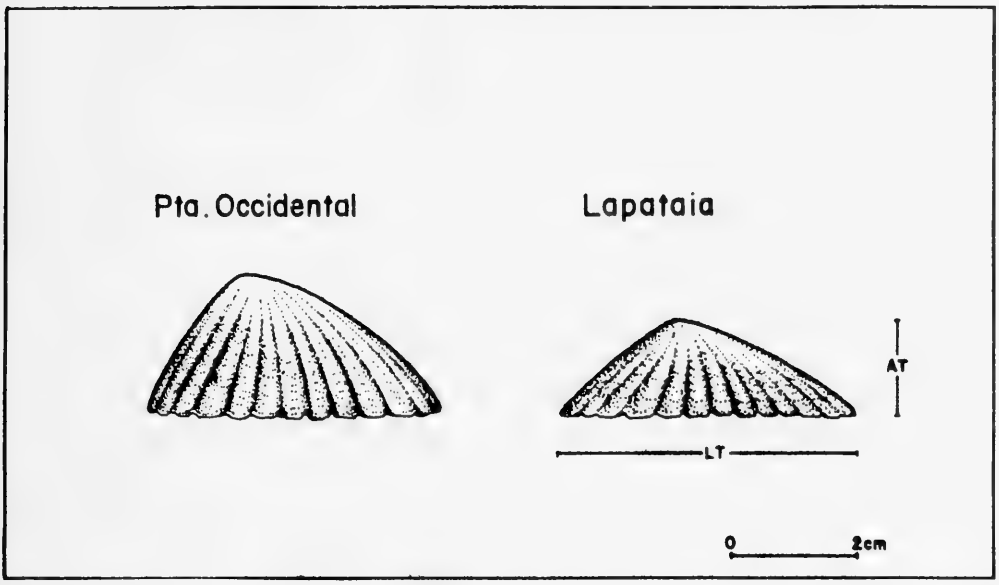

FIG. 2: Vista lateral de las valvas de *Nacella (Patinigera) deaurata* provenientes de ambas localidades de muestreo.

TABLA 1: Regresión de AT, PV y VI sobre LT para zonas expuestas (PO) y protegidas (BL).

Localidad	Y = a + b * X	r	P	N
(A) PO	AT = −5.32 + (0.52 * LT)	0.96	< 0.001	161
(B) BL	AT = −2.52 + (0.37 * LT)	0.96	< 0.001	167
Localidad	1g Y = a + (b * lg X)	r	P	N
(C) PO	1g PV = −5.43 + (3.68 * lg LT)	0.98	< 0.001	161
(D) BL	1g PV = −4.68 + (3.11 * lg LT)	0.98	< 0.001	167
(E) PO	1g VI = −5.04 + (3.58 * lg LT)	0.99	< 0.001	161
(F) BL	1g VI = −4.86 + (3.40 * lg LT)	0.98	< 0.001	167

TABLA 2: LT/AT. Test de homogeneidad de las pendientes ($H_0 : b_1 = b_2$) siendo b_1 la pendiente de la ecuación (A) y b_2 la pendiente de la ecuación (B) de la Tabla 1.

Fuente de variacion	Suma de cuadrados	Grados de libertad	Cuadrado Medio	F	P
Localidad	64.552	1	64.552	22.646	≤0.000
LT	12599.998	1	12599.998	4420.336	≤0.000
Localidad * LT	354.555	1	354.555	124.385	≤0.000
Error	923.549	324	2.85		

lándose las ecuaciones de regresión correspondientes. Cuando fue necesario se realizó la transformación logarítmica de los datos a fin de ajustarlos a la ecuación de la recta.

RESULTADOS

Se analizó la relación entre LT y los diferentes parámetros estructurales, calculándose las ecuaciones de regresión correspondientes por el método de los cuadrados mínimos. Las relaciones A/LT, P/LT y AB/LT no presentan diferencias significativas entre las pendientes de las rectas de regresión correspondientes a cada localidad de muestreo.

Relación LT—AT

La relación LT—AT se ajusta a una recta en las dos zonas de muestreo consideradas

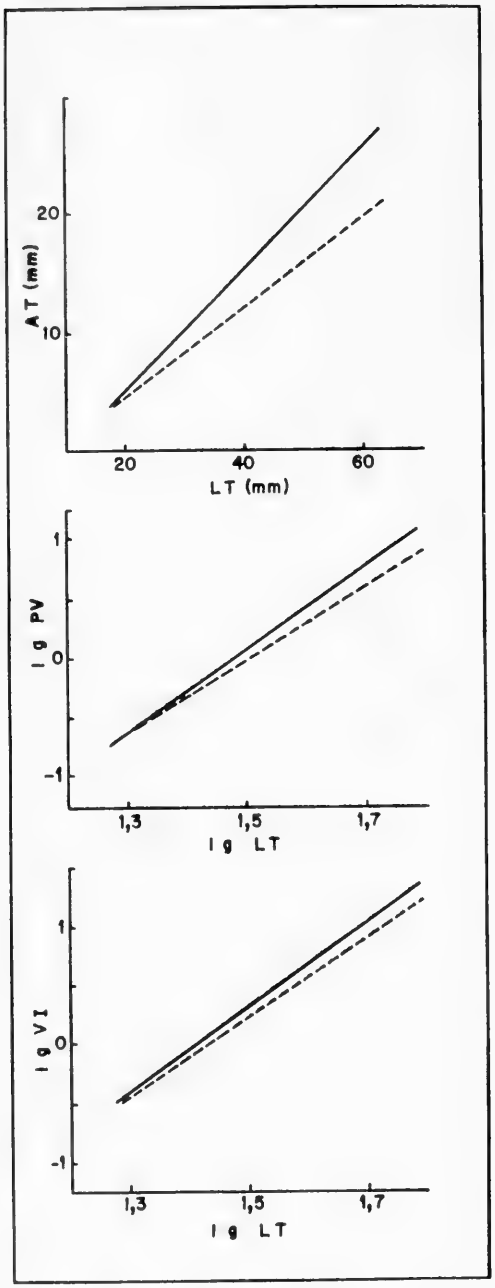

FIG. 3: Rectas de regresión entre AT/LT, PV/LT y VI/LT para Punta Occidental (_____) y Bahía Lapataia (- - - -).

(Tabla 1). La comparación entre las pendientes de las rectas de regresión de ambas localidades muestra diferencias significativas (Tabla 2). A igual LT las valvas de Punta Occidental son más altas que las de Lapataia (Fig. 3).

Relación LT—PV

Esta relación se ajusta a una curva potencial tanto en Punta Occidental como en Lapataia por lo que se realizó la transformación logarítmica de la misma (Tabla 1). La comparación entre las dos rectas resultantes muestra que las pendientes son diferentes (Tabla 3) siendo mayor el PV en Punta Occidental, para las LT consideradas (Fig. 3).

Relación LT—VI

Se ajusta de igual manera a una curva potencial en las dos localidades, por lo que se hizo la transformación logarítmica correspondiente (Tabla 1), comparándose las dos rectas; éstas muestran pendientes significativamente diferentes (Tabla 4). Se observa que el VI es mayor para cada clase de LT en Punta Occidental (Fig. 3).

DISCUSION

El análisis de las posibles influencias ambientales sobre la morfología valvar se ha intentado en repetidas oportunidades, con resultados a veces contradictorios, especialmente por la dificultad para analizar por separado la influencia de la turbulencia del agua y de la exposición a la desecación.

La relación entre la resistencia ofrecida a las corrientes de agua y la forma de la valva de diferentes especies de lapas fue analizada experimentalmente por Denny (1989). Este sostiene que la influencia de la forma de la valva en relación a la resistencia ofrecida a las corrientes no es tan crítica para la sobrevida y por lo tanto es de un restringido valor adaptativo. Orton (1932) sugiere que la acción de las olas sobre la altura de las valvas de las lapas tendría un efecto insignificante sobre la forma de las mismas en *P. vulgata*. Tampoco Balaparameswara Rao y Ganapati (1971) hallan diferencia de altura en *Cellana radiata* que habita costas desprotegidas con respecto a la población que vive en zonas protegidas.

Por el contrario, Ebling et al. (1962) en *Patella aspersa* encontraron lapas con valvas cuya altura aumentaba significativamente en las poblaciones que vivían permanentemente sumergidas y sometidas a fuertes corrientes.

TABLA 3: LT/PV. Test de homogeneidad de las pendientes ($H_0 : b_1 = b_2$) siendo b_1 la pendiente de la ecuación (C) y b_2 la pendiente de la ecuación (D) de la Tabla 1.

Fuente de variación	Suma de cuadrados	Grados de libertad	Cuadrado Medio	F	P
Localidad	0.51	1	0.51	56.098	≤0.000
lgLT	108.086	1	108.086	11879.686	≤0.000
Localidad *lgLT	0.742	1	0.742	81.584	≤0.000
Error	2.948	324	0.009		

TABLA 4: LT/VI. Test de homogeneidad de las pendientes ($H_0 : b_1 = b_2$) siendo b_1 la pendiente de la ecuación (E) y b_2 la pendiente de la ecuación (F) de la Tabla 1.

Fuente de variación	Suma de cuadrados	Grados de libertad	Cuadrado medio	F	P
Localidad	0.027	1	0.027	6.046	≤0.014
lgLT	114.137	1	114.137	25969.286	≤0.000
Localidad *1gLT	0.072	1	0.072	16.357	≤0.000
Error	1.424	324	0.004		

Walker (1972) en *Patinigera polaris* y Simpson (1985) en *Nacella macquarensis* relacionan la intensidad alométrica del incremento de la altura de la valva respecto de la longitud con la mayor turbulencia del agua. En *Cellana radiata* provenientes de diferentes niveles mareales, Balaparameswara Rao y Ganapati (1971) concluyen que presentan mayor altura los individuos que están sujetos a mayor desecación.

Vermeij (1973, 1978) halla que en varias especies de lapas la altura de la valva es mayor en las que habitan los niveles superiores de la costa, sugiriendo que una valva más alta incrementaría la capacidad de reserva de agua y la resistencia a la desecación. Coincidentemente, Bannister (1975) prueba experimentalmente que *P. lusitanica,* que habita en la zona superior del intertidal, resiste mejor la desecación que *P. caerulea,* que vive en la zona inferior del mismo; la mayor resistencia es vinculada al incremento de altura de la valva, que determina un mayor volumen interno.

Las poblaciones de *N. (P.) deaurata* investigadas habitan el intertidal inferior y el subtidal somero, por lo que la desecación no influiría en la altura de las valvas como ocurre en otras especies. En esta especie, comparando lapas de igual LT provenientes de zonas expuestas (PO) y protegidas (BL) se comprueba una AT significativamente mayor para las primeras (Tabla 2, Fig. 3).

Balaparameswara Rao y Ganapati (1971) comparan *C. radiata* que vive en el intertidal superior e inferior y en zonas expuestas y protegidas. Estos autores encuentran que son más pesadas las valvas de las que habitan el intertidal superior, pero no hallan diferencias en zonas con distinta exposición.

En *N. (P.) deaurata* se produce un incremento del peso de la valva con el aumento de LT, expresándose esta relación en una curva potencial (Tabla 1). De la comparación entre poblaciones de zonas expuestas y protegidas se desprende una diferencia significativa, siendo las primeras más pesadas (Tabla 3, Fig. 3)

Baxter (1983) no encuentra diferencias en la relación volumen-longitud en *P. vulgata* habitando sitios con poca y mucha exposición al oleaje.

Las valvas de *N. (P.) deaurata* presentan, para una misma longitud, mayor volumen interno en las zonas expuestas (Punta Occidental) que en las protegidas (Bahía Lapataia) siendo las diferencias significativas (Tabla 4, Fig. 3). No se encontraron diferencias significativas entre el A, P y AB de la valva, en lapas de igual LT provenientes de ambas zonas de muestreo. Al no diferenciarse los parámetros mencionados se evidencia que el mayor volumen que presentan las lapas provenientes de Punta Occidental se debe a la mayor altura de las valvas.

Kopp (1980) relaciona la mayor exposición a la desecación durante la baja marea en el mejillón *Mytilus californianus* con individuos que presentan valvas más anchas y pesadas. Una alometría similar, generando valvas más altas y pesadas en las lapas que están ex-

puestas a cierto tipo de stress (desecación, exposición al oleaje) es encontrada por Orton (1932). Este autor argumenta que los estímulos para mantener la valva fuertemente adherida al sustrato ocasionan la retracción del borde del manto. De esa manera disminuiría el crecimiento periférico y por lo tanto aumentaría el crecimiento en altura de la valva. Kopp (1980) establece una relación análoga entre la forma de la valva y la extensión o retracción del borde del manto, apoyándose en pruebas experimentales.

Se considera que un proceso similar daría lugar a un mayor engrosamiento de la valva que conduciría a un aumento de su peso. El incremento en altura sin cambio en la superficie o perímetro de la base aumentaría el volumen interno.

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A NEW DEEP-WATER HYDROTHERMAL SPECIES OF *NUCULANA* (BIVALVIA: PROTOBRANCHIA) FROM THE GUAYMAS BASIN

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ABSTRACT

A new deep-water species of *Nuculana* is described that occurs in the southern trough of the Guaymas Basin and is associated with a hydrothermal vent system. The species, *N. grasslei,* is characterized by a large, ornamented prodissoconch, but in other respects it differs little in its gross morphology from other species of *Nuculana.* Such specializations that do occur relate to the hostile sulphurous environment in which it lives. Particularly important in this regard is the thickened periostracum and the large volume of pigmented blood.

Keywords: *Nuculana,* Protobranchia, hydrothermal vents.

INTRODUCTION

This paper describes the gross morphology of a new species of *Nuculana* taken from the southern trough of the Guaymas Basin in the Gulf of California at a depth of 2000 m, adjacent to a position where hydrothermal fluid at between 270–314°C percolates through a thick layer of pelagic sediment and through chimneys (Lonsdale et al., 1980; Simoneit & Lonsdale, 1982; Grassle et al., 1985; Berg & Van Dover, 1987).

Juvenile and adult specimens were taken during a series of dives by DSRV Alvin in January 1982 and August 1985 (listed in Jones, 1985, and Berg & Van Dover, 1987). In the Guaymas Basin, there are black smokers, and the sediments from the study area smell strongly of hydrogen sulphide. On this sediment, large patches of the filamentous bacterium *Beggiatoa* are present. The soft sediment benthic communities comprise a few species in great numbers, but their composition varies over short distances (Grassle et al., 1985). Samples of plankton containing larvae of the *Nuculana* were taken within the 5 m of water column above the sea bed (Berg & Van Dover, 1987). The methods employed to collect the specimens are reported by Grassle et al. (1985) and Berg & Van Dover (1987).

I am very grateful to Dr. J. Frederick Grassle for allowing me to examine this material, to Dr. Cindy Lee Van Dover for permission to copy from SEM photographs of larvae, and to the director and staff of the Woods Hole Oceanographic Institution for their help over many years.

DESCRIPTION

Genus *Nuculana* Link 1807

Type species (OD):
Arca rostrata Brugière, 1789,
ex Chemnitz MS, = *Arca pernula Müller, 1779.*

Shell robust, moderately and posteriorly elongate; rostrum truncate, usually bicarinate, moderately compressed, strong concentric sculpture; umbo anterior; posterior ventral margin slightly sinuate; occasionally with radial ribs; escutcheon present; hinge teeth chevron-shaped; ligament external with central internal part.

Nuculana grasslei, new species

Type locality: Guaymas Basin, south trough, 27°03′N, 111°23′W, 2003 m.

Holotype: USNM No. 859482	1 specimen
Paratypes: USNM No. 859481	specimens selected by J. A. A. from the type locality.

Named in honour of Dr. J. F. Grassle, friend and colleague of many deep-sea voyages and participant in the Guaymas Expedition.

[1]Address for correspondence.

Material

Dive No.	Depth (m)	Specimens Examined	(Number Collected)	Position	Equipment	Date
Alvin 1168	2003	25	(50)	27°03′N, 111°23′W	SS	10–1-82
		3	(3)		TC	
Alvin 1169	1998	8	(16)	27°03′N, 111°25′W	BC	11-1–82
Alvin 1170	2019	—	(7)	27°01′N, 111°25′W	BC	12-1–82
Alvin 1174	2011	—	(1)	27°01′N, 111°24′W	BC	17-1–82
Alvin 1175	1997	—	(1)	27°03′N, 111°23′W	BC	18-1–82
Alvin 1176	2022	4	(152)	27°01′N, 111°25′W	TC	19-1–82
Alvin 1607	2012	4	(4)	27°05′N, 111°24.5′W	TC	29-7–85
Alvin 1608	2002	1	(1)	27°07′N, 111°24.4′W	TC	31-7–85
Alvin 1614	2004	2	(2)	27°07′N, 111°24.4′W	BC	6–8-85
Alvin 1628 (1–5 above bottom)	2000	—	(5 postlarva)	27°00′N, 111°24.5′W	PT	23–8-85
Alvin 1629 (3–4 above bottom)	2000	—	(1 postlarva)	27°00′N, 111°25.5′W	PT	23–8-85

BC—Box Core (225 cm^2 area sampled)
TC—Tube Core (35 cm^2 area sampled)
SS—Scoop Sample (63 mm mesh bag over metal frame) non-quantitative
PT—Plankton Tow (0.4 m^2, 183 μ mesh) non-quantitative

Samples reported in Grassle et al. (1985) and Berg & Van Dover (1987).

Shell Description (Figs. 1–4)

Shell elongate, stout, bluntly rostrate, equivalve—although central portion of ventral margin of right valve may slightly overlap left valve as a consequence of strong concentric ornamentation; broad concentric ridges extend over central region of shell from faint posterior radial ridge to close to anterior margin, those close to umbonal region less conspicuous than those ventral to them; fine, closely spaced concentric striae extend anterior and posterior to ridges, with line of ridges marked by heavier striae; two faint radial ridges extend from umbo to posterior ventral margin; umbo anterior (position at approximately 38% total length), relatively large, beaks inturned; antero-dorsal margin smoothly curved near umbo, but in large specimens somewhat flattened anteriorly; postero-dorsal margin more or less straight or even slightly concave in large specimens, angulate at point opposite posterior limit of hinge plate; posterior margin broadly truncate and slightly gaping; ventral margin for most part an even, shallow curve, except posteriorly between limits of radial ridges, where it is sinuate (this corresponds to position of feeding aperture); escutcheon and lunule outlined by faint ridges; hinge plate moderately broad, continuous ventral to umbo; hinge teeth chevron-shaped, number increasing with increasing shell length, 17 anterior and 25 posterior teeth in specimen 26.3 mm total length, of these 6 or 7 on each side of umbo are more leaf-like than those more posterior, 11 anterior and 15 posterior in specimen 13.7 mm total length; ligament predominantly opisthodetic, small internal part attached to resilium, which occupies a dorsal position on hinge plate and separates anterior and posterior hinge tooth series; external part comprises small portion anterior to umbo and moderately elongate portion posterior to umbo, latter somewhat extended by fused periostracum; periostracum golden-yellow, much thickened and strongly held within periostracal groove.

Prodissoconch large, 275–283 μm total length, ornamented with 9–10 reticulated concentric ridges and 10–11 radial reticulations.

Length of largest shell examined: 26.3 mm.

Internal Morphology

The gross morphology of the body organs is typically nuculanid in form (Fig. 5) and differs little from descriptions of shallow-water species (Yonge, 1939).

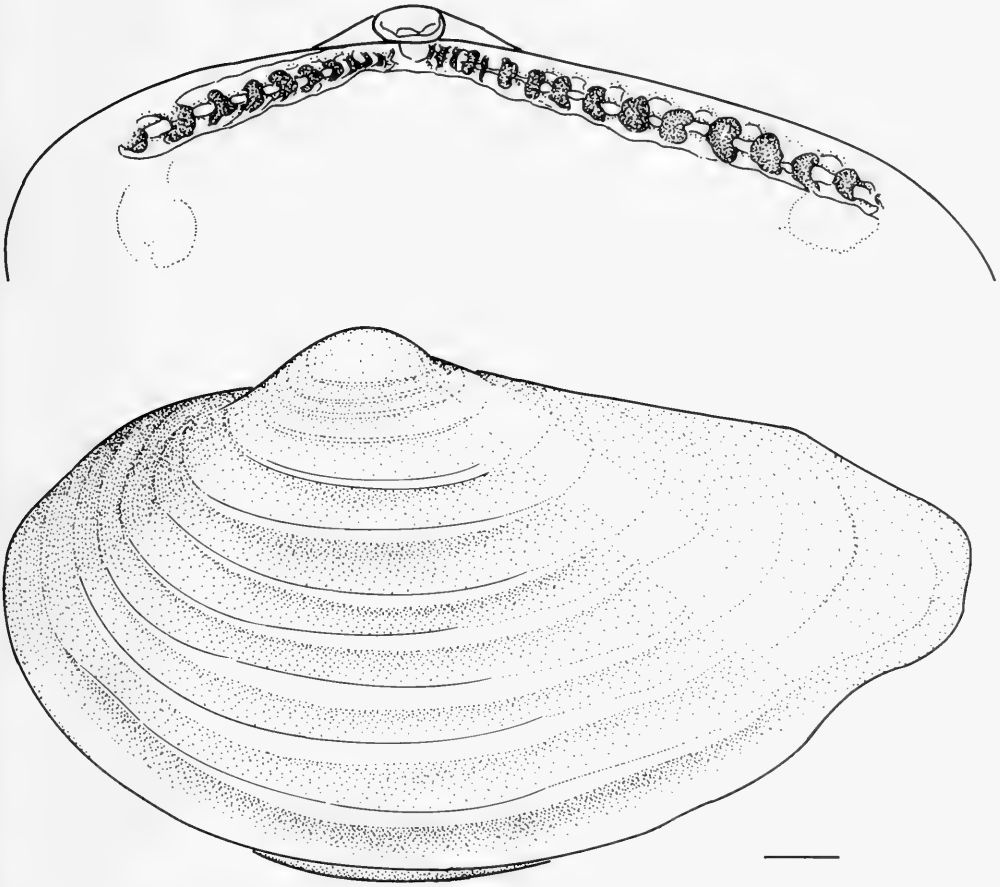

FIG. 1. *Nuculana grasslei.* Lateral view of the shell of the holotype from the left side and an internal view of the hinge region of the right valve of a specimen of similar size (bar = 1 mm).

The mantle is relatively unspecialized. Three typical folds are present at the mantle margin. Antero-ventrally the middle sensory fold is somewhat enlarged to form a simple anterior sense organ. Posteriorly there is a shallow siphonal embayment enclosing combined inhalent and exhalent siphons. The inhalent siphon is unfused both dorsally and ventrally (Fig. 6). Nevertheless, the integrity of the siphonal lumena is maintained by the apposition of thickened central and ventral longitudinal ridges on the inner siphonal surface. The inhalent siphon is somewhat shorter than the exhalent. There is no siphonal tentacle present, as is the case in other species of *Nuculana* (e.g. Yonge, 1939); however, a small lobe is present at the posterior limit of the left and right inner mantle folds where they meet the ventral margins of the mantle embayment. These are not homologous to the protobranch tentacle and probably represent the termination of the main rejection tract of the mantle that is present on the inner surface of the inner muscular mantle fold. Their function presumably is to guide pseudofaeces to the inhalent siphon so they may be ejected on contraction of the shell valves. There is a simple feeding aperture immediately anterior to the siphonal embayment. Here the middle sensory and the inner muscular lobes of the mantle are widened and somewhat folded. The feeding aperture of *N. grasslei* is much simpler than that of many deep-sea nuculanid protobranchs (Allen & Hannah, 1989). Numerous fine radial muscles are present within the mantle to the inside of the marginal folds. The adductor muscles are relatively small and unequal in

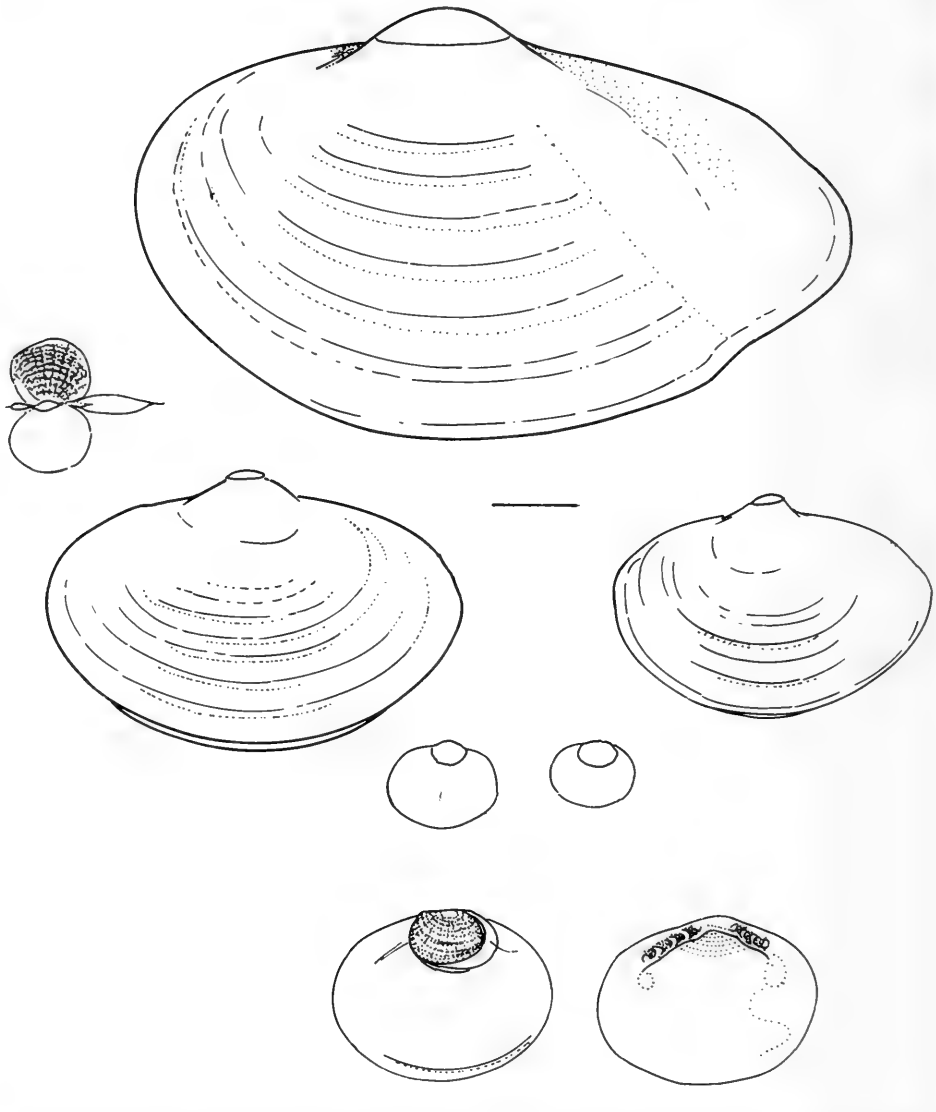

FIG. 2. *Nuculana grasslei.* Lateral views of shells from the right side to show variation in shape with increasing shell size. The figure includes a dorsal view of the hinge region of the next but largest shell illustrated and enlarged internal and external views of valves of a juvenile shell (bars = 1 mm).

size. The posterior muscle is oval in cross section, with "quick" and "catch" portions of equal size. The anterior muscle is crescent-shaped, with a narrow elongate "catch" portion running the length of the anterior face.

The gills are well developed and extend horizontally and parallel to the postero-dorsal shell margin from the mid-visceral region to the siphonal embayment. In the largest specimen examined, there are approximately 150 broad gill plates on each demibranch. These are comparable to those described by Yonge (1939). The plates of each demibranch alternate in their attachment to the axis. Each axis extends posteriorly beyond the posterior plate as an extremely long, fine filament. Unlike the condition in other nuculanid protobranchs, these do not appear to be attached to the

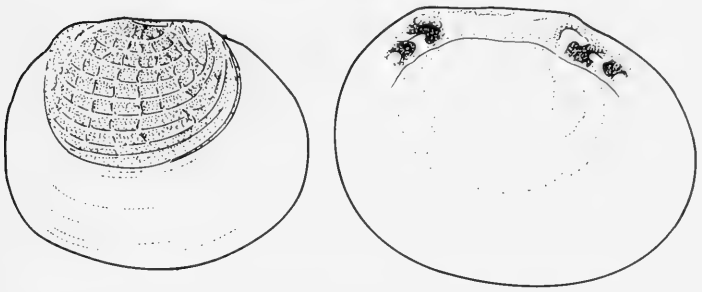

FIG. 3. *Nuculana grasslei.* Drawing from SEM photographs of the lateral external surface of the left valve and the internal surface of the right valve of a planktonic postlarva (with kind permission of Dr. C. L. Van Dover) (bar = 0.1 mm).

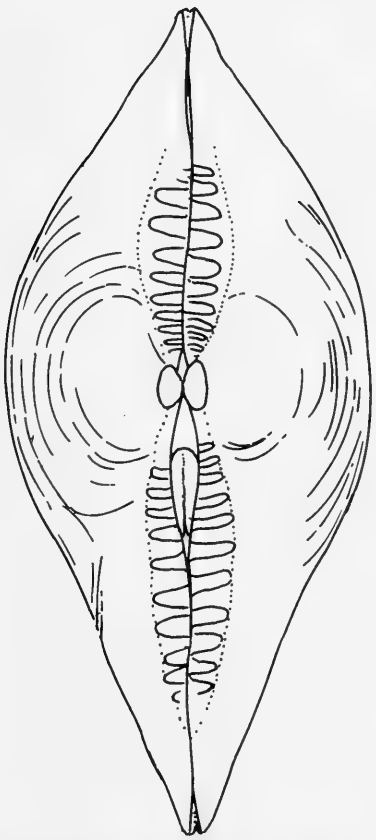

FIG. 4. *Nuculana grasslei.* Dorsal view of shell to show external detail of hinge region (bar = 1.0 mm).

respective left and right central ridges separating the inhalent from the exhalent siphon. Whether this is a consequence of preservation and a tenuous attachment has been lost cannot be determined at present. They presumably act as do axial extensions in other protobranchs, as guides to the transport of faecal rods from anus to exhalent siphon. It may be speculated that in this particular case they have become greatly extended to ensure disposal far distant from the feeding aperture.

The palps are moderate in size, with relatively broad sorting ridges on their inner faces. As in the case of the gill plates, the number of ridges on each face varies with the size of the specimen—39 in a specimen 26.3 mm total length and 14 in a specimen 3.0 mm total length. The palp proboscides are broad and long, even in the contracted, preserved state. In life they must be capable of considerable extension beyond the shell.

The foot and viscera are extensive. The muscular foot is broad. The sole is deeply divided and fringed with papillae. There is a small "byssal" gland in the heel of the foot at the point where it joins the sole. The pedal retractor muscles are not particularly well developed. There is a posterior pair inserted antero-dorsal to the posterior adductor muscle and two pairs of anterior retractor inserted postero-dorsal to the anterior adductor muscle.

The mouth lies somewhat posterior to the ventral edge of the anterior adductor muscle. The oesophagus is elongate and opens dorsally on the anterior face of the stomach. The stomach and combined style sac are moderately large and lie vertically within the body. Because of the brittle nature of the preserved specimens and because the digestive diverticula adhere closely to the stomach wall, little detail of the stomach was observed. Nevertheless, a well-developed dorsal hood and an extensive gastric shield are present. A small number of grooves comprising the posterior sorting area were identified. There is no doubt

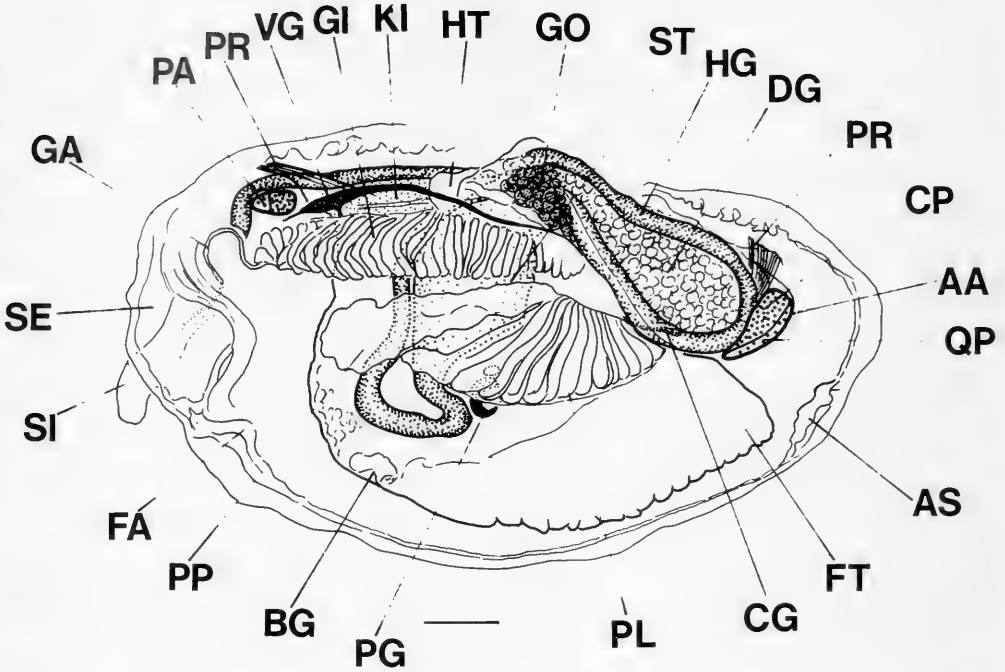

FIG. 5. *Nuculana grasslei.* Semidiagrammatic drawing of the internal morphology of a specimen from the right side (bar = 1.0 mm). AA, anterior adductor muscles; AS, anterior sense organ; BG, "byssal" gland; CG, cerebral ganglion; CP, "catch" portion of adductor muscle; DG, digestive diverticula; FA, feeding aperture; FT, foot; GA, extension of gill axis; GI, gill; GO, gonad; HG, hindgut; HT, heart; KI, kidney; PA, posterior adductor muscle; PG, pedal ganglion; PL, palp; PP, palp proboscis; PR, pedal retractor muscle; QP, "quick" portion of adductor muscle; SE, siphonal embayment; SI, combined siphon; ST, stomach; VG, visceral ganglion.

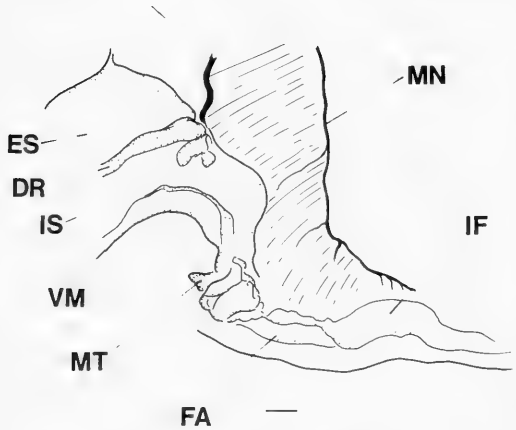

FIG. 6. *Nuculana grasslei.* Enlarged detail of the siphon and postlarval margin of the left mantle (bar = 0.1 mm). DR, dividing ridge; ES, exhalent siphon; FA, feeding aperture; IF, inner mantle fold; IS, inhalent siphon; MT, mantle tentacle; SN, siphonal nerve; VM, ventral margin of inhalent siphon.

that the morphology of the stomach differs little from the typical deep-sea nuculanid stomach (Allen & Hannah, 1989). The hindgut takes a typical course. From the style sac, it passes posterior to the stomach to the dorsal margin of the viscera. It then describes a loop on the right side of the body (Fig. 7), reaching the internal face of the anterior adductor muscle before passing posteriorly along the mid dorsal margin of the body, through the pericardium and ventricle of the heart, over the posterior adductor muscle to the anus. There is a typhlosole along the length of the hindgut; the faecal rods are typically compact with a groove moulded by the typhlosole. The digestive diverticula are very extensive with fine tubules that permeate the entire visceral mass.

The heart is exceptionally large. Paired lateral auricles are each supplied anteriorly via a major vessel from the gill axis. The blood volume also appears to be large. In all specimens, the contraction of the body on preser-

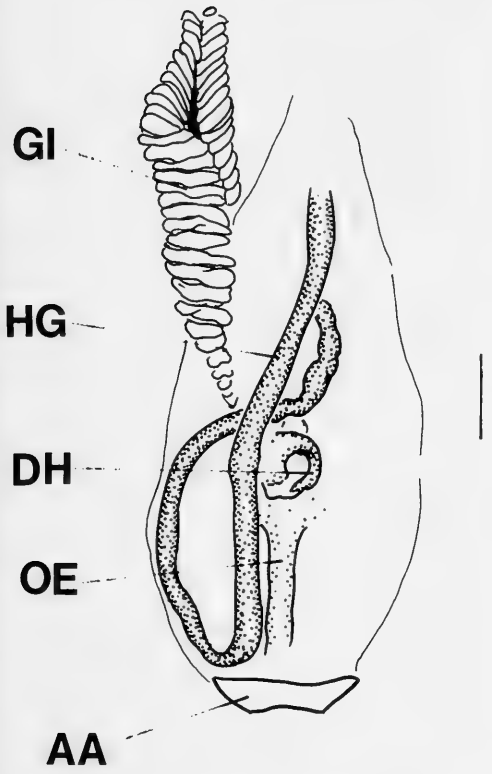

FIG. 7. *Nuculana grasslei*. Dorsal view of the internal morphology of a specimen to show the course taken by the hind gut and the disposition of the right gill (bar = 1.0 mm). AA, anterior adductor muscle; DH, dorsal hood; GI, gill; HG, hind gut.

vation has forced blood to various parts of the body, particularly the sinuses of the mantle margin and the gill and gill axis. These are swollen with congealed red-pigmented blood.

The kidney consists of paired brown-pigmented intercommunicating sacs, lying between the heart and the posterior adductor muscle. It is particularly well developed.

The nervous system follows the typical protobranch plan. The paired cerebral ganglia are slender and not well developed. Similarly, the visceral ganglia, although somewhat larger than the cerebral, are also small in comparison with other deep-sea nuculanids. From each visceral ganglion, there is a major nerve to the gill axis, to the siphon, and to the mantle edge (Fig. 5). The pedal ganglia are large and lie at the interface of foot and viscera, anterior and close to the ventral limit of the hindgut.

Paired gonads were seen in specimens >18 mm total length. The major portion of the gonad lies anterior to the heart and dorsal and posterior to the stomach. From there, it spreads thinly across the lateral surface of the digestive gland. The gonadial ducts traverse the lateral faces of the kidney to open in the supramantle cavity. No fully mature gonad was present in the specimens examined.

Shell Growth

Because of the wide difference in the size of the specimens examined, it was possible to obtain some information on the change in shape of the shell with increasing size.

The prodissoconch is oval and large (275–283 μm total length) equivalve and approximately equilateral (Fig. 3). The prodissoconch of the post-larva illustrated by Berg & Van Dover (1987), and by kind permission redrawn here for comparison with the prodissoconchs present on the adult shells, has a reticulated ornamentation that is presently without parallel in the Protobranchia and almost so in bivalves in general.

Post-prodissoconch shell growth immediately begins to take on adult proportions. The anterior growth is less than the posterior, and the disparity in the numbers of teeth on the hinge plates is immediately apparent, with two anterior and three posterior teeth present in the smallest post-larval shells (480 μm total length) in the collection. The teeth are on a broad and continuous hinge plate (Figs. 1, 2). The outline of the shell gradually changes with growth, and by the time the shell is 10 mm long the adult proportions are established (Figs. 2, 8). Thus, the percentage ratio of height over length to length over the first five millimeters of growth changes from 75% to 65%. At the same time, the shell becomes more rostrate, with the post-umbonal length increasing in relation to total length, while the shell becomes more slender. This change in shape with size is typical of all deep-sea protobranchs (Allen & Hannah, 1989).

With increasing size (age), the umbonal region of the shell becomes increasingly eroded. All specimens of more than 10 mm total length show erosion to some degree. In the case of the larger specimens (Fig. 9), an area equivalent to the outline of a 10-mm shell may be affected and to such an extent that all that remains is the thin innermost layer of shell. In this extreme condition, the umbo is completely lost, with the ligament and the remains of the hinge plate in which the hinge

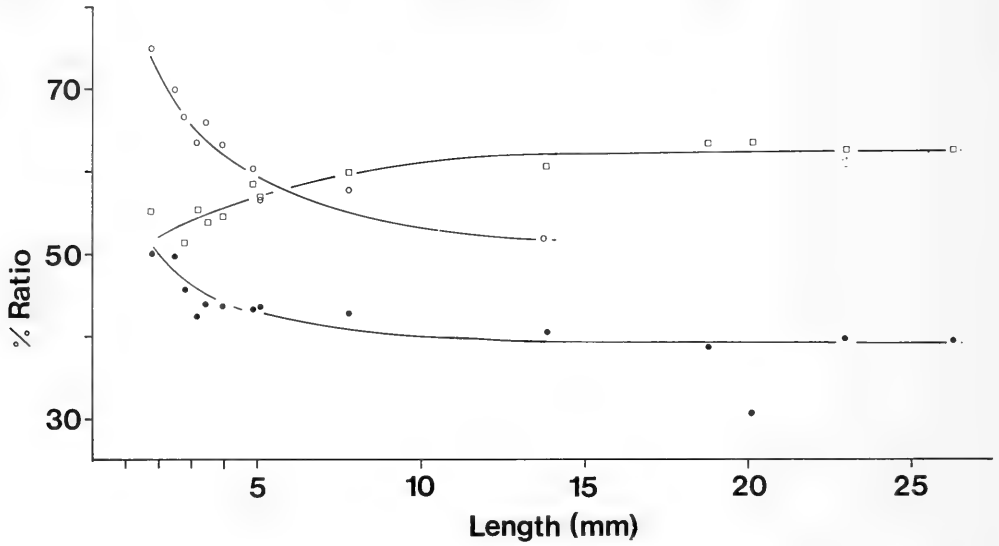

FIG. 8. *Nuculana gasslei.* Plot of the percentage ratios of height to length (open circles), width to length (closed circles) and post umbonal length to length (open squares) against length.

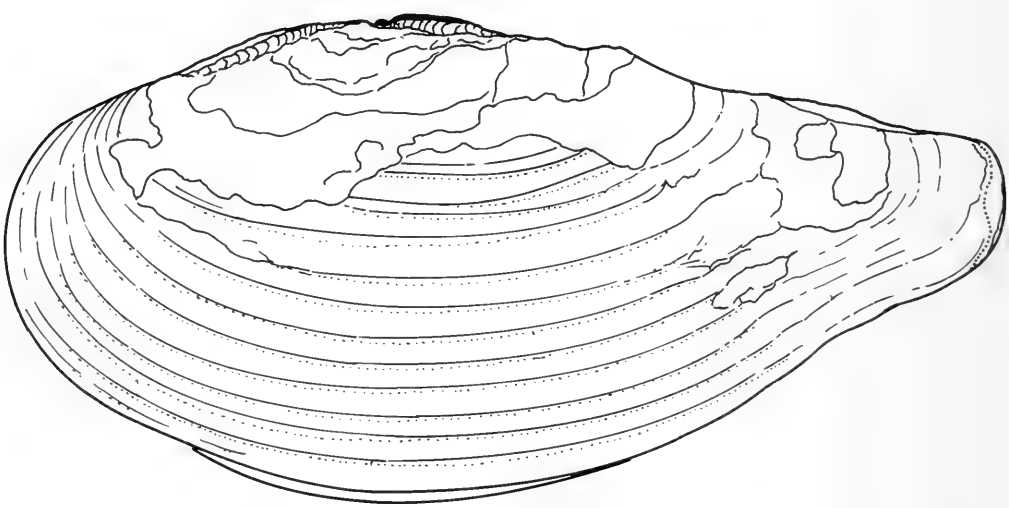

FIG. 9. *Nuculana grasslei.* Lateral view of a large shell from the left side to show the extent of corrosion (bar = 1.0 mm).

teeth are clearly visible, standing out as a crest to the shell (Fig. 9). In addition, the area over the insertion of the posterior adductor muscle also becomes eroded.

Comparisons have been made with known species, with particular attention being paid to those from off the Pacific coast of America and from deep water. The combined shell characters of *N. grasslei* are unlike those of any other described species (Abbott, 1974; Bernard, 1983; Dall, 1890, 1896, 1897, 1908, 1916; Dall & Bartsch, 1910; Hertlein & Strong,

1940; Moore, 1983; Oldroyd, 1935; Willett, 1944). The main points of recognition of *N. grasslei* include the shell outline, in which the postero-dorsal margin is angulate and the postero-ventral margin is sinuous, the large and anteriorly placed umbo, the slightly flattened antero-dorsal margin, and the form and spacing of the concentric ribs. Furthermore, no other description includes reference to an ornamented prodissoconch, though this does not preclude unnoted occurrence in other species. It must be said that the prodissoconch in *N. grasslei* is striking, and a similar presence in other species is unlikely to have been overlooked by earlier authorities.

Although large by deep-sea protobranch standards (few species obtain a length of more than 5 mm), *N. grasslei* is not large in comparison with other species of *Nuculana*. For example, *N. pernula* (Müller, 1779) from shallow Arctic seas is similar in size, as too is *N. taphria* Dall, 1897, from the shallow water of California and Baja California.

Discussion

The investigation reported here is limited to the gross morphological description of a new deep-sea hydrothermal species. Detailed microscopical examination was not made in the knowledge that Dr. Richard Gustafson of Rutgers University was studying various organs in detail.

For the most part, the functional morphology of *N. grasslei* differs little from that of other species of *Nuculana* from slope or shelf seas. There are no characters that differ so significantly to warrant separation at generic level. Nevertheless, there are a few unusual characters that relate to the habitat of the species and at least one that is unrelated to the habitat of the adult. The former include the thick periostracum and the large volume of pigmented blood; the latter refers to the ornamented prodissoconch.

The periostracum varies in thickness but measures up to 40 μm a figure that is twice that of *N. minuta* (Müller, 1776) of a similar size (pers. obs.). It is probable that the thickened nature of the periostracum relates to the sulphurous nature of the habitat. Muds smelling of hydrogen sulphide must be acidic and thus corrosive to the shell. The thickened periostracum clearly protects the shell up to a third of the life of the animal as measured by shell length, i.e. to the size when gonads are developing. Similarly, the large blood volume must also relate the the nature of the habitat. Hydrogen sulphide will affect oxygen levels of the overlying sea water as well as that within the sediment. A large oxygen carrying capacity of the blood would be expected on *a priori* grounds. It is known that protobranchs in particular can survive anoxic conditions for long periods of time (Doeller et al., 1988; pers. obs.). Thus, all things being equal, it would be expected that protobranchs could survive the conditions pertaining at seeps and vents with little modification. In fact, there is circumstantial evidence that protobranchs can survive reducing conditions in marine muds better than most bivalves, possibly with the exception of members of the Lucinacea. In recent laboratory experiments, three species of *Nucula* have survived anoxic conditions for more than three weeks (pers. obs.).

Although common to all species of *Nuculana,* the lack of the siphonal tentacle is perhaps of interest, as too is the relatively poorly developed nervous system. Again, it may be speculated that this may be preadaptive in that *N. grasslei* lives in sediments in which there is ample food material in the form of bacterial mats at the surface. In such a situation, specialized sensory assistance in food gathering is of minimal importance.

The ornamented prodissoconch is striking. On first reflection, little evolutionary advantage would seem to accrue from this reticulation. As in all bivalves it is protective, not in terms of predation, but in terms of the protection it affords against the dissolution of the shell at a weak and vulnerable point. When the prodissoconch is eventually lost from the surface of the growing adult shell, it exposed a small area of calcium carbonate to the umbo, a part of the shell that is relatively thin. In the case of *N. grasslei,* the prodissoconch remains in place for a relatively long period, protecting the shell against corrosion until the animal is beginning to mature. As soon as it is lost, corrosion occurs at the place where it had been. What function the reticulate ornamentation plays is much less certain. Reticulate ornamentation is characteristic of some protobranchs (e.g. *Nucula sulcata* Bronn, 1831) (Allen, 1954). Whereas in the adult ornamentation may assist in the maintenance of the position of the shell within the sediment (Stanley, 1970), it hardly seems likely in the case of the newly settled prodissoconch.

Unlike better known vent bivalves, *Calyptogena magnifica* Boss & Turner, 1980, and *Bathymodiolus thermophilus* Kenk & Wilson,

1985, *N. grasslei* is not exceptionally large. This may be related to its deposit rather than its suspension feeding habits, its digestive physiology, and to the apparent lack in the gill of symbiotic chemoautotrophic bacteria of the type present in *Calyptogena* and *Bathymodiolus,* although other types of bacteria are present (Gustafson, pers. comm.). These latter may bear relationship to the large volume of pigmented blood observed in the specimens examined. The pigment is almost certainly haemoglobin. This is known to be present in other vent bivalves and in some other nuculanid protobranchs (Wittenberg, 1985). It would appear that this is part of an efficient oxygen carrying system in relatively low oxygen pressures (Wittenberg, 1985).

The large size of the prodissoconch indicates a large heavily yolked egg, probably in the order of 200+ μm. (No adults with mature ova were present in the samples.) It is not unusual for vent invertebrates to have lecithotrophic larvae (Gage & Tyler, 1991). Although this does not appear to restrict the ability of vent species in general to colonize new vents as they occur, at present *Nuculana grasslei* is known only from the Guaymas Basin in the Gulf of California.

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LETTERS TO THE EDITOR

REPLY TO "SUPRASPECIFIC NAMES OF MOLLUSCS: A QUANTITATIVE REVIEW"

M. A. Edwards[1] & M. J. Thorne[2]

ABSTRACT

The article 'Supraspecific names of Molluscs; a quantitative review' by Phillipe Bouchet and Jean-Pierre Rocroi, contains some misapprehensions about the Zoological Record. This article seeks to correct them.

Key words: Literature coverage, Mollusca, Taxonomic names, Zoological Record

"Critics will certainly find it easy to discover deficiencies in the volume, but we may doubt whether they will realize the extent of the work involved in it." (Sharp, 1902)

This comment, made by the then editor of the *Zoological Record,* is, apparently, as true today as it was nearly a century ago.

The recent article by Bouchet & Rocroi (1992) discusses the numbers of supraspecific names in Mollusca, and takes the *Zoological Record* to task for what they estimate to be an omission rate of 20% in respect of those names, particularly in the period 1960–1989.

Those responsible for the *Zoological Record* are not averse to criticism, but the Mollusca must be considered in the context of the wide field of literature on all animal groups which the *Record* endeavours to search with the limited resources at its disposal. Although the annual growth in the number of new molluscan names may have remained reasonably stable, the growth in the literature most certainly has not.

Each annual volume of the *Zoological Record* covers the recent literature relating to nearly 50 different animal groups. To locate relevant work, over 6,500 serials are searched, as available, together with some 1,500 or more books and reports; from these, 65–70,000 individual items are indexed each year. In addition, names described in works published in earlier years are constantly coming to light. These are included in that volume of the *Record* being indexed at the time of discovery, which makes an omission rate impossible to define in the long term.

Reference is made to the imperfect coverage of some literature, in particular that from China, Japan and the former Soviet Union. While this is not disputed, it must be appreciated that access to this material is often difficult, and the linguistic skills required to index it are expensive to obtain. Nevertheless, details of additional publications are always welcome. (Of those titles mentioned in the article, the two primary publications are covered in the *Record,* but the Chinese secondary publication is not because abstracts are not normally indexed.)

Each section of the *Zoological Record* carries a request to authors to provide copies of recent publications for indexing purposes, and considerable efforts are made to obtain literature not previously covered.

It is inevitable, however, that workers in a particular field in touch with colleagues will have more complete listings than the *Record,* and no doubt more opportunities to visit libraries abroad, to "browse" through reprint collections, and to check bibliographic compilations which may span many years. To do this on the scale required for all animal groups indexed in the *Record* would be beyond the resources available.

Bouchet & Rocroi also say that the *Record*

[1]The Zoological Society of London, Regent's Park, London NW1 4RY, England.
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is "supposedly the most complete indexing system," "a nomenclator considered to be the most complete . . ." and go on to state that the "unexpectedly high omission rate . . . should cause concern to all taxonomists. Because this nomenclator is the main bibliographical source of many (palaeo) zoologists . . .". They then suggest that names should be registered before they can be declared nomenclaturally available.

The *Record* has never claimed to be complete, that would be impossible, but it is evidently still considered to be "the main bibliographical source" and no other more comprehensive work in the zoological field is known. As regards the registration of names, *Zoological Record* staff are working with the International Commission on Zoological Nomenclature to establish such a register, though of course for *Zoological Record* purposes names would still have to be indexed whether or not they were registered.

Compilation and production of the *Zoological Record* is an excessively expensive undertaking. Throughout its long history there have always been appeals for funds but little response from those who, while insisting on its continuation, are unwilling to provide sufficient financial support and rely on the publishers (The Zoological Society and now BIOSIS) to subsidize it.

If the article by Bouchet & Rocroi helps to highlight the difficulties faced by the *Zoological Record* and thereby increases interest in and support for this unique publication, it will have served a useful purpose. Otherwise the biological community should seriously consider what the effects might be should the *Record* cease publication.

LITERATURE CITED

BOUCHET, PHILIPPE & JEAN-PIERRE ROCROI, 1992, Supraspecific names for molluscs: a quantitative review. *Malacologia,* 34:75–86.

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PHYLOGENETIC ANALYSIS OF THE RAPANINAE (NEOGASTROPODA: MURICIDAE)

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ABSTRACT

The generic level revision and phylogenetic analysis of the gastropod subfamily Rapaninae Gray, 1853 (Prosobranchia: Neogastropoda: Muricidae), presented here is based primarily on gross anatomy (female and male reproductive systems, alimentary system, mantle cavity organs), radular, opercular, and protoconch morphology, and shell ultrastructure. Results reveal that Rapaninae includes most members previously allocated to the Thaidinae Jousseaume, 1888. The type species of most recognized rapanine genera were studied for character selection. Eighteen characters were determined for cladistic analyses, and results were compared with additional data derived from egg capsule morphology and biogeographic data.

The cladistic analyses show (1) that the former Thaididae/nae of authors is polyphyletic and should be divided into two (monophyletic) groups; (2) that family status is not justified for either of these groups; (3) that *Rapana* Schumacher, 1817, is monophyletic with Thaidinae, resulting in synonymization of Thaidinae Jousseaume, 1888, with Rapaninae Gray, 1853; and (4) that several genera belonging to the Rapaninae merely deserve subgeneric status.

The genera *Nucella* Röding, 1798, *Forreria* Jousseaume, 1880, *Trochia* Swainson, 1840, *Acanthina* Fischer von Waldheim, 1807, and *Haustrum* Perry, 1811, are placed in Ocenebrinae Cossmann, 1903 (*sensu* Kool, 1993); the genera *Cymia* Mörch, 1860, *Rapana* Schumacher, 1817, *Stramonita* Schumacher, 1817, *Concholepas* Lamarck, 1801, *Dicathais* Iredale, 1936, *Drupa* Röding, 1798, *Plicopurpura* Cossmann, 1903, *Pinaxia* H. & A. Adams, 1853, *Nassa* Röding, 1798, *Vexilla* Swainson, 1840, *Cronia* H. & A. Adams, 1853, *Morula* Schumacher, 1817, *Thais* Röding, 1798, *Purpura* Bruguière, 1789, and *Mancinella* Link, 1807, are placed in Rapaninae. The taxa *Vasula* Mörch, 1860, *Tribulus* Sowerby, 1839, and *Neorapana* Cooke, 1918, are allocated subgeneric status under *Thais*.

> "My Thais, thou hast seen these filthy snails crawling towards thee with their sticky sweat . . . Thais, Thais, Thais, . . . say if thou wilt go mad with them!"
>
> Anatole France, *Thais*

INTRODUCTION

Of all large littoral prosobranchs, none are more conspicuous and perplexing, in a taxonomic sense, than gastropods belonging to the Rapaninae ["Rapananina"] Gray, 1853, herein shown to include Thaidinae Jousseaume, 1888 (*sensu* Kool, 1989 [= Thaididae/nae of authors, *in partem*]). Rapaninae, *sensu* Kool (from this point onward referred to as Rapaninae), comprises many more genera than Rapaninae of authors. The Rapaninae is a group of predatory gastropods belonging to the family Muricidae Rafinesque, 1815, in the superfamily Muricoidea (*sensu* Ponder, 1973; see below). Most rapanines live in the rocky intertidal zone where wave energy can be very high, but members of the genus *Rapana* Schumacher, 1817, are subtidal. Rapanines prey on a variety of invertebrates (mollusks, polychaetes, crustaceans, cnidarians, etc.; see Kool, 1987), although some are known to eat invertebrate and vertebrate carrion; some species are specialists (for example, coral feeders), others generalists.

My initial assumption was that the Thaididae/nae of authors was a conglomerate of disparate taxa, and that para- and polyphyly would be rampant in this "waste-basket group." Although Rapaninae have been commonly used for ecological (Spight, 1982; J. D. Taylor, 1984), environmental (Bryan et al., 1986, 1987), genetic (Palmer, 1984, 1985), physiological (Carriker et al., 1978), and biochemical (Huang & Mir, 1972) research, little is known about the evolutionary relationships among the members of this group, and its status among other muricid groups.

Taxonomic History

Traditionally, the superfamily Muricoidea Rafinesque (*sensu* Thiele [as Muricacea]) has been divided into several different families (Table 1). Ponder (1973) advocated inclusion of several other neogastropod families in Muricoidea, so that Muricoidea, *sensu* Thiele, is almost equivalent to Muricidae, *sensu* Ponder. Unless noted otherwise, Muricidae will herein be equivalent to Muricoidea, *sensu* Thiele.

Members of the Muricidae have an often spiny shell, usually bearing a distinct, sometimes long, anterior siphonal canal. An anatomical feature shared by most Muricidae is the accessory boring organ, located in the foot, and used for chemically dissolving shell material. Naticids have an accessory boring organ as well, but this structure apparently has arisen independently in these distinct groups. Most Muricidae have a long radular ribbon with a row of tri- or pentacuspid rachidian (central) teeth, each of which is flanked by a lateral tooth. The tri- and pentacuspid rachidian morphology occurs also in other Neogastropoda (for example, Buccinidae).

The taxonomy and phylogeny of the Muricidae have been in a state of confusion for over two centuries. Taxonomic problems within the Muricidae as a whole impede our understanding of all groups within this taxon. For example, due to the vague boundaries of many higher muricid taxonomic groups, the limits of lower groups can not be set, and *vice versa.* Keen (1971a: 35) pointed out that "distinctions between subfamilies within the Muricidae are not always clear-cut, . . ." This taxonomic confusion results in a lack of understanding of the phylogeny of all muricid groups.

Familial and subfamilial arrangements of Muricidae differ greatly among authors. A selection of arrangements and authors is listed in Table 1. For example, Cossmann (1903) recognized five subfamilies within the Muricidae: Ocenebrinae [authors and dates of taxa given in Table 1], Muricinae, Trophoninae, Typhinae, and Rapaninae; he included the members of the Thaididae/nae of authors in the Purpuridae as a separate family. Thiele (1929) included two families, Muricidae and Magilidae, and did not list subfamilies. Wenz (1941) included the same two families, but subdivided the Muricidae into the subfamilies Muricinae, Rapaninae, Columbariinae, and Drupinae (Thaidinae of authors). Keen (1971a) recognized the families Muricidae, Columbariidae, Sarganidae, Coralliophilidae, Moreidae, and Thaididae; she subdivided the Thaididae into the subfamilies Thaidinae, Rapaninae, and Drupinae. Radwin & D'Attilio (1971) subdivided the Muricidae into the families Muricidae, Columbariidae, Rapanidae, Coralliophilidae, and Thaididae. Ponder (1973) reduced the number of superfamilies in the Neogastropoda and included the Buccinidae, together with 16 other families in the Muricoidea, and followed Cossmann's (1903) subdivision of the Muricidae. Harasewych (1983) showed that the Columbariinae do not belong within the Muricidae but instead in the Turbinellidae. Ponder & Warén (1988) include in Muricidae the subfamilies Muricinae, Thaidinae (with Rapaninae in synonymy), Coralliophilinae, Sarganinae, and Moreinae.

Of the subgroups of the Muricidae, the group formerly known as Thaidinae (or as Thaididae) Jousseaume, 1888 (original spelling "Thaisidae"), is probably the most problematic and in need of comprehensive revision. Some authors have ranked this group as a subfamily, but many have given it family rank (Table 2).

The family-subfamily controversy is a result of a poor understanding of genus-level relationships within the Rapaninae and of relationships between Rapaninae and the other muricid taxa. The generic allotment for the many rapanine species is highly suspect, as generic boundaries are usually ill-defined. Many muricid genera of uncertain status have been placed in Thaididae/nae of authors, resulting in a conglomerate of disparate taxa. Therefore, Thaididae/nae of authors, as well as other higher level muricid taxa, are probably para- and/or polyphyletic.

Taxonomic controversy in Rapaninae has existed from the time when rapanine genera were given their own group-name and ranking. Menke (1828) considered the group as a superfamily and used the name Purpuracea. Swainson (1835, 1840) referred to this group as Purpurinae. Broderip (1839) ranked this group as a family (Purpuridae). The family-level designation has been used most frequently since then. Other synonyms of Thaididae/nae of authors (and thus *in partem* of Rapaninae, as defined herein) are Concholepadidae Perrier, 1897, Purpuradae Leach, 1852, Thaisidae Jousseaume, 1888, Thaidae Cooke, 1919, Drupinae Wenz, 1941, Thaisidinae Kuroda & Habe, 1971, Thaidiidae Atap-

attu, 1972, and Nucellinae Kozloff, 1987 (see also Ponder & Warén, 1988).

The oldest rapanine generic name still in use is *Purpura,* introduced by Martini (1777). Due to the controversial history of *Purpura* (see treatment of this genus), Keen (1964) proposed that the names "Purpurinae," "Purpuridae" and "Purpuracea" be placed on the Official Index of Rejected and Invalid Family-Group Names in Zoology and to place Thaididae Suter, 1913 [originally as "Thaisidae"], on the Official List of Family-Group Names in Zoology. The Commission acted on this petition (ICZN, Opinion 886, 1969) and placed Purpuracea Menke, 1828, and Purpurinae Swainson, 1840 [*sic*], on the Official Index of Rejected and Invalid Family-Group Names in Zoology. Furthermore, the Committee ruled that Purpuridae Broderip, 1839, and Thaididae Suter, 1913, be placed on the Official List of Family-Group Names in Zoology, and that Purpuridae not have priority over Thaididae. From this point on, the stem "Thaid-" has been used most frequently for rapanine gastropods (Table 2). As Cernohorsky (1980) pointed out, "Thaididae Jousseaume, 1888" (originally as "Thaisidae"), predates Thaididae Suter. Lehtinen (1985) petitioned to adopt the original spelling "Thaisidae" to avoid homonymy with the spider family Thaididae Lehtinen, 1967 (based on the genus *Thaida*), but later withdrew his petition.

Convergent Shell Morphology: Roots of Taxonomic Discord

The main reason for the plethora of taxonomic arrangements for muricid groups is a poor understanding of muricid phylogeny. The characters on which all past taxonomic schemes were based are distilled primarily from external shell morphology. These features are readily visible but are misleading in that they may have resulted from convergent and/or parallel evolution.

Many authors have pointed out that shell morphology within a species is effected by environmental influences. For example, environmental factors often dictate a particular shell shape and/or shell color. Examples of ecophenotypic variation are given in a number of papers on muricids (primarily the genus *Nucella* Röding) (Agersborg, 1929; Vermeij, 1975, 1979, 1982; Palmer, 1979; Vermeij & Currey, 1980; Etter, 1987; Day, 1990) and on other gastropod groups as well (S. J. Gould, 1971; Cain, 1981). If environmental influences are strong enough to cause high selection pressures at the population level, selective forces may also have caused convergence in shell shape among species. Shell convergence among species may thus be high, and any taxonomic scenario for the Muricidae (or other gastropod group) based exclusively or primarily on shell morphology is therefore highly suspect.

Evidence for the phenomenon of environmentally induced shell shape is given for the species *Nucella lapillus.* Cooke (1895, 1919) pointed put that stunted, short-spired specimens of *Nucella lapillus* occurred in very exposed areas, whereas those living in sheltered areas had high-spired shells with a relatively small aperture. Crothers' (1973, 1974) studies on ecophenotypic variation of *Nucella lapillus* reported similar results to those of Cooke. Kitching et al. (1966) were able to demonstrate experimentally that morphs of *Nucella* with wide apertures had greater adhesive power to cling to intertidal rocks than did the morphs with narrower apertures, thus providing an adaptationist explanation for variation in shell shape. Other characters derived from shell morphology correlating with environment are color patterns and sculpture (Agersborg, 1929; Etter, 1987).

Besides wave action, other environmental influences reportedly play a role in determining aspects of shell morphology. Balaparameswara Rao & Bhavarayana (1976) were able to correlate shell morphology statistically in *Drupa tuberculata* with temperature and desiccation at different intertidal levels. Moore (1936) suggested that the great intraspecific variation in shell shape in *Nucella* was due to differential feeding. Bandel (1984) showed that juveniles of *Stramonita haemastoma floridana* would "change" into typical *Stramonita haemastoma* in the laboratory when food levels were kept artificially high. Hallam (1965) stated that a combination of such factors as food availability, salinity, oxygen concentration, temperature, turbidity and agitation, and population density, may induce stunting in mollusks and other invertebrates. Wilbur & Owen (1964), in discussing allometric growth in mollusks, pointed out that growth rates for different bodily parts may not be equal; thus shell shape may depend on a snail's age. They also showed that this allometry may also partly be due to a combination of several environmental factors.

Many authors have noted population differences in shell shape in different muricidae

TABLE 1. Important supraspecific taxonomic arrangements for muricids.

Authors	Taxonomic Names
Fischer, 1887	PECTINIBRANCHIATA MURICIDAE Rafinesque, 1815 CORALLIOPHILIDAE Chenu, 1859
Cossmann, 1903	RHACHIGLOSSA MURICIDAE Rafinesque, 1815 MURICINAE Rafinesque, 1815 OCENEBRINAE Cossmann, 1903 TROPHONINAE Cossmann, 1903 (incl. *Forreria*) TYPHINAE Cossmann, 1903 RAPANINAE Gray, 1853 PURPURIDAE Broderip, 1839 (incl. thaidines *s.l.*) CORALLIOPHILIDAE Chenu, 1859
Thiele, 1929	MURICACEA Rafinesque, 1815 MURICIDAE Rafinesque, 1815 MAGILIDAE Thiele, 1925
Wenz, 1941	MURICACEA Rafinesque, 1815 MURICIDAE Rafinesque, 1815 RAPANINAE Gray, 1853 (incl. *Forreria*) COLUMBARIINAE Tomlin, 1928 MURICINAE Rafinesque, 1815 DRUPINAE Wenz, 1941 (incl. thaidines *s.l.*) MAGILIDAE Thiele, 1925 (incl. *Coralliophila*)
Radwin & D'Attilio, 1971	MURICACEA Rafinesque, 1815 COLUMBARIIDAE Tomlin, 1928 RAPANIDAE Gray, 1853 CORALLIOPHILIDAE Chenu, 1859 THAIDIDAE Jousseaume, 1888 MURICIDAE Rafinesque, 1815 (7 subfamilies)
Keen, 1971a	MURICACEA Rafinesque, 1815 MURICIDAE Rafinesque, 1815 (5 subfamilies) COLUMBARIIDAE Tomlin, 1928 CORALLIOPHILIDAE Chenu, 1859 MOREIDAE Stephenson, 1941 SARGANIDAE Stephenson, 1923 THAIDIDAE Jousseaume, 1888 THAIDINAE Jousseaume, 1888 DRUPINAE Wenz, 1941 RAPANINAE Gray, 1853
Ponder, 1973	MURICACEA Rafinesque, 1815 MURICIDAE Rafinesque, 1815 (not specific about subfamilial divisions) BUCCINIDAE Rafinesque, 1815 (and all other rachiglossate families usually attributed superfamilial status by other authors).
Golikov & Starobogatov, 1975	MURICOIDEA Rafinesque, 1815 MURICIDAE Rafinesque, 1815 VASIDAE H. & A. Adams, 1853 CORALLIOPHILIDAE Chenu, 1859 THAIDIDAE Jousseaume, 1888

(*continued*)

TABLE 1. (*Continued*)

Ponder & Warén, 1988	MURICOIDEA Rafinesque, 1815 MURICIDAE Rafinesque, 1815 MURICINAE Rafinesque, 1815 (incl. Trophoninae, Ocenebrinae, etc.) THAIDINAE Jousseaume, 1888 (incl. Rapaninae) CORALLIOPHILINAE Chenu, 1859 MOREINAE Stephenson, 1941 ?SARGANINAE Stephenson, 1923

TABLE 2. Ranking of thaidine higher taxa since Thaididae, Jousseaume, 1888, by a selection of authors.

Family Rank
Thaididae: Hedley, 1918; Iredale, 1937; Clench, 1947; Korobkov, 1955; Pchelintsev & Korobkov, 1960; Keen, 1964, 1971a, b; Strausz, 1966; Jung, 1969; Radwin & D'Attilio, 1971, 1972; Vokes, 1972; Golikov & Starobogatov, 1975; Petuch, 1982; Harasewych, 1984; Kensley, 1985; Kensley & Pether, 1986.
Thaisidae: Suter, 1909; Stewart, 1927; Iredale & McMichael, 1962; Powell, 1961; Miller, 1970.
Thaidiidae: Atapattu, 1972.
Thaidae: Cooke, 1919.
Purpuridae: Cossmann, 1903; Lamy, 1928; Coomans, 1962; Settepassi, 1971; Abbott, 1974.
Concholepadidae: Perrier, 1897.
Subfamily Rank
Thaidinae: Cernohorsky, 1969; Beu, 1970; Emerson & Cernohorsky, 1973; Rosewater, 1975; Rehder, 1980; Emerson & D'Attilio, 1981; Fujioka, 1985a.
Thaisidinae: Kuroda & Habe, 1971.
Drupinae: Wenz, 1941; Hertlein, 1960.
Purpurinae: Baker, 1895.
No Separate Rank
Muricidae: Thiele, 1929; Demond, 1957; Barnard, 1959; Arakawa, 1962, 1964, 1965; D. W. Taylor & Sohl, 1962; Habe, 1964; Wu, 1965a, 1968, 1973, 1985; Habe & Kosuge, 1966; Maes, 1966, 1967; Powell, 1979.

but have not investigated causes for this phenomenon (Colton, 1916, 1922; Kincaid, 1957; Berry & Crothers, 1968, 1970; Cowell & Crothers, 1970; Hoxmark, 1970, 1971; Largen, 1971; Crothers, 1973; Spight, 1973).

If environment causes high intraspecific variation in shell morphology among muricids (and gastropods generally), it is not surprising that convergence in shell shape is a frequently recognized phenomenon (Ponder, 1973; Davis, 1979; Signor, 1982; Harasewych, 1984; Vermeij & Zipser, 1986). Similar shell shapes may have evolved in response to similar environmental pressures. Thus, convergence in shell shape is probably the major underlying cause of existing taxonomic controversies within the Thaididae/nae of authors and other muricid groups.

Of course, shell morphology can be deceiving in another way as well: major differences in external shell morphology may obscure a possibly close phylogenetic relationship, which may—as does convergence—result in paraphyletic and/or polyphyletic groups.

Radular morphology is the second-most utilized criterion on which to base taxonomic groups within Thaididae/nae, although radular characters are almost always used in conjunction with shell characters (Cooke, 1919; Thiele, 1929; Clench, 1947; Arakawa, 1962, 1964; Wu, 1968, 1985; Radwin & D'Attilio, 1971, 1972, 1976; Emerson & Cernohorsky, 1973; Bandel, 1984; Harasewych, 1984; Fujioka, 1985a). Troschel (1866–1893) used radular characters as the sole basis for his classification.

Although radular characters in Thaididae/nae of authors and other molluscan groups have been applied cautiously, no studies correlating radular morphology and diet existed until recently (Kool, 1986, 1987) to indicate whether this caution is justified. Radular characters have often been regarded as, at most, moderately indicative of relationship, in par-

ticular, when radular characters do not show congruence with shell shape. In this case, adaptationist explanations usually have been invoked in which radular morphology is postulated to have evolved as a direct response to dietary habits (Arakawa, 1964 [Rapaninae, *sensu* Kool]; Wu, 1965a [Rapaninae, *sensu* Kool]; Powell, 1964 [Turridae]; see also Kool, 1987). Several authors (Arakawa, 1962; Radwin & D'Attilio, 1972; Wu, 1973; Fujioka, 1985a) have mentioned intrageneric differences in rapanine radulae. However, the generic determinations and boundaries used by these authors were based on shell morphology, and may therefore have been invalid. A detailed investigation by Kool (1987) showed that radular morphology in Thaididae/nae of authors does not reflect diet, but is indicative of relationships as determined by anatomy [i.e. "soft" anatomy (not including radula)].

However, some degree of caution is necessary. Sexual dimorphism in radulae has been reported for several genera in Rapaninae: *Nassa* (Maes, 1966), *Drupella* Thiele, 1925 (Arakawa, 1957; Fujioka, 1982), *Morula* (Fujioka, 1984), and *Cronia* (Fujioka, 1984). Furthermore, Fujioka (1985a) and DiSalvo (1988) observed ontogenetic changes in the radulae of several rapanine species, and Fujioka (1985b) also found seasonal aberrant radular formation to occur in two species of rapanines. Anatomical [not including radula] data are probably the most reliable morphological data in reflecting phylogenetic relationships. Molluscan anatomists, such as Ponder (1973), Houbrick (1978), and Davis (1979), have demonstrated the importance of anatomical characters as opposed to characters derived from external shell morphology in establishing phylogenetic relationships. It is now generally agreed that a reliable phylogenetic explanation for any molluscan group must be based on a robust set of anatomical data.

In contrast to the vast amount of descriptive data on shell morphology, and the information available on radular morphology, very little is known about the anatomy of representatives of the Rapaninae and other muricid groups. Most anatomical studies are either superficial or focus on specific aspects of anatomy, such as the alimentary system (Righi, 1964; Wu, 1965a; Rajalakshmi Bhanu et al., 1980, 1981a, b; Carriker, 1981; Shyamasundari et al., 1985), and the reproductive system (Houston, 1976; Gallardo & Garrido, 1989; Srilakshmi, 1991). Haller (1888) presented an exceptionally detailed anatomical study of *Concholepas concholepas* (Bruguière, 1789), and anatomical information is also available on *Nucella* (Fretter, 1941; A. Graham, 1941, 1949; Fretter & Graham, 1962; Harasewych, 1984; Houston, 1976) and *Acanthina* (Wu, 1985). Several anatomical reports exist on a variety of other muricid taxa, e.g. *Urosalpinx* Stimpson, 1865 (Carriker, 1943, 1955; Carriker et al., 1972), *Trophon* Montfort, 1810 (Harasewych, 1984; E. H. Smith, 1967), and *Rapana* (Chukhchin, 1970).

Recently, the topic of "imposex" (the occurrence of male characters in female snails, in particular a penis) in especially Muricidae has received much attention (Féral, 1976; Hall & Feng, 1976; Bryan et al., 1986, 1987; Gibbs & Bryan, 1986; Gibbs et al., 1987; Bright & Ellis, 1990). The occurrence of imposex is highly correlated with environmental pollution by the chemical tributyltin.

Another non-conchological feature that may be of use in unraveling evolutionary relationships among rapanines is egg capsule morphology. Aspects of egg capsule morphology of muricids have been treated by a variety of authors (Lebour, 1936, 1945; Amio, 1957; Ganaros, 1958; D'Asaro, 1966, 1970a, b, 1986; Gohar & Eisaway, 1967; Bandel, 1976; Tirmizi & Zehra, 1983). The most comprehensive work on muricid egg capsules to date is by D'Asaro (1991), who provided detailed descriptions for the egg capsule morphology of a wide variety of muricids.

Hypothesis and Objectives

The working hypothesis of this study is that a classification resulting from cladistic analyses of a data set of primarily anatomical characters will differ from all previous classifications and will be far more reliable than those based primarily on shell shape. The new classification will reveal which names and taxonomic levels should be applied to one or more monophyletic groups.

This first comprehensive comparative anatomical study will establish a testable inference of phylogeny and a classification not only for those taxa traditionally included in Thaididae/nae of authors, but also for other muricid groups. Furthermore, this study will provide a framework onto which other taxa can be added more easily, after limits of different taxa are set by identification of synapomorphies.

MATERIALS AND METHODS

Compilation of Morphological Data

Eighteen type species (herein referred to as: *Concholepas concholepas* (Bruguière, 1789), *Cronia amygdala* (Kiener, 1835), *Cymia tecta* (Wood, 1828), *Dicathais orbita* (Gmelin, 1791), *Drupa morum* Röding, 1798, *Haustrum haustorium* (Gmelin, 1791), *Mancinella alouina* (Röding, 1798), *Morula uva* (Röding, 1798), *Nassa serta* (Bruguière, 1789), *Neorapana muricata* (Broderip, 1832), *Nucella lapillus* (Linnaeus, 1758), *Pinaxia versicolor* (Gray, 1839), *Purpura persica* (Linnaeus, 1758), *Stramonita haemastoma* (Linnaeus, 1767), *Thais nodosa* (Linnaeus, 1758), *Tribulus planospira* (Lamarck, 1822), *Vasula melones* (Duclos, 1832), and *Vexilla vexilla* (Gmelin, 1791)], and one "non-type species," *Plicopurpura patula* (Linnaeus, 1758), representing 19 genera usually placed in Thaididae/nae of authors, were studied in detail (Appendix 1). Two additional type species, also usually placed in Thaididae/nae of authors, *Acanthina monodon* (Pallas, 1774) and *Trochia cingulata* (Linnaeus, 1771), were examined on a relatively low number of characters. Furthermore, one taxon belonging to Rapaninae of authors, *Rapana rapiformis* (Born, 1778), one taxon belonging to Muricinae, *Muricanthus fulvescens* (Sowerby, 1841), and one taxon *incertae sedis, Forreria belcheri* (Hinds, 1844), were examined in detail. A fossil taxon *incertae sedis, Ecphora* cf. *quadricostata* (Say, 1824) was examined also. Twenty-four of the above-mentioned taxa (excluding *Ecphora*) were subjected to cladistic analyses performed with Hennig86 (Farris, copyright 1988).

The database used to address questions of muricid phylogeny consisted primarily of anatomical data, but also included data from protoconch, operculum, radula, and shell ultrastructure. Anatomical variation within and among species was determined by dissection of a variety of specimens. Most voucher specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; others are at the Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A, or at the Museum of Comparative Zoology, Harvard University.

Field work was done at many geographical locations throughout the Pacific and western Atlantic oceans, and in numerous habitats (rocky intertidal, mangrove forest, etc.), allowing a variety of ecological and behavioral observations (spawning, feeding, etc.). When possible, egg capsules of rapanine species were collected during spawning.

Both living and preserved specimens were used in this study. Living animals were maintained in tanks of running sea water and observed periodically before being sacrificed. Prior to dissection, animals were de-shelled using a vice and observed under a dissecting microscope. In some cases, a 7.5% isotonic solution of magnesium chloride was used to relax the animals. Snails were dissected while alive to observe color patterns, gross anatomy, and variability within an individual in structures such as the penial flagellum. Dissected animals were fixed in 10% formalin and preserved in 70–75% ethyl alcohol for further study. Preserved museum material was frequently in poor condition due to incomplete penetration of preservative, and provided limited information.

Some morphological data were obtained from histological sections and study of critical-point dried specimens using the Hitachi S-570 and Cambridge Stereoscan (100 and 250 MK II) scanning electron microscopes at the U.S. National Museum of Natural History. Pallial gonoducts were embedded in paraffin and sectioned at 7, 10, or 15 micrometers, depending on the size of the animal and the degree of detail desired. They were normally stained using triple PAS stain, although other stains (Masson's and Cason's) were occasionally used.

Morphological analyses resulted in a data matrix consisting of 18 characters and 64 character states. These characters were derived from the protoconch, shell ultrastructure, operculum, mantle cavity complex (ctenidium, osphradium), female and male reproductive and alimentary systems, and radula, and were used in cladistic analyses.

Because shell morphology is known to be under the influence of environmental selection pressures, the only shell characters used in cladistic analyses are those taken from larval shells and shell ultrastructure (see below).

Description of Characters

A variety of philosophies advocate different ways of choosing and justifying characters for reconstructing phylogeny. For example, some authors argue that characters displaying parallelism and convergence should not be used in phylogenetic analyses. However, parallel-

isms and convergences are only recognizable after analyzing the branching patterns of phylogenetic trees. Once a convergence between two synapomorphic states is recognized, the character in question should not be automatically discarded, because this results in loss of information and may in addition, lead to a reduction in resolution within or among branches of the tree. A case of homoplasy should be re-evaluated and re-divided into character states (perhaps with the tree topology based on other characters as a guide). Parallelisms and convergences, after all, provide valuable information about the manner in which different organisms adapt to possibly similar circumstances, and they indicate areas requiring more detailed study. Furthermore, those character states of a (partially homoplasious) character that are not homoplasious and occur only once in a branching sequence are additional synapomorphies and add to the resolution of the cladogram.

Convergence in external shell morphology is known to exist. Judging from the variety of taxonomic arrangements based on shell morphology and the results from the cladistic analyses presented herein, characters taken from the external morphology of the teleoconch have been very misleading in assessing relationship (Kool, 1988b). For these reasons, I have not included characters from external shell morphology in the cladistic analyses presented here. However, with the obtained branching pattern as a frame work, "good" (i.e. reflecting relationship) characters from the external shell morphology can be identified and could be added in future analyses.

Most of the characters used in the phylogenetic analysis are anatomical characters (reproductive system, alimentary system [excluding radula], mantle cavity, etc). The other characters were taken from shell ultrastructure, protoconch, operculum, and radula.

To avoid duplication of figures (often only differing in only minor details [e.g. length of accessory salivary glands]), general lay-outs of different morphological systems with their individual structures and organs are illustrated in Figures 3 (whole animals, reproductive systems, alimentary system, mantle cavity organs), 4 (female reproductive system), 5 (male reproductive system), and 6 (rachidian tooth).

I made no *a priori* assumptions about the validity of characters in reconstructing phylogeny and used all characters analyzed. For example, a variety of authors has expressed suspicion about the phylogenetic significance of radular morphology in a variety of groups (Kool, 1987). Diet is often suspected to be the driving force behind the evolution of radular characters. Although this may be true for some groups, the matter has never been thoroughly investigated. I have shown elsewhere (Kool, 1987) that there is very little correlation between radular morphology and dietary habits in rapanine gastropods, but that high correlation is present between relationship (based on anatomy) and radular morphology. The results of this study (Kool, 1987) show that inclusion of radular characters is indeed justified for reconstructing phylogeny and that characters, which were often assumed *a priori* to be under the influence of environmental factors and thus non-reflective of relationship, need testing against an independent data set (reflecting phylogeny) prior to unqualified prejudice against that particular suite of characters.

The list of characters follows the sequence in which these characters are described in each species.

Protoconch: Most of the protoconchs (and, where possible, the embryonic shell) were described from scanning electron micrographs, but a few descriptions were based on published drawings. Whorls, seen in apical view, were counted from the end of protoconch II spiraling inward. In some cases, the exact number of whorls could not be given due to poor preservation of the protoconch. Most data were derived from SEM micrographs of a single specimen, but other data from light microscopy were frequently added.

Characters:

1. Number of whorls and sculpture
   (a) multispiral (more than two and a quarter whorls); sculptured (e.g. Figs. 10D, 19C)
   (b) paucispiral (fewer than two whorls); smooth (e.g. Figs. 15C, 28C)
   (c) multispiral; smooth (e.g. Fig. 9C)
   (d) paucispiral; sculptured (e.g. Fig. 23D)
2. Transition into teleoconch
   (a) outward-flaring lip (e.g. Fig. 10D, E)
   (b) smooth transition (e.g. Fig. 26B, C)

Shell Morphology: Shell measurements (height and width) were taken from large adult specimens in the USNM collection and do not

represent maximum sizes. Height was measured from the apex (tip of earliest whorl) to the most distal point of the anterior siphonal canal, or apertural lip, whichever yielded the highest number; aperture height includes the apertural lip. Shell width is defined here as the distance between the apertural lip (or close to it to avoid inclusion of spines or knobs) and the other side of the body whorl (not including spines or knobs). Percentage measurements of the body whorl and aperture are relative to total shell height, and percentage is rounded off to a whole number and a multiple of five. A consistently present incision in the posteriormost portion of the apertural lip was considered as a posterior siphonal canal. A large number of museum lots was examined for color descriptions.

Shell ultrastructural data were obtained using scanning electron microscopy. Shell fragments of at least two specimens (depending on ambiguity or difficulty of interpretation of data) provided data on the kinds and combinations of shell layers. Fragments were cut out from the central region of the apertural lip with a diamond saw at some distance (about one-half of a whorl away) from the apertural lip edge, and broken collabrally. The fracture surfaces were observed and the different layers identified. In some cases, the fracture surface was polished; this process facilitates recognition of the different layers.

In the descriptions of the ultrastructure of the shells, the layers are listed in consecutive order beginning with the innermost layer (adjacent to the animal). All layers described for any of the taxa treated herein are present in, for example, *Purpura;* Figure 18F can be used for general reference. An approximate range for the thickness of each layer is given relative to all shell layers combined.

Characters:

3. Calcitic outer layer
   (a) absent (e.g. Figs. 13F, 24D)
   (b) present, thick > 25% of total (e.g. Figs. 15G, 26F)
   (c) present, thin < 20% of total (e.g. Figs. 8G, 25D, 18F, e)
4. 45° innermost aragonitic layer
   (a) absent (e.g. Fig. 25D)
   (b) present (e.g. Figs. 14E, 11G, H, 18F, a)

Operculum: In the descriptions of the opercular morphology, terms such as "bracket-shaped" and "arch-shaped" are used to describe the shape of growth lines on both the outside surface, referred to as "free surface" and the inside surface, referred to as "attached surface." In older specimens, the bracket-shaped growth lines often lose their horizontal portions, resulting in growth lines running straight from top to bottom. The terms "left side" and "right side" (on either surface) are used in reference to an operculum with its apex situated upward (the apex actually being the posteriormost end of the operculum). The vertical position of the nucleus varies among taxa; the description "in center right" denotes a nucleus located midway on an imaginary line running from the apex to the lower end of the operculum. The size of the operculum corresponds closely to the size of the shell aperture (given in shell description), unless noted otherwise. No notation of color and color patterns was made; color often reflects the age and thickness of the operculum and varies among individuals of the same species.

Character:

5. Morphology of operculum (shape, position of nucleus)
   (a) operculum ovate; terminal nucleus in lower right (Fig. 1A)
   (b) operculum D-shaped, upper end rounded; lateral nucleus in lower right (Fig. 1D)
   (c) operculum D-shaped, tapered at lower end, and with S-shaped left (adjacent to columella) edge; lateral nucleus in lower right (Fig. 1F)
   (d) operculum inverted tear-shaped; lateral nucleus in lower right (Fig. 1B)
   (e) operculum D-shaped; lateral nucleus in center right (Fig. 1C)
   (f) operculum ovate-elongate, tapered at lower end; lateral nucleus in upper right (Fig. 1E)

Foot and Mantle Cavity: The anatomical descriptions are given as follows. In a first paragraph, most of the external characteristics are listed (coloration and morphology of tentacles [e.g. Fig. 3B, t], head-foot region, kidney [e.g. Fig. 3B, C, k], hypobranchial gland [e.g. Fig. 3B, C, hg], nephridial gland [anteriorly of the kidney; usually visible on left side of live animals]), followed by data on accessory boring organ and (for females) ventral pedal gland (e.g. Fig. 4A, B, abo, pg).

The second and third paragraphs treat the osphradial and ctenidial morphologies (e.g. Fig. 3D, os, ct). The length of the osphradium

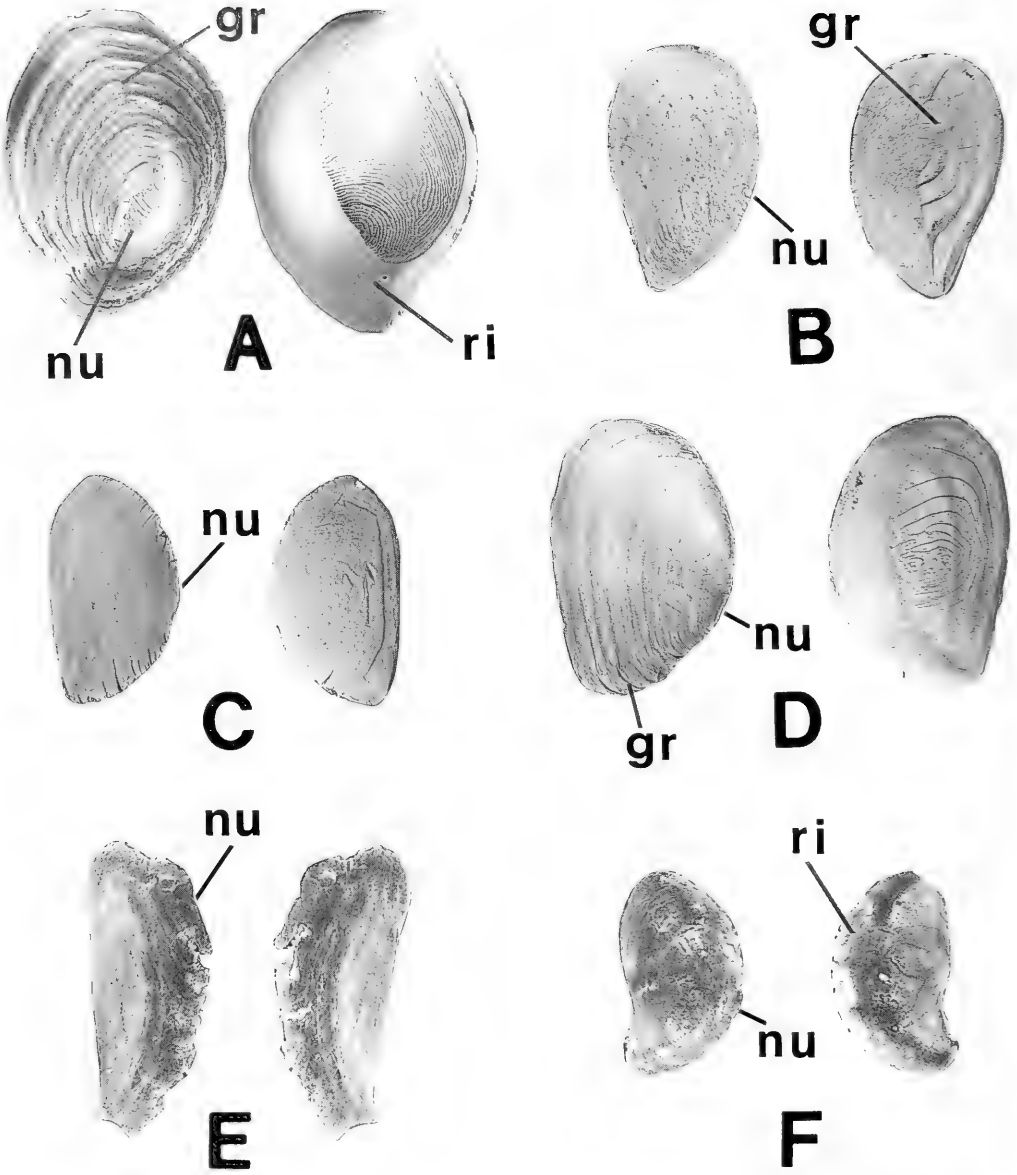


FIG. 1. Morphologies of muricid opercula, showing free surface (facing to the outside) and attached surface (facing inside), respectively. A, *Muricanthus fulvescens.* B, *Rapana rapiformis.* C, *Thais nodosa.* D, *Forreria belcheri.* E, *Vexilla vexillum.* F, *Cronia amygdala;* gr, growth lines; nu, nucleus; ri, rim of callus.

is measured from the posteriormost end (Fig. 3D, pos) to the anteriormost tip (Fig. 3D, ant) along the central axis separating both pectins. Similarly, the length of the ctenidium (gill) is measured along the ctenidial efferent blood vessel (Fig. 3D, cv). Absolute measurements are not given; only relative size (osphradium vs. ctenidium). The term "symmetrical in shape" is used rather than "symmetrical" because although there often is symmetry along the longitudinal (central) axis in the overall shape of both pectins, in none of the taxa examined was the number of osphradial lamellae equal between the left and the right

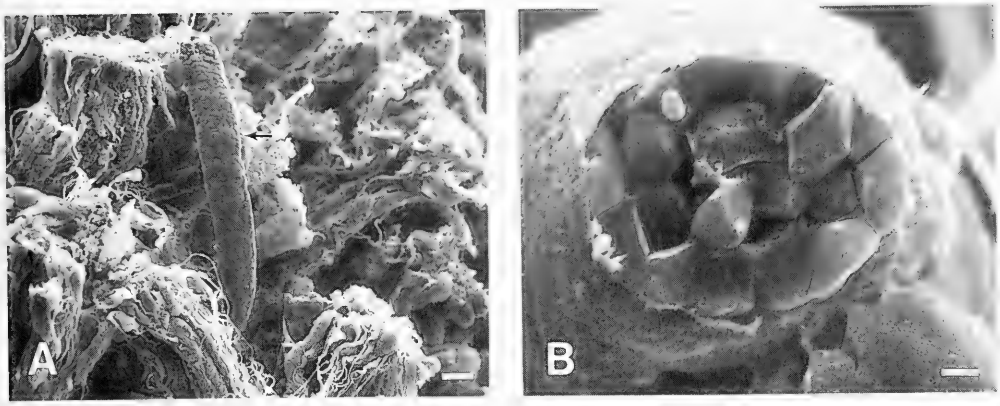


FIG. 2. Rod structures located in hypobranchial gland of *Morula nodulosa*. A, surface of hypobranchial gland with rod structure in center (arrow), SEM (bar = 20 μm). B, cross section through rod structure, SEM (bar = 2 μm).

pectin; the right pectin (directly adjacent to the ctenidium) consistently bears (about 25%) more lamellae than the left one. The general shape of the ctenidium (usually elongate half-moon-shaped [Fig. 3D, ct], or D-shaped) and osphradium (usually ovate-elongate) with left (Fig. 3D, los) and right pectins, is variable at least within some taxa, as is the morphology and number of individual lamellae of both organs. The edge of the ctenidial lamella adjacent and parallel to the support rod is referred to as the ventral edge (Fig. 3D, lr); the other free edge as the lateral edge (Fig. 3D, le). The size of the ctenidial lamellae is described as a relation between width and depth (the latter term was chosen over "height" because the lamellae *in situ* hang down).

Characters:

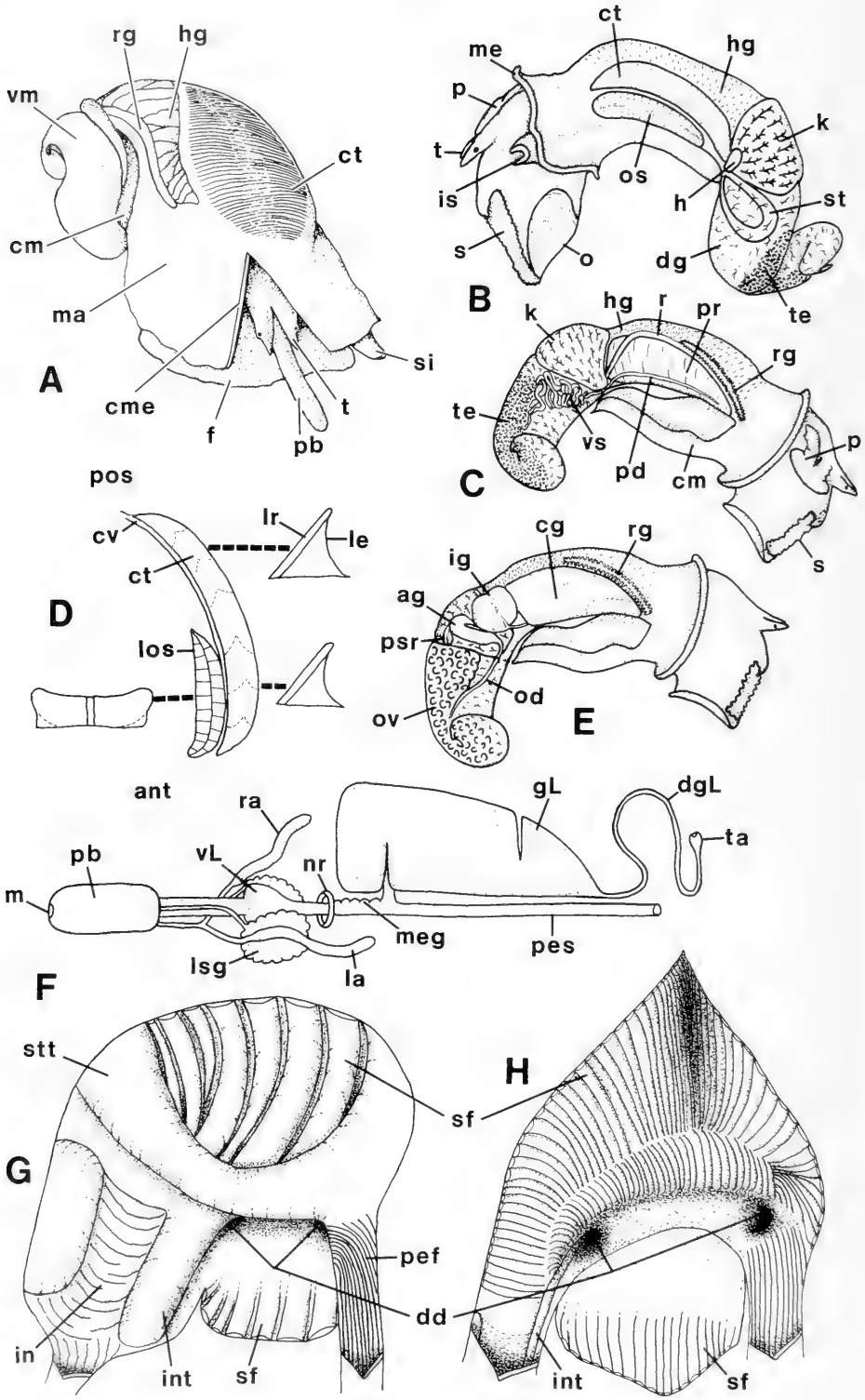
6. Rodlike structures in hypobranchial gland
   (a) absent
   (b) present (Fig. 2A, B)
7. Ventral pedal gland and accessory boring organ
   (a) sharing one duct (e.g. Fig. 4B)
   (b) having separate ducts (e.g. Fig. 4A)
   (c) accessory boring organ absent
8. Osphradial length relative to ctenidial length
   (a) osphradial length less than one-half ctenidial length
   (b) osphradial length at least one-half ctenidial length

Female Reproductive System: The reproductive organs of the female pallial gonoduct are listed and described in the same order in which the dissections were made (anterior to posterior), beginning with the vaginal opening and the vagina (Fig. 4C, v), followed by the bursa copulatrix (Fig. 4C, bc), capsule gland with left and right lobes (Figs. 3E, cg, 4C, lc, rc), ventral channel (Fig. 4C, vc), ovi-sperm duct (connecting capsule gland with albumen gland; Fig. 4E–H, osd), ingesting gland (Fig. 3E, ig), albumen gland (with or without posterior seminal receptacles; Figs. 3E, ag, 4E–H), and the gonad (Fig. 3E, ov).

Characters:

9. Bursa copulatrix
   (a) sacklike, separate from lumen of capsule gland (Fig. 4C, bc)
   (b) continuous with capsule gland (Fig. 4D, bc)
10. Posterior seminal receptacles around albumen gland
   (a) absent (Fig. 4F, G)
   (b) 1–3 with duct branching off ovi-sperm duct (Fig. 4E, psr)
   (c) many (usually at least 7 or 8) (Fig. 4H, psr)
11. Morphology of albumen gland
   (a) diverticulum of oviduct (Fig. 4F)
   (b) arch-shaped, elongate (Fig. 4G)
   (c) staff-shaped (Fig. 4E)
   (d) omega-shaped, roundish (Fig. 4H)

Male Reproductive System: Descriptions of the organs of the male reproductive system follow the same format as those of the female system. The penis (Figs. 3B, C, p, 5A–F, I) is described, followed by the penial vas deferens (Fig. 5A, B, D, pvd), cephalic vas defer-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ens, prostate (Figs. 3B, pr, 5G, H), prostate duct (Fig. 3B, pd), seminal vesicles (Fig. 3C, vs) and the testis (Fig. 3B, C te). The term "large" as referred to penis size is to be taken relative to tentacle size; a penis which measures more than twice the size of the tentacles is referred to as "large." Changes in penial morphology within the same individual are a common phenomenon in most species. The penis can be extended or condensed, and its shape can thus be altered. In a relaxed state, however, the penial shape does not vary much among individuals of the same species. Penial variation in living specimens facilitated evaluation of penial shapes in preserved specimens.

Characters:

12. Morphology of penis
    (a) elongate, gradually tapering (Fig. 5A)
    (b) straight to lightly curved, with pseudo-papilla (Fig. 5B)
    (c) strongly recurved, with large side lobe (Fig. 5E, I)
    (d) strongly recurved, club-shaped (Fig. 5F)
    (e) strongly recurved, with flagellate pseudo-papilla (Fig. 5D)
    (f) slightly recurved, gradually thinning to flagellate morphology (Fig. 5C)
13. Morphology of penial vas deferens
    (a) duct well developed, semi-closed by interlocking lateral ridges (Fig. 5A, pvd)
    (b) duct minute, open, adjacent to posterior edge of penis
    (c) duct minute, semi-closed by loosely overlapping ventral and dorsal sides of penis; adjacent to posterior edge of penis (Fig. 5B, pvd)
    (d) coiling duct within a larger duct (duct-within-a-duct system) (Fig. 5D, pvd)
14. Morphology of vas deferens of prostate (pallial vas deferens)
    (a) open to mantle cavity in posterior portion (Fig. 5H, prv)
    (b) closed to mantle cavity (Fig. 5G, prv)

Alimentary System: The alimentary system (exclusive of radula) is treated in two paragraphs; one for structures of the anterior portion of the alimentary system (Fig. 3F), such as the proboscis (pb), accessory salivary glands (ra, la), salivary glands (lsg), valve of Leiblein (vL), mid-esophageal glandular folds [on portion of mid-esophagus between nerve ring (nr) and duct to gland of Leiblein; meg], gland of Leiblein (gL), the other for the posterior structures, such as the stomach (e.g. Fig. 3G, H), rectal gland (Fig. 3C, E, rg), and anal opening. Size references for the accessory salivary glands are relative to shell height (see below). Size of the proboscis is given relative to the size of the gland of Leiblein ("large" translates into almost equal in size to gland of Leiblein). The portion of the mid-esophagus containing glandular folds is referred to as "long" when it stretches from the nerve ring to the duct to the gland of Leiblein. The posterior blind duct of the gland of Leiblein is either long (duct longer than one-half of length of gland), or short (duct shorter than one-fourth of length of gland); no intermediate values were found.

The posterior portion of the stomach is herein considered that portion with is directly adjacent to the esophagus; a lateral extension means an extension of the central mixing area of the stomach. The term "stomach typhlosole" (Fig. 3C, stt) refers to the foldlike

FIG. 3. Anatomy of selected rapanines and their organs. A–C, E, whole animals removed from shell. A, *Plicopurpura patula,* male with mantle skirt cut longitudinally to expose head (×1). B, *Morula uva,* male, left side (×10). C, *Morula uva,* male, right side (×10). D, ctenidium and osphradium of *Morula uva,* with lamellae (×15). E, *Morula uva,* female, right side (×10). F, generalized representation of anterior portion of alimentary tract found in rapanines. G–H, morphologies of muricid stomach and intestine, inside views. G, *Nucella lapillus.* H, *Muricanthus fulvescens;* ag, albumen gland; ant, anterior end; cg, capsule gland; cm, columellar muscle; cme, cut mantle edge; ct, ctenidium; cv, ctenidial efferent vessel; dd, digestive diverticula; dg, digestive gland; dgL, posterior duct of gland of Leiblein; f, foot; g, gonad; gL, gland of Leiblein; h, heart; hg, hypobranchial gland; ig, ingesting gland; in, intestine; int, intestinal typhlosole; is, incurrent siphon; k kidney; la, left accessory salivary gland; le, lateral edge; los, left osphradial pectin; lr, lamellar support rod (ventral edge); lsg, left lobe of salivary gland; m, mouth; ma, mantle; meg, mid-esophageal folds; nr, nerve ring; o, operculum; od, oviduct; ov, ovary; p, penis; pb, proboscis; pd, prostate duct; pef, longitudinal folds of the posterior esophagus; pes, posterior esophagus; pos, posterior end; pr, prostate; psr, posterior seminal receptacles; r, rectum; ra, right accessory salivary gland; rg, rectal gland; s, sole; sf, folds on gastric wall of stomach; si, siphon; st, stomach; stt, stomach typhlosole; t, tentacle; ta, terminal ampulla; te, testes; vL, valve of Leiblein; vm, visceral mass; vs, vesicula seminalis.

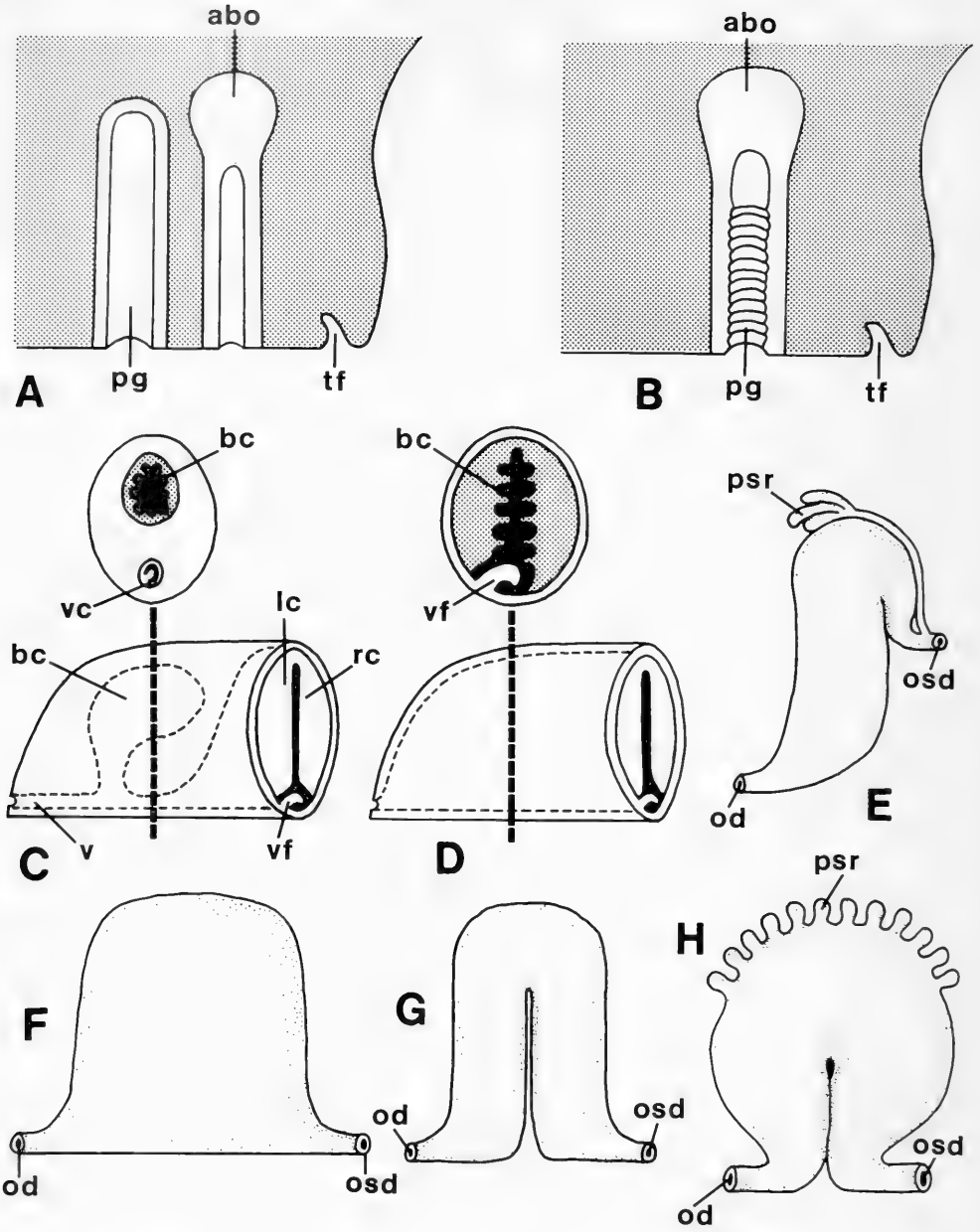

FIG. 4. Morphologies of muricid female reproductive structures. A, B, sagittal cross sections through anterior foot of female, viewed from right. A, ventral pedal gland and accessory boring organ separate (e.g. *Nucella lapillus*). B, ventral pedal gland and accessory boring organ combined (e.g. *Thais nodosa*). C, schematic representation of anterior pallial gonoduct of female non-thaidine muricid (e.g. *Nucella lapillus*), viewed from left, with cross section. D, schematic representation of anterior pallial gonoduct of female thaidine (e.g. *Plicopurpura patula*), viewed from left, with cross section. E–H, albumen gland morphologies in Muricidae, viewed from right. E, e.g. *Morula uva*. F, e.g. *Muricantus fulvescens*. G, e.g. *Nucella lapillus*. H, e.g. *Stramonita haemastoma;* abo, accessory boring organ; ag, albumen gland; bc, bursa copulatrix; lc, left lobe of capsule gland; od, oviduct; osd, ovi-sperm duct; pg, ventral pedal gland; psr, posterior seminal receptacles; rc, right lobe of capsule gland; tf, transverse furrow; v, vagina; vc, ventral channel; vf, ventral flange.

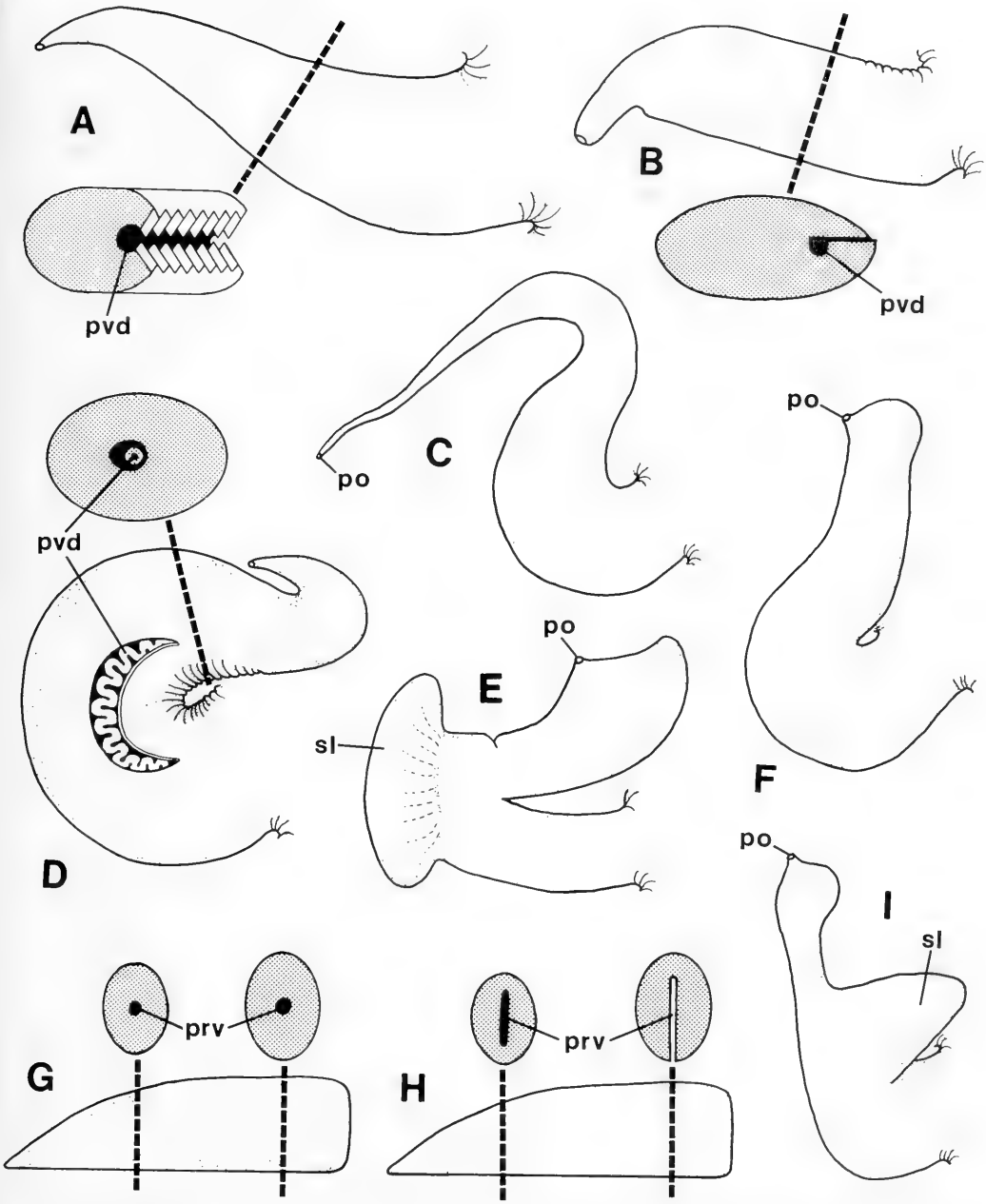

FIG. 5. Morphologies of muricid male reproductive structures. A–F, I, penial morphologies in Muricidae. A, *Muricanthus fulvescens,* with cross section. B, *Nucella lapillus,* with cross section. C, *Nassa serta.* D, *Thais nodosa,* with cross section. E, *Morula uva.* F, *Cymia tecta.* I, *Cronia amygdala.* G–H, schematic representation of prostate morphologies in Muricidae, with cross section. G, e.g. *Thais nodosa.* H, e.g. *Nucella lapillus;* po, penial opening; prv, prostate vas deferens; pvd, penial vas deferens; sl, side lobe.

structure which usually borders the posterior mixing area and can be continuous with what Fretter & Graham (1962) refer to as "typhlosole 2," located in the intestine (e.g. Fig. 3G, int).

Characters:

15. Length of accessory salivary glands
    (a) right gland minute, nearly undetectable; left one absent
    (b) both left and right glands very long (nearly one-half of shell height)
    (c) both glands short to medium (less than one-quarter of shell height; Fig. 3F, la, ra)
    (d) both glands absent
    (e) right gland very long (nearly one-half of shell height); left gland absent
16. Length of posterior blind duct of gland of Leiblein
    (a) duct at least one-half of length of gland (Fig. 3F, dgL)
    (b) duct shorter than one-half (usually less than one-fourth) of length of gland

Radula: Radulae (2–6 per species) were dissected from living and preserved animals, cleaned in potassium hydroxide, and examined using scanning electron microscopy. For the sake of consistency, only scanning electron micrographs were used for analyzing radular structures. Four micrographs were taken of the central portion of each radular ribbon. The first two micrographs (one including lateral teeth, one excluding lateral teeth) were taken perpendicular to the radular ribbon. The radula was then tilted laterally to an angle of 40° to obtain a lateral view of the morphology of the cusps and denticles on the rachidian tooth. Finally, the radula was tilted laterally to an angle of about 85° to examine the edge of the rachidian tooth and the angles, sizes and locations of its cusps and denticles, in an area from which the lateral teeth had been cut away with a surgical knife.

The morphology of the radula is described starting with the rachidian tooth (Fig. 6B), followed by the lateral teeth. The cusps (three or five) on the rachidian are described beginning with the central cusp (Fig. 6B, cc), followed by the inner lateral denticle (ild), lateral cusp (lc), the marginal area (ma), marginal denticles (d), and marginal cusp (mc). The marginal area is defined as the more or less horizontal area on the outside of the lateral cusp, extending to—if present—the marginal cusp. Size of lateral cusps is given relative to size of central cusp ("nearly equal" translates into 75% or more of central cusp length). The position of the inner denticle(s) is against the base of the inner edge of the lateral cusp, unless noted otherwise. Size of inner lateral denticle is relative to lateral cusp. Size of lateral teeth is given relative to rachidian width. An approximate range of the length of the radular ribbon is given, where available, relative to shell height.

Characters:

17. Orientation of marginal cusp of rachidian tooth
    (a) marginal cusp absent or in same plane as lateral cusp (and marginal denticles, if present) (e.g. Fig. 7F)
    (b) marginal cusp in different plane than lateral cusp (forming an approximately 75° angle), on antero-posteriorly widened base (e.g. Fig. 15E, F)
18. Morphology of rachidian tooth
    (a) marginal area and cusps absent; inner lateral denticle small, free from and between lateral and central cusps; lateral cusps nearly equal in length to central cusp (Fig. 24E)
    (b) marginal area and cusps absent; inner lateral denticle larger than lateral cusp, free from and between lateral and central cusps; lateral cusps nearly equal in length to central cusp (Fig. 11D)
    (c) marginal area absent, marginal cusps small; one or more small inner lateral denticles; lateral cusps nearly equal in length to central cusp (Figs. 15E, F, 26D, E)
    (d) marginal area absent, marginal cusps small; inner lateral denticle small; central cusp much longer than lateral cusps and reclining, forming angle with them (Fig. 8H)
    (e) marginal area wide, smooth, marginal cusps absent; inner lateral denticle small, free from but adjacent to lateral cusp; central cusp much longer than lateral cusps (e.g. Fig. 8D)
    (f) marginal area and cusps absent; several faint inner lateral denticles; lateral cusps nearly equal in length to central cusp (Fig. 25C, E)
    (g) marginal area absent, marginal cusps small; one or more inner lateral denticles; lateral cusps nearly

equal in length to central cusp (e.g. Fig. 7F)

(h) marginal area wide, with multiple denticles and small marginal cusps; inner lateral denticle small; lateral cusps nearly equal in length to central cusp (e.g. Fig. 18D)

(i) marginal area and cusps absent; inner lateral denticle absent; central cusp much longer than lateral cusps (Fig. 11I)

(j) short marginal area with small marginal cusps; inner lateral denticle small or absent; lateral cusps nearly equal in length to central cusp which is wide at base (e.g. Fig. 22E)

Note: both *Neorapana* and *Tribulus* have larger, wider central cusps relative to the lateral cusps. These lateral cusps (those of *Neorapana* without inner lateral denticle) are bent somewhat sideways, which, in the case of *Neorapana,* resulted in the loss of any marginal area. If the Hennig86 program would allow for scoring of more than ten character states, a separate character state would have been assigned to *Neorapana* and *Tribulus.* However, overall morphology of the rachidian tooth strongly suggests homology among the four genera scored for with "(j)."

Taxa which could not be scored due to a limited number of character-state entries in Hennig86 are mentioned below. They are all synapomorphic and thus would not have influenced the topology of the tree.

Nassa—similar to "(i)," but female specimens with small free-standing inner lateral denticle (Fig. 13G).

Plicopurpura—similar to "(i)," but with slit in central cusp (Fig. 17E).

Vexilla—similar to "(i)," but with base of central cusp nearly as wide as rachidian (Fig. 23C).

Phylogenetic Analysis

Data pertaining to the reproductive and alimentary systems, mantle cavity, radula, operculum, protoconch, and shell ultrastructure were subjected to cladistic analyses. No data were derived from external shell morphology.

Three steps were necessary to commence the cladistic analysis: (1) identification of potentially homologous characters; (2) division of each individual character into character states; and (3) polarization of character states, for which the outgroup method was applied. Homology was regarded as two very similar structures with similar location and function.

The outgroup method was used to determine the ancestral state of each character. The outgroup criterion is based on the assumption that character states present in the sister group (outgroup) and the group studied (ingroup) is the plesiomorphic or "primitive" condition (Hennig, 1966). The outgroup method was thus used to determine the "zero state." Use of an outgroup further allows application of the parsimony criterion; it is assumed that the hypothesis based on the lowest number of character changes ("steps") is the best solution for the available data, because it explains the data in the most economical way and is thus based on the smallest number of assumptions made about the evolutionary process (Farris, 1979, 1982; Lipscomb 1984).

The muricine *Muricanthus fulvescens* (Sowerby, 1841) (also known as *Murex fulvescens* and *Hexaplex fulvescens*) appeared suitable to serve as outgroup in the cladistic analysis for several reasons: (1) the Muricinae is a sister group of the Rapaninae; (2) many live-collected and well-preserved specimens were available to provide all data necessary for anatomical studies; (3) most of the structures and characters derived from rapanine anatomy are present also in *Muricanthus* Swainson, 1840, although their "states" may be very different.

The character states of multi-state characters were left unordered; because no realistic assumptions about character state evolution could be made *a priori.* For example, ontogenetic criteria could not be applied because only adult specimens of the type species were available.

Only a few continuous (or quantitative) characters (e.g. size, or numbers) were used due to the arbitrary nature of "cut-off points." Qualitative characters were more easily divided into character states.

The Hennig86 cladistic computer package was used to derive a repeatable, testable, relatively objective, most parsimonious, and most informative hypothesis with the available database. The results herein were very similar to previous results (Kool, 1989) obtained with a slightly different data set using other computer packages (PAUP [Swofford, copyright 1985]; and PHYSYS [Farris & Mickevich, copyright 1985]).

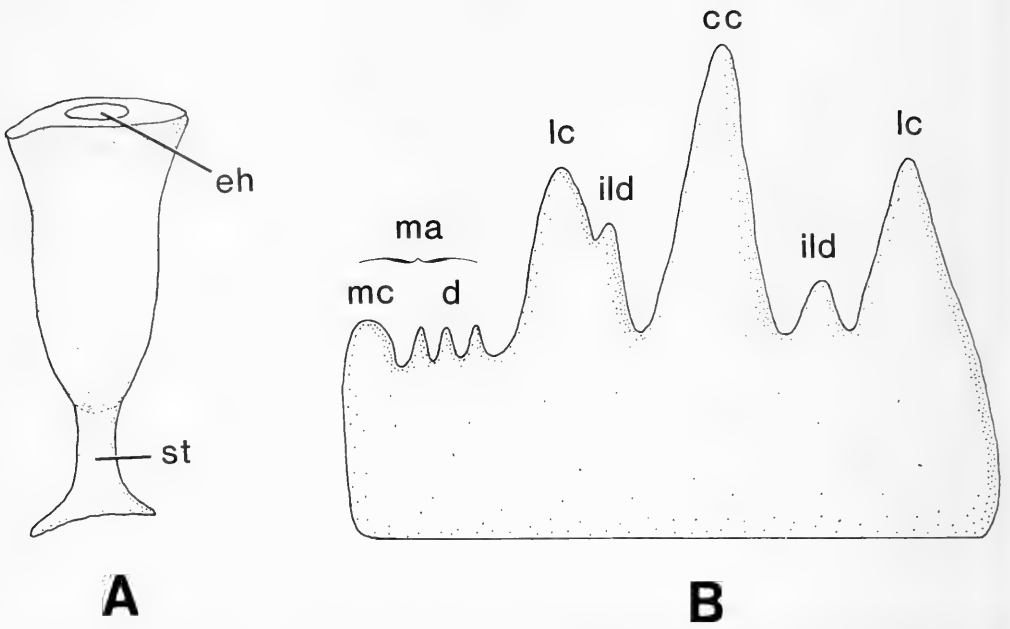

FIG. 6. A, egg capsule of *Cymia tecta,* apical view. B, schematic representation of composite rachidian tooth of muricids (frontal view); cc, central cusp; d, denticles on marginal area; eh, exit hole; ild, inner lateral denticle; lc, lateral cusp; ma, marginal area; mc, marginal cusp; st, stalk.

One of the advantages of using cladistics is the predictive power of the obtained trees. To test the robustness and predictive power of the phylogeny proposed herein, a few taxa were examined on those characters which revealed themselves during early stages of the analysis as unique synapomorphies for certain clades. This "spot checking" allowed for unambiguous placement of taxa for which only limited data were available. Based on the cladistic analyses, limits were set for each group after synapomorphies for each group were identified.

Cladograms never yield a final solution for evolutionary relationships among taxa, and the phylogeny presented herein should be taken only as a testable hypothesis for the evolutionary history of the Rapaninae (as defined herein) and its position in the Muricidae.

RESULTS

The genera formerly included in Thaididae/nae are treated in alphabetical order. A chronologically arranged synonymy of each genus is given, including author, date, page, and information on the type species. The type species of the valid genus name is given, followed by the correct binomen and a synonymy. New combinations are omitted. A "Remarks" section provides for a short discussion of the taxonomic history and placement by different authors (usually including Cossmann, 1903, Thiele, 1929, and Wenz, 1941) of the genus and (type) species.

Different aspects of morphology (protoconch, teleoconch, anatomy, radula, egg capsules) of each species are described in detail, followed by (if available) data on the biology (ecology and geographic distribution) of each taxon. Not treated is the fossil history of each taxon, as most of this information, given by Thiele (1929) and Wenz (1941), is out of date and highly suspect (see "Congruence with Fossil Record").

A less detailed treatment is provided for *Muricanthus fulvescens,* used as outgroup, *Forreria belcheri,* a taxon *incertae sedis,* and *Rapana rapiformis.* I should mention that it was not known initially that *Rapana* was monophyletic with most members of Thaidinae of authors. Only limited data were available on the taxa *Acanthina monodon* and *Trochia cingulata* (both usually included in Thaididae/nae of authors), but the available

data were used in the cladistic analysis, partially to test for character robustness.

Although many of the descriptions of the anatomy of the type species are based on dissections of living animals, most observations were based on preserved specimens. Illustrations of anatomy are schematic in order to standardize and elucidate the shared morphologies rather than to show individual idiosyncrasies due to intraspecific variation.

Descriptions of taxa traditionally grouped in Thaididae/nae of authors

Genus *Concholepas* Lamarck, 1801
(Fig. 7A–F)

Concholepas Lamarck, 1801: 69.
Concholepa Deshayes, 1830: 256 (error for *Concholepas*).
Conchopatella Herrmannsen, 1847: 291 (introduced in synonymy).

Type Species: Concholepas peruviana Lamarck, 1801, by monotypy, = *Concholepas concholepas* (Bruguière, 1789); synonym: *Buccinum concholepas* Bruguière, 1789.

Remarks: Lamarck introduced the species *C. peruviana* as type of the genus *Concholepas* and may have considered it a different species from *Buccinum concholepas* Bruguière. More likely, he renamed it without regard for priority to avoid tautonomy (an unpopular nomenclatural procedure at the time). However, these two taxa are synonymous, and the earlier name, *C. concholepas,* has priority. The genus has one living and several fossil representatives (Vokes, 1972; Kensley, 1985). Haller (1888) gave an extensive description of the anatomy of this species, emphasizing the nervous system.

Shell: Protoconch (Fig. 7C, D) squat (wider than high), smooth, of 2.5–3 whorls, with slightly impressed suture, and with outward-flaring lip (DiSalvo, 1988) (eroded from figured specimen) and sinusigeral notch. Teleoconch (Fig. 7A, B) of 2–3 whorls and exhibiting high rate of whorl expansion. Adult shell up to about 125 mm in height, 95 mm in width. Suture slightly impressed, nearly canaliculate on final whorl. Body whorl and aperture reaching beyond apex. Body whorl robust, rounded "patelliform," sculptured with 11–13 spiral, lamellose cords, with one spiral thread in interspaces. Lamellose sculpture most common in juveniles, often persisting in adults. Aperture oval, extending beyond shell spire. Apertural lip with crenate edge, corresponding to spiral cords. Anterior siphonal canal short, wide and open; posterior siphonal canal absent. Columella flat or somewhat concave, continuous with apertural lip, and reaching from beyond apex to anterior siphonal canal. Siphonal fasciole similar to axial ribs but more elevated. One or two labial toothlike structures adjacent to siphonal fasciole on apertural lip. Shell uniformly dark reddish brown; aperture white; columella white, occasionally with light brown areas.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (15–20%); aragonitic layer with crystal planes oriented parallel to growing edge (15–20%); calcitic layer (60–70%) (Fig. 7E).

Operculum: D-shaped (about one-third size of aperture), with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface usually with one bracket-shaped growth line and with callused, glazed rim (about 35–40% of opercular width) on left.

Anatomy: (based on preserved animals only): Cephalic tentacles long and wide. Tentacles a uniform, medium brown. Head-foot and sole of foot mottled dark brown. Mantle edge smooth and following shell contour, with very long brown incurrent siphon. Pinkish and yellow hypobranchial gland positioned within thin, upright, lateral epithelial ridges. Kidney dull caramel brown. Pedal gland in females well developed, with accessory boring organ in proximal portion.

Osphradial length less than one-fourth ctenidial length; osphradial width less than ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, extending farther anteriorly than osphradium. Anterior ctenidial lamellae distinctly wider than deep; posterior lamellae deeper than wide. Lateral and ventral edges of ctenidial lamellae concave, lateral edge occasionally straight. Distal tips of ctenidial support rods extending beyond lateral edge as papillate projections.

Vaginal opening situated on tapering anterior end of pallial oviduct and located directly beneath anal opening. Bursa copulatrix an

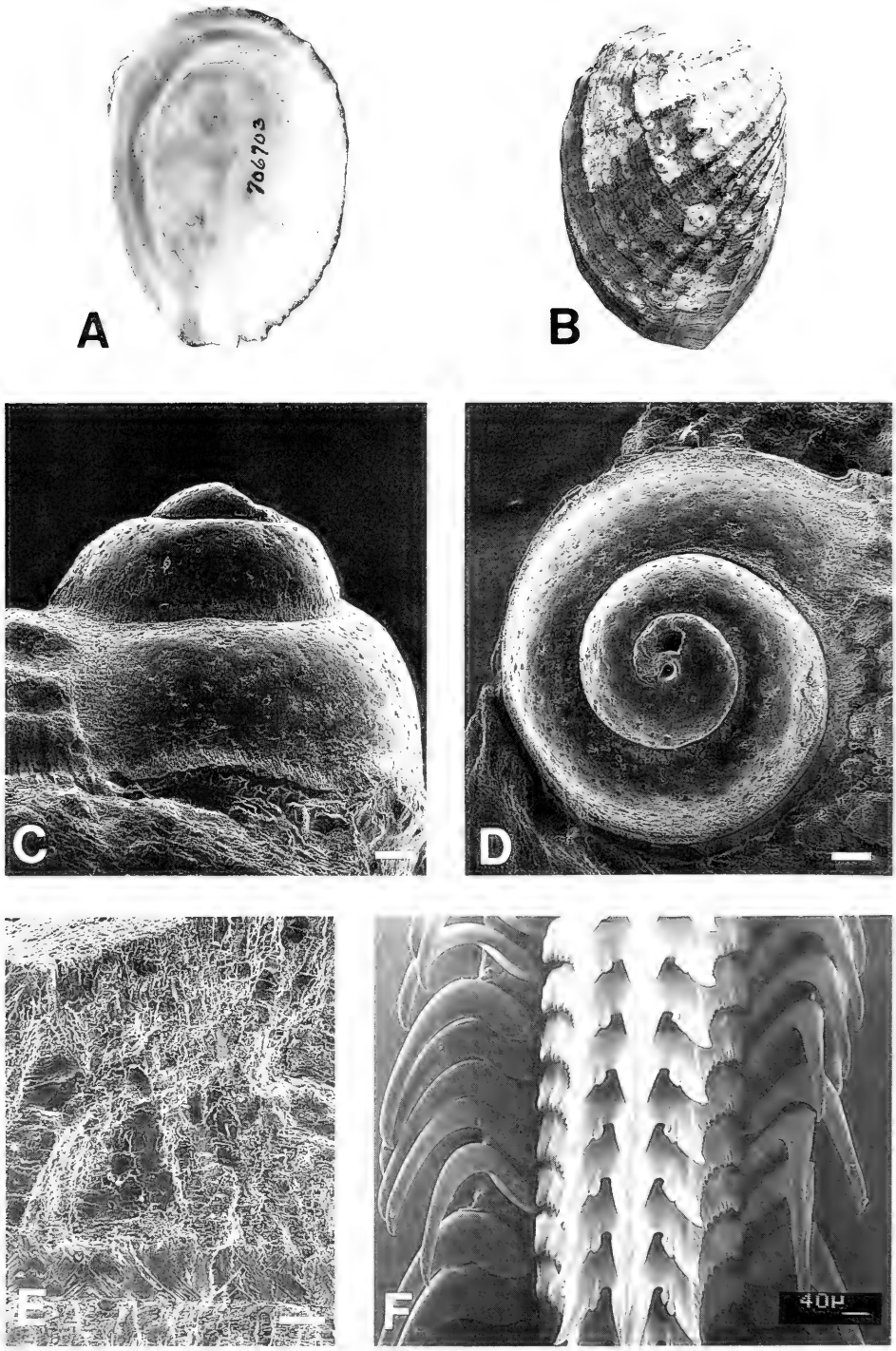

FIG. 7. *Concholepas concholepas.* A, shell (67 mm), apertural view. B, shell (67 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, SEM (bar = 50 µm). F, radula, SEM.

open chamber in interior vagina and open to anterior portion of capsule gland. Posterior part of pallial oviduct with ventral sperm channel consisting of two ventrally located flanges each facing one another and perpendicular to capsule gland lobes. Ventral channel in anterior portion of pallial oviduct very small. Ingesting gland located between capsule gland and albumen gland, continuing on left side of albumen gland, comprising many small, interconnected chambers, and lined with dark yellow epithelium. Seminal receptacles on dorsal periphery of albumen gland small, elongate-oval, white. Albumen gland small, omega-shaped. The external lay-out of the female reproductive system in this species and the species following hereafter is superficially similar to that shown in Figure 3E and in Kool (1988b, fig. 3C).

Penis dorso-ventrally flattened, wide, with large folds along posterior border (in young individual examined), or angular (in older ones). Penial shaft curved, with long and thin flagellate tip. Vas deferens as thin duct-within-a-duct system (Fig. 5D, pvd) occupying about one-fifth of penial width. Prostate gland solid, white, adjacent to spongy, white, rectal wall. Duct of prostate closed off from mantle cavity but sometimes visible through epithelium. Seminal vesicles comprised of small, white or orange outpocketings. Testicular duct following periphery of gonad.

Proboscis whitish, thinner than width of gland of Leiblein. Paired accessory salivary glands of equal length, long, worm-shaped, slightly less than one-half of shell height. Left accessory gland located under and separate from salivary gland but loosely connected to it by many strings of connective tissue. Right accessory gland ventral to proboscis and slightly ventral to salivary glands. Salivary glands cream brown, consisting of many small portions, larger in mass than accessory salivary glands, partially located between gland of Leiblein and proboscis, or partially between nerves emanating from nerve ring. Valve of Leiblein elongate, irregularly shaped, surrounded by salivary glands but not attached to them. Salivary ducts attached some distance from valve of Leiblein; valve separated from nerve ring. Portion of mid-esophagus with glandular folds long; folds well developed. Major portion of posterior esophagus free and looped along side of gland of Leiblein, but small area of posterior esophagus closely attached to it. Gland of Leiblein coiled counterclockwise, forming two folds, brown grey, of hard consistency, with thick outer covering with "interwoven" strings of connective tissue. Blind posterior duct of gland of Leiblein more than one-half length of gland itself. The lay-out of the alimentary system in this and the following species is similar to that shown in Figure 3F.

Stomach buried in digestive gland, with center projecting deep into visceral mass, and with lateral extension. Interior epithelium forms many (about 20) distinct folds, the largest central and perpendicular to typhlosole. Folds on right portion of stomach curve into central fold; folds of left portion perpendicular to stomach typhlosole. One diverticulum present. Stomach typhlosole well developed, continuing onto stomach wall. Intestinal typhlosole wide and shallow. Several minute folds on right side of intestinal typhlosole in intestinal groove. Anal opening distinct, wide, varying from thin- to thick-walled. Anal papilla poorly developed. Rectal gland well developed, green, adjacent to entire length of pallial gonoduct.

Radula: Central cusp on rachidian with wide, somewhat constricted base (Fig. 7F); lateral cusps pointing outward; inner lateral denticle located on base of lateral cusp and one-half its length; several knobby outer denticles on base of lateral cusp; marginal cusp very small. Lateral teeth long, thin, wide-based, nearly total rachidian width.

Egg Capsules: Large, about 20 mm in height (Gallardo, 1973), elongate, slightly curving, with undulating surface, and resting on short, thin stalk, about 1 mm in length. Capsules arranged in clusters, close to one another, each containing up to 13,000 eggs (Gallardo, 1979). Eggs up to 158–160 μm in diameter (Gallardo, 1979).

Ecology: Concholepas concholepas is one of the few rapanine gastropods of direct economic importance and of culinary value to man, who is this species' major predator on the west coast of South America (Castilla & Duran, 1985). Thus, a substantial number of papers have been published on its ecology (Gallardo, 1973, 1979, 1980; Gallardo & Perron, 1982; Castilla & Cancino, 1976; Castilla & Duran, 1985). Egg capsules are usually found in the sublittoral zone; planktotrophic veliger larvae hatch from them probably spending up to several weeks in the plankton

before settlement (Gallardo, 1979). Adults live and spawn in the rocky intertidal zone, where they feed on barnacles and mussels (Gallardo, 1979; Kool, 1987). DuBois et al. (1980) reported specimens living at a depth of 40 m. DiSalvo (1988) describes the veliger stages. Beu (1970) suggested that fossil relatives of the Recent species lived in much deeper waters.

Distribution: Eastern Pacific, from central Peru to southern Chile (Beu, 1970; Disalvo, 1988).

Genus *Cronia* H. & A. Adams, 1853
(Fig. 8A–D)

Cronia H. & A. Adams, 1853: 128 (as a subgenus of *Purpura*).

Type Species: Purpura amygdala Kiener, 1835, by monotypy, = *Cronia amygdala* (Kiener, 1835); synonyms: ?*Buccinum avellana* Reeve, 1846; ?*Purpura aurantiaca* Hombron & Jacquinot, 1852; ?*Purpura pseudamygdala* Hedley, 1902.

Remarks: The taxon *Cronia* was introduced by H. & A. Adams (1853: 128) as a subgenus of *Purpura* "Aldrovandus" [correct author: Bruguière, 1789), with one species listed. Cossmann (1903: 68) placed *Cronia* as a section under the subgenus *Polytropalicus* Rovereto, 1899, genus *Purpura.* Dall (1909: 50) allotted *Cronia* to *Thais.* Thiele (1929: 294) and Wenz (1941: 1113) placed *Cronia* as a subgenus under *Drupa.* Fujioka (1985a) and Cernohorsky (1982, 1983) used *Cronia* as a full genus.

The species described below resembles Kiener's (1835) figures of *Purpura amygdala* but appears more similar to Hedley's (1902) figures of *Purpura pseudamygdala.* Kiener's figures of *Purpura amygdala* bear more resemblance to the figures of Hedley's *Purpura pseudamygdala* than to Hombron & Jacquinot's figures of *Purpura aurantiaca,* which is most likely conspecific with *Buccinum avellana* Reeve, 1846. I strongly suspect all four "species" to be geographical or ecophenotypic variants of the same species. Cooke (1919: 107) explained that Hedley restricted the *amygdala* form to the southeast coast of Australia, and introduced *Cronia pseudamygdala* for the "species" from Queensland. Closer examination of the types, ranges of variation, and the anatomy of these four "morphs" is necessary before definite statements on this matter can be made.

Shell: Protoconch tall, conical, smooth, of about four adpressed whorls, and with outward-flaring lip and sinusigeral notch (Hedley, 1902: pl. 29, figs. 4–5). Teleoconch (Fig. 8A, B) of 6–7 adpressed, high-spired, fusiform whorls. Adult shell up to about 30 mm (including 3 mm siphonal canal) in height and 15 mm in width. Body whorl about 65–70% of shell height, rounded, heavily sculptured with five pronounced spiral cords, one of them directly below suture, and with 3–4 fine, delicately lamellose spiral lines at regular intervals from one another, between each pair of major spiral cords. Spiral cords bear 8–9 knobs at regular intervals towards the base. Knobs aligned to form about nine thick axial ribs per whorl. Aperture elongate, about 60% of shell height. Apertural lip slightly thickened, with seven denticles. Anterior siphonal canal well developed, short, deep and semi-closed; posterior siphonal canal absent. Siphonal fasciole well developed, delicately lamellose, free from callus on lower columella. Columella with heavy callus deposition. Shell grey brown; knobs on axial ribs white or light brown; aperture light orange brown, especially on columella and lip edge.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (70–75%) (Fig. 8C).

Operculum: D-shaped, with S-shaped left edge, tapered at lower end, with lateral nucleus in lower right (compare Fig. 1F). Free surface with staff-shaped growth lines; attached surface with about 5–7 arch- and bracket-shaped growth lines and with callused, glazed rim (about 30–40% of opercular width) on left.

Anatomy (based on living and preserved material): Head-foot and siphon brown with green, yellow and white specks, cephalic tentacles long. Mantle edge smooth, following aperture contour; incurrent siphon long. Hypobranchial gland large, perpendicular to mantle wall, with small, thin, black, rodlike structures embedded in it (compare Fig. 2A, B). Kidney green in males, brown in females. Nephridial gland green in females. Pedal gland as simple duct, combined with large accessory boring organ (Fig. 4B).

Osphradial length equal to or slightly more

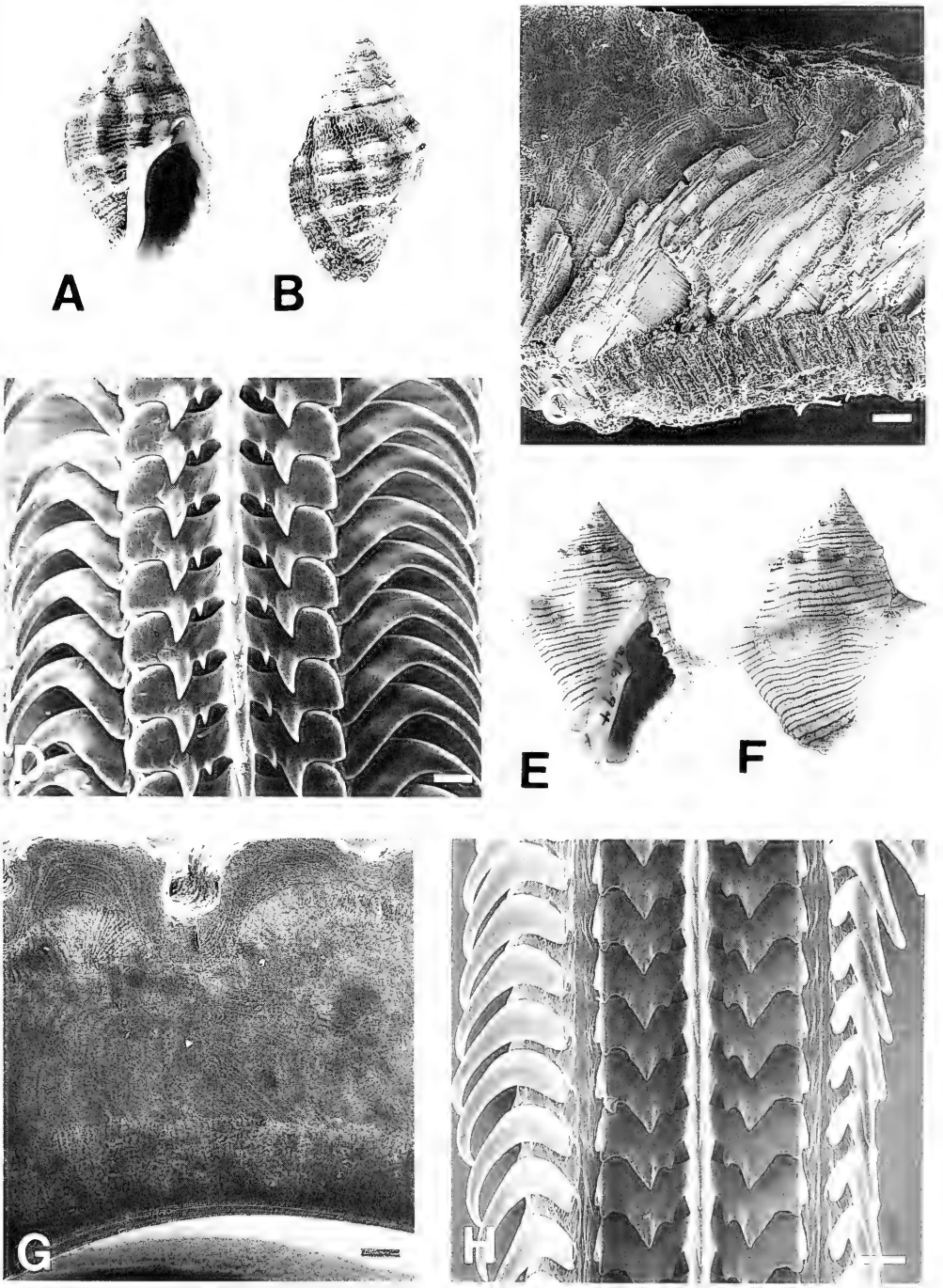

FIG. 8. A–D, *Cronia amygdala*. A, shell (28 mm), apertural view. B, shell (28 mm), abapertural view. C, shell ultrastructure, SEM (bar = 0.10 mm). D, radula, SEM (bar = 30 μm). E–H, *Cymia tecta*. E, shell (55 mm), apertural view. F, shell (55 mm), abapertural view. G, shell ultrastructure, polished surface, SEM (bar = 0.30 mm). H, radula, SEM (bar = 45 μm).

than one-half ctenidial length; osphradium and ctenidium about equal in width. Osphradium symmetrical in shape along lateral axis; right pectin wider than left. Osphradial lamellae attached along more than one-half of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior and posterior ctenidial lamellae wider than deep. Lateral and ventral edges of ctenidial lamellae usually sharply concave. Distal tips of well-developed ctenidial support rods not extending beyond lateral edge.

Vaginal opening round, situated on distal end of short, attached tube and located below and posterior to anal opening. Bursa copulatrix a dorso-ventral slit, continuous with capsule gland and ventral channel (Fig. 4D). Ventral sperm channel formed by large rolled flange originating from ventral epithelium and lying below both capsule gland lobes. Duct from ovi-sperm duct enters mushroom-shaped, orange-brown (in living animals) ingesting gland, which lies between capsule gland and albumen gland (compare Fig. 3E). Second duct branching off ovi-sperm duct more posteriorly, forming single, elongated, grey seminal receptacle lying above albumen gland (compare Fig. 3E, psr). Sperm apparent from iridescence in receptacle. Albumen gland omega-shaped, usually turned sideways, lying on posterior portion.

Penis with large side lobe (Fig. 5I), basically oval in cross section, with bulbous tip on long thin shaft. Triangular muscular side lobe (Fig. 5I, sl) pointing toward head and tentacles. Penial duct as duct-within-a-duct system (compare Fig. 5D, pvd) occupying about one-fourth of penial width. Testicular duct brown and seminal vesicles weakly developed. Prostate duct closed to mantle cavity. Prostate solid, light brown (in living animals), directly adjacent to rectum, without layer of connective tissue separating both structures. Testis brown.

Proboscis much wider than width of gland of Leiblein. Paired accessory salivary glands both equally short (2 mm), stubby, much less than half of shell height. Left accessory salivary gland embedded in intertwined salivary glands; right accessory salivary gland separated from salivary glands. Salivary glands intertwined, light orange, larger than accessory salivary glands and with granular appearance. Valve of Leiblein elongate, free from salivary glands. Salivary gland ducts attached to esophagus at base of valve of Leiblein, which lies adjacent to nerve ring. Glandular folds on mid-esophagus resulting in slight thickening of mid-esophagus. Duct between esophagus and gland of Leiblein poorly developed. Posterior esophagus separated from gland of Leiblein along entire length. Gland of Leiblein coiled counterclockwise, forming two folds, flat, creamy brown, soft, appearing granular. Posterior blind duct about one-half of length of gland of Leiblein.

Stomach very large, with large sorting area having weak lines arranged randomly. Large, posteriorly located, unciliated area and two digestive diverticula present. Intestinal typhlosole well developed, but stomach typhlosole variable in size. Anal opening inconspicuous; anal gland poorly developed, running dorsally along less than one-half of pallial gonoduct.

Radula: Ribbon length about 20% of shell height (Fig. 8D). Rachidian with long, thin central cusp; lateral cusp with convex inner edge and smooth, concave outer edge; inner lateral denticle small, separate from lateral cusp; large, smooth, horizontal area between lateral cusp and edge of rachidian. Lateral teeth curved, smooth, slightly larger than half the rachidian width.

Egg Capsules: Unknown.

Ecology: Specimens of *Cronia amygdala* were collected on an intertidal offshore coral reef fringing a mangrove forest at Cockle Bay, Magnetic Island, Queensland, Australia. Abe (1983) reported *Cronia margariticola* (Broderip) to be a scavenger, preying upon a wide variety of food items, or feeding on eggs of *Thais clavigera* (Küster).

Distribution: West, north, and east Australia (Eisenberg, 1981) and Pacific Ocean (Cernohorsky, 1972).

Genus *Cymia* Mörch, 1860
(Fig. 8E–H)

Cuma Humphrey, 1797 (rejected work).

Cuma Swainson, 1840: 87 (*non* Milne-Edwards, 1828) [type: *Cuma sulcata* Swainson, 1840, by monotypy, = *Cymia tecta* (Wood, 1828)].

Cymia Mörch, 1860: 97 (replacement name for *Cuma* Swainson; as subgenus of *Rapana*).

Cumopsis Rovereto, 1899: 105 (unnecessary replacement name for *Cuma* Swainson; as subgenus of *Purpura*).

Cyma Rovereto, 1899: 105 (error for *Cymia*).

Type Species: Cuma sulcata Swainson, 1840, by monotypy, = *Cymia tecta* (Wood, 1828); synonyms: *Buccinum tectum* Wood, 1828; *Purpura angulifera* Duclos, 1832.

Remarks: Swainson (1840: 87) placed *Cuma* in the subfamily Pyrulinae, family Turbinellidae, and included only one species, *Cuma sulcata.* Mörch introduced *Cymia* as a replacement name for *Cuma* Swainson, which was pre-occupied, and placed it under *Rapana.* Rovereto (1899: 105) synonymized *Cuma* Swainson with his replacement name, *Cumopsis,* allotted it to *Purpura,* and did not list any other species to be included in this subgenus. Korobkov (1955: 299) considered *Cymia* to be a subgenus of *Thais.*

Shell: Protoconch unknown. (Protoconch of *Cymia brightoniana* Maury "a little more than one whorl" [Jung, 1969: 497]). Teleoconch (Fig. 8E, F) heavy, fusiform, oblong, of 7–8 adpressed whorls, with high spire and shallow suture. Early whorls sculptured with spiral, incised lines. Adult shell up to about 70 mm in height, 50 mm in width. Body whorl about 65–70% of shell height, sculptured with 8–10 large, spinose knobs on periphery of very pronounced, centrally located shoulder of each whorl. Suture adjacent to and following lower contours of these knobs. Twenty-five to 30 deeply incised spiral grooves on body whorl, several crossing knobs. Aperture moderately large, about 70% of shell height. Apertural lip thin, reflecting pattern caused by incised lines. Anterior siphonal canal short, wide, open; posterior siphonal canal poorly developed or absent. Heavy, central fold on columella. Siphonal fasciole curving, well developed, only partially covered by moderate callus layer on fasciole. Shell white, yellow, grey-brown; aperture and columella white to very light orange.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (30–35%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–20%); calcitic layer (15–20%) (Fig. 8G).

Operculum: D-shaped, with strongly concave left edge (to accommodate fold on shell fasciole), with lateral nucleus at center right (compare Fig. 1C). Free surface with bracket-shaped growth lines indented in center; attached surface with about 4–6 arch- and bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on preserved animals only): Cephalic tentacles short, stubby, with black blotches. Head-foot mottled black. Mantle edge crenate (following aperture lip contour). Incurrent siphon protruding farther than mantle edge. Sole of foot with many, primarily laterally crossing, shallow grooves, resulting in pustulate pattern. Pedal gland large, separated from accessory boring organ, but adjacent to it. Small lateral folds on wall of distal part of pedal gland; proximal part smooth. Accessory boring organ large, compact, chamber-shaped, adjacent to pedal gland in females.

Osphradial length less than one-half ctenidial length; osphradium and ctenidium about equal in width. Osphradium symmetrical in shape along longitudinal axis; usually wider anteriorly. Osphradial lamellae attached along large portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium, or osphradium extending slightly farther anteriorly. Anterior ctenidial lamellae wider than deep; posterior lamellae deeper than wide. Lateral and ventral edges of ctenidial lamellae variable in shape. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening elongated, located directly below anal opening. Bursa copulatrix between vaginal opening and capsule gland. Vertical flange large, folded, emanating from dorsal wall of bursa. Flange thin, straight, vertical, folded at tip prior to entering capsule gland. Bursa copulatrix continuous with anterior part of capsule gland. Flange minute, folded at 45° angle in most of capsule gland. Large second bursa between capsule gland and small albumen gland of the omega- or arch-shaped type. Ingesting gland with single chamber.

Penis (Fig. 5F) large, thick, strongly recurved, angular in cross section, with terminal papilla. Penial vas deferens tubular, about one-third of penis width. Cephalic vas deferens poorly developed. Prostate gland round in cross section, clearly separated from rectal wall, and with prostate duct closed off from mantle cavity. Posterior sperm storage area small but elongate, running horizontally on border line of gonad and digestive gland, dorsal to prostate.

Proboscis muscular, thick, half as wide as gland of Leiblein. Paired accessory salivary glands very long, thin, of equal length, more than one-half of shell height. Right accessory salivary gland in dorsal right anterior corner of buccal cavity; left gland intertwined with salivary glands between proboscis and gland of Leiblein. Salivary gland mass dorsal, much smaller than accessory salivary glands. Valve of Leiblein elongate, free from salivary gland mass, adjacent to nerve ring. Salivary gland ducts attached to anterior portion of esophagus directly anterior to valve of Leiblein. Mid-esophageal folds indiscernible. Nerve ring adjacent to thin, long duct joining esophagus and gland of Leiblein. Posterior esophagus adjacent to lower left of gland of Leiblein. Gland of Leiblein spiral, forming two folds oriented antero-posteriorly, dark brown, of hard consistency. Posterior blind duct approximately one-half of length of gland of Leiblein, running into dorsal branch of the afferent renal vein but not reaching kidney.

Stomach U-shaped, but with large posterior widening. Sorting area with 10–15 folds extending over only half its surface. Sorting area adjacent to intestinal typhlosole with minute folds and ridges parallel to it. Two digestive diverticula present. Intestinal typhlosole large. Rectum embedded in spongy tissue. Anal papilla covering anal opening. Rectal gland long and thin; anal opening well developed.

Radula: Ribbon length about 25% of shell height (Fig. 8H). Rachidian tooth with narrow central cusp; central cusp reclining, thus pointing in different direction than lateral cusp; inner lateral denticle nearly united with lateral cusp, which thus appears very wide; outer edge of lateral cusp straight, without denticulation; area between lateral cusp and edge of rachidian narrow, without denticles; wide marginal cusp pointing forward and parallel to lateral extension on rachidian base. Lateral teeth smooth, about three-fourths of rachidian width.

Egg Capsules: About 6 mm in height, elevated on wide stalk 1 mm long (Fig. 6A). Capsule vase-shaped, with oval, flat top; one side more elevated than other (normally continuing gradually in top layer of capsule); exit hole central, oval, located at slightly horizontal tip of capsule. All capsules appearing to be interconnected with basal membrane. Egg capsules examined (ANSP 355766) deposited on free side of operculum.

Ecology: Specimens were found living on intertidal rocks on mud flats, but also on mud among mangrove roots.

Distribution: Eastern Pacific, from Costa Rica to Ecuador (Keen, 1971b).

Genus *Dicathais* Iredale, 1936
(Fig. 9A–F)

Dicathais Iredale, 1936: 325.

Type Species: Buccinum orbita Gmelin, 1791, by original designation, = *Dicathais orbita* (Gmelin, 1791); synonyms: *Buccinum succinctum* Martyn, 1784 (non-binominal); *Purpura textilosa* Lamarck, 1816; *Purpura scalaris* Menke, 1828 (*non* Schubert & Wagner, 1829); *Purpura aegrota* Reeve, 1846; *Dicathais vector* Thornley, 1952.

Remarks: Iredale (1936: 325) removed *succincta* from the genus *Neothias* Iredale, 1912 (type: *N. smithi* Brazier, 1889, by original designation; emended [unjustified] by Iredale to *Neothais* [1915: 473]), recognized *orbita* Gmelin as its valid name and designated *Dicathais orbita* as type of *Dicathais.* Wenz (1941: 1124) synonymized *Dicathais* with *Neothias.*

Controversy exists about the number of *Dicathais* species. Cooke (1919: 97) observed differences between the radulae of "*Thais succincta* (= *orbita*)" and "*T. textilosa.*" These and three other names (*aegrota, scalaris,* and *vector*) are now considered to be geographical variants of one another (Phillips et al., 1973; Powell, 1979). The form here described is typical *Dicathais orbita.*

Shell: Protoconch (Fig. 9C, D) low, smooth, of about four adpressed whorls, with outward-flaring lip and sinusigeral notch. Teleoconch (Fig. 9A, B) of 5–6 adpressed whorls. Adult shell up to about 85 mm in height, 60 mm in width. Spire less than one-third shell height. Suture impressed, canaliculate in final whorl. Penultimate and body whorls sculptured with eight, solid spiral cords and with many minute spiral, incised lines; body whorl about 85% of shell height. Aperture large, ovate, about 70–75% of shell height. Apertural lip thin, deeply scalloped due to spiral cords. Interior of apertural lip deeply grooved. Columella rounded or concave, with callus layer more pronounced toward posterior end. Anterior siphonal canal a short but deep notch; posterior siphonal canal absent. Siphonal fasciole curved, about equally, or slightly more ele-

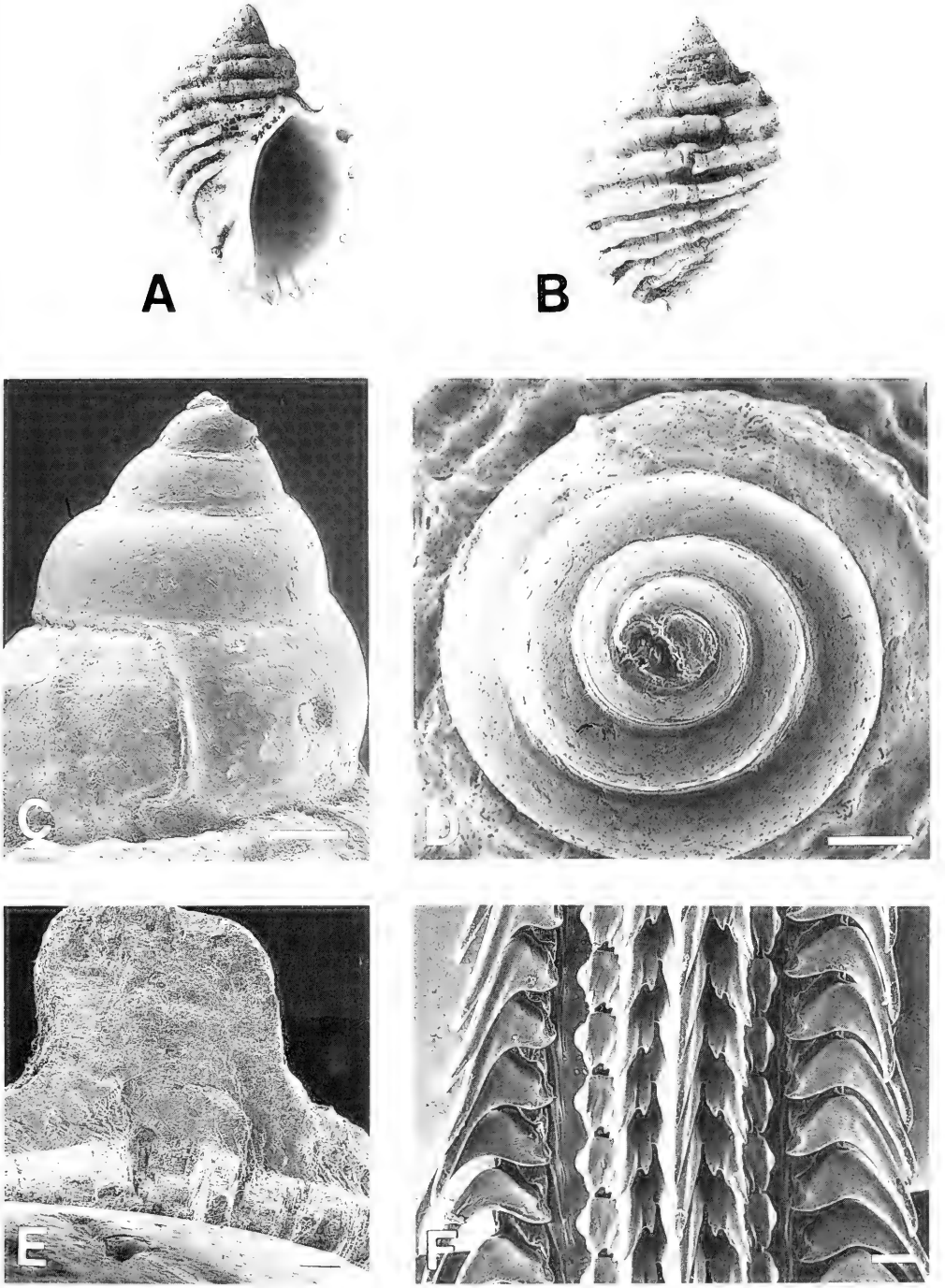

FIG. 9. *Dicathais orbita*. A, shell (58 mm), apertural view. B, shell (58 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.20 mm). D, protoconch, apical view, SEM (bar = 0.20 mm). E, shell ultrastructure, SEM (bar = 30 μm). F, radula, SEM (bar = 40 μm).

vated than spiral cords and adjacent to edge of lower, more heavily callused portion of columella. Shell white yellow to light brown (the latter especially in juveniles); aperture white yellow and columella white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (25–50%); aragonitic layer with crystal planes oriented parallel to growing edge (20–25%); calcitic layer (20–55%) (most pronounced at ribs) (Fig. 9E).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface usually with one bracket-shaped growth line and with callused, glazed rim (about 35–45% of opercular width) on left.

Anatomy: (based on living and preserved animals): Cephalic tentacles long, uniform black. Head-foot mottled black. Mantle edge crenate, following contour line of spiral ribs. Incurrent siphon long, uniform dark brown to black. Accessory boring organ large, dorsal to pedal gland.

Osphradial length about one-half ctenidial length; osphradial width between one-fourth and one-half ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along very small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior and posterior ctenidial lamellae usually wider than deep. Lateral and ventral edge of ctenidial lamellae concave.

Vaginal opening a slit, situated on end of thick, tubular, partially detached, distal end of pallial gonoduct, and located directly below anal opening. Bursa copulatrix a channel, with flange, emanating from ventral lobe of capsule gland, forming oval, semi-closed ventral channel. Farther posteriorly ventral lobe of capsule gland absent and ventral channel located under right lobe of capsule gland. Ingesting gland on left of posterior part of capsule gland, with central and many smaller white-walled chambers; gland nearly as large as capsule gland, visible on exterior of body as large, dirty white granular mass. Row of pink, iridescent seminal receptacles on dorsal periphery of albumen gland. Albumen gland shape difficult to discern in adults; morphology in juveniles resembling both omega-shaped and arch-shaped types. Pseudo-penis usually present, either as small appendix or equal in size and shape to penis of male specimens.

Penis large, strongly recurved, with long flagelliform tip, occupying entire space between tentacles and pallial complex, oval in cross section, with penial vas deferens as duct-within-a-duct system occupying nearly total width of penis. Cephalic vas deferens well developed, with internal, meandering tubular duct (similar to penial vas deferens). Prostate solid, dirty white, with accumulations of white granules. Prostate duct as closed tube adjacent to thin, cream-colored rectal wall.

Proboscis very large, unpigmented, slightly less than, or equal in width to, gland of Leiblein. Paired accessory salivary glands long and thin, each adjacent to salivary glands; left accessory salivary gland sometimes slightly longer than right one, and both about one-fourth of shell height. Salivary gland lobes inseparable; right portion under proboscis, extending to right anterior corner of buccal cavity. Valve of Leiblein elongate, irregularly shaped, separate from salivary gland mass. Salivary ducts attached to esophagus some distance from valve of Leiblein. Portion of mid-esophagus with glandular folds long, but poorly developed, except for short, widened section of mid-esophagus; widened section located adjacent to duct of gland of Leiblein. Duct between esophagus and gland of Leiblein thin. Posterior esophagus embedded in lower left side of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, cream-colored, covered with thick, strawlike outer membrane. Posterior blind duct slightly less than length of gland of Leiblein.

Stomach with large posterior projection. Ten to fifteen sizable folds on stomach wall. Two digestive diverticula present. Stomach typhlosole indistinct, poorly developed. Intestinal typhlosole thick, well developed. Long, wide rectal gland dark green. Rectal wall, at minute anal opening, pointing dorsally.

Radula: Ribbon length about 40–45% of shell height (Fig. 9F). Central cusp on rachidian constricted at base; lateral cusps with large inner denticle attached midway; lateral cusps convex on inner edge, concave on outer edge; several faint, knobby, outer denticles on upper half of lateral cusp, and well-developed denticles at base; lateral cusp edge continuing down to well-developed marginal cusp; rachidian base with lateral exten-

sion. Lateral teeth nearly equal in length to rachidian width.

Egg Capsules: About 9 mm in height, 6 mm wide, interconnected by basal membrane (Hedley, 1905). Dorsal surface of capsule elongate, rhomboidal, with elongate slit along longest axis. Hedley (1905) found egg capsules of "*Purpura*" *succincta* deposited on the ascidian *Cynthia praeputialis* Heller. Each capsule contains up to about 5,000 eggs (Phillips, 1969).

Ecology: Dicathais orbita has been observed clinging tightly to rocks between large seasquirts in the low intertidal zone of Botany Bay, Australia. It feeds on the barnacle *Tesseropora rosea* (Kraus) and displays patterns of vertical migration between shelter areas (lower intertidal) and high concentrations of prey (high intertidal) (Fairweather, 1988). It has also been observed on rocks, partially buried in sand. The western Australian variant *Dicathais "aegrota"* lives on limestone reef platforms where wave action is heavy (Phillips, 1969). It therefore seeks shelter in pockets and crevices, or partly buries itself (or gets buried) in the sand. Feeding usually occurs at high tide and at night (Phillips, 1969). Its varied prey consists mostly of mollusks (primarily *Cronia "avellana"*) and malacostracan crustaceans (Phillips, 1969). Large trematode parasites were present in several specimens I collected in Botany Bay (New South Wales, Australia), which had made these individuals sterile. Phillips (1969) also found trematodes in *D. "aegrota."* Some known predators of *Dicathais* are octopods, other *Dicathais* individuals (at least under laboratory conditions), and perhaps crustaceans. *Cronia "avellana"* and Crustacea are known to feed on *Dicathais* egg capsules (Phillips, 1969).

Distribution: Australia, Tasmania, Norfolk Island, Lord Howe Island, Kermadec Island, and New Zealand (Philips et al., 1973; Powell, 1979).

Genus *Drupa* Röding, 1798
(Fig. 10A–E)

Drupa Röding, 1798: 55.

Canrena Link, 1807: 126 [type: *Murex neritoideus* Linnaeus, 1767 by subsequent designation, Iredale, 1937: 256, = *Drupa morum* Röding, 1798, *in partem*].

Sistrum Montfort, 1810: 594 [type: *Sistrum album* Montfort, 1810, by original designation, = *Murex ricinus* Linnaeus, 1758, = *Drupa ricinus* (Linnaeus, 1758)].

Ricinula Lamarck, 1816: 1, pl. 395 [type: *Ricinula horrida* Lamarck, 1816, by subsequent designation, Children, 1823: 56 (as *Ricinula horida*), = *Drupa morum* Röding, 1798].

Ricinulus Lamarck; Chenu, 1859: 174 (invalid emendation for *Ricinula* Lamarck).

Ricimula A. A. Gould, 1855: 263 (error for *Ricinula* Lamarck).

Ricinella Schumacher, 1817: 240 [type: *Ricinella purpurata* Schumacher, 1817, by subsequent designation, Iredale, 1937: 256, = *Drupa rubusidaeus* Röding, 1798].

Pentadactylus Mörch, 1852: 87 [*non* Schultze, 1760, *nec* Gray, 1840] [type: *Murex ricinus* Linnaeus, 1758, by subsequent designation, Baker, 1895: 186, = *Drupa ricinus* (Linnaeus, 1758)].

Drupina Dall, 1923: 303 [type: *Ricinula digitata* Lamarck, 1816, by original designation, = *Drupa grossularia* Röding, 1798].

Type Species: Drupa morum Röding, 1798, by subsequent designation, Rovereto, 1899: 105; synonyms: *Nerita nodosa* Linnaeus, 1758 (*in partem*); *Murex neritoideus* Linnaeus, 1767 (*in partem*); *Ricinula globosa* Martyn, 1784 (non-binominal); *Ricinula horrida* Lamarck, 1816; *Ricinella violacea* Schumacher, 1817; *Ricinula horida* Lamarck, Children, 1823 (error for *horrida*).

Remarks: Cossmann (1903: 68) considered *Ricinula* (= *Drupa*) a full genus. Thiele (1929: 295) subdivided the genus *Drupa* into the subgenera *Drupa* (sections *Drupa, Morula,* and *Drupina*), *Cronia* (sections *Cronia, Morulina, Usilla, Muricodrupa*), *Phrygiomurex, Maculitriton,* and *Drupella.* Wenz (1941: 1113) included the subgenera *Drupa, Morulina, Usilla, Cronia, Muricodrupa, Phrygiomurex, Maculitriton, Morula,* and *Drupella* in *Drupa.* Keen (1971b: 553) placed *Drupa* in the Drupinae. Emerson & Cernohorsky (1973) divided *Drupa* into the subgenera *Drupa, Ricinella* and *Drupina* on the basis of shell morphology.

Shell: Protoconch similar to that of *Drupa grossularia* (Fig. 10D, E), tall, conical, consisting of at least 3.5 adpressed whorls [exact count could not be made from available specimen], with small subsutural plicae, interconnected by three thin spiral ridges, but other-

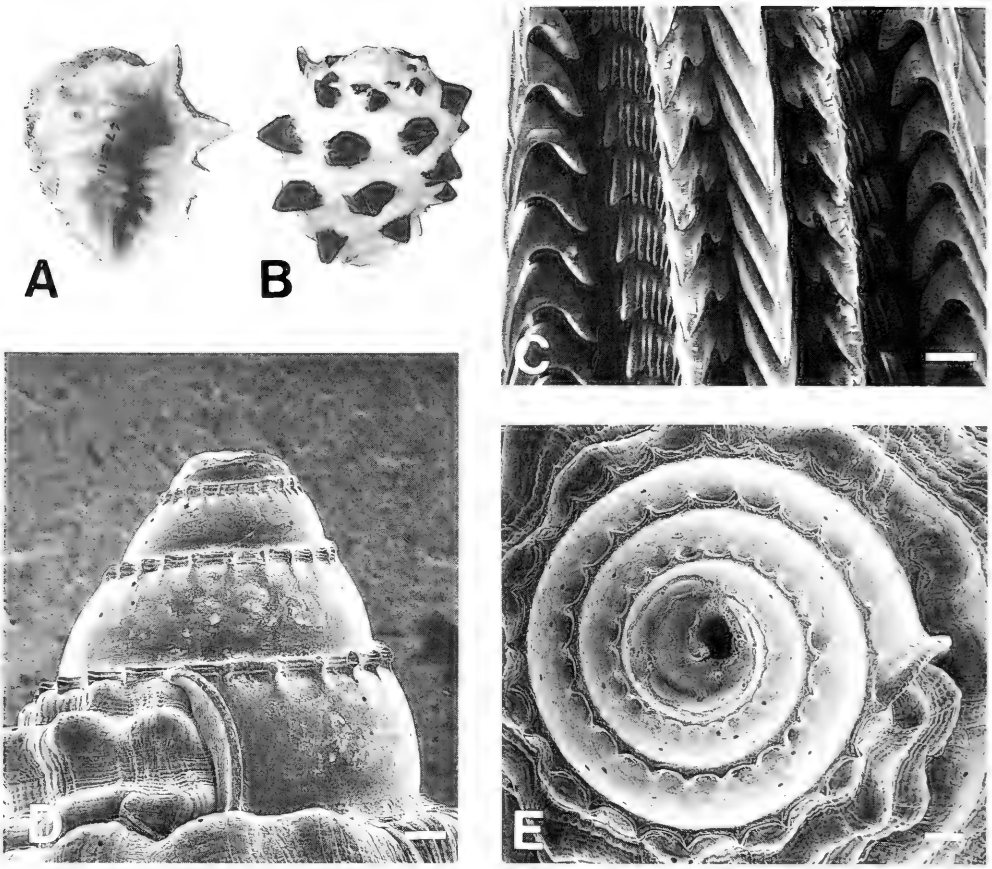

FIG. 10. A–C, *Drupa morum.* A, shell (35 mm), apertural view. B, shell (33 mm), abapertural view. C, radula, SEM (bar = 25 μm). D–E, *Drupa grossularia.* D, protoconch, side view, SEM (bar = 0.10 mm). E, protoconch, apical view, SEM (bar = 0.10 mm).

wise smooth, and with outward-flaring lip; sinusigeral notch covered by teleoconch. Teleoconch (Fig. 10A, B) globose but flat on apertural side, low-spired, of 3–4 adpressed whorls. Adult shell up to about 40 mm in height, 35 mm in width. Body whorl about 85–90% of shell height, dome-shaped, robust, thick, and sculptured with five rows of spiral bands of seven heavy, sometimes spinelike, axially arranged knobs. Largest knobs on second and third row, knobs on fifth row weakest. Thin, lamellose, spiral, microscopic riblets over entire whorl. Aperture about 95–100% of shell height; apertural opening narrow, elongate. Interior of apertural lip heavily callused, with pair of wide teeth, each pair comprising 2–4 denticles; in addition, two weak, separate denticles near anterior siphonal canal; interior of aperture with weak denticles at previous growth intervals. Anterior siphonal canal a short and open notch; posterior siphonal canal absent. Columella heavily callused, curving inward in center, and with three strong columellar teeth. Three to four well-developed knobs on siphonal fasciole. Shell white, knobs dark brown to black; aperture and columella purple.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (0–15%; lacking in some specimens); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–35%); aragonitic layer with crystal planes oriented parallel to growing edge (40–55%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–10%). Presence of calcitic layer questionable.

Operculum: D-shaped, tapered at lower end, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 4–7 bracket-shaped growth lines and with callused, glazed rim (about 35–40% of opercular width) on left.

Anatomy (based on living and preserved animals): Mantle edge, siphon and cephalic tentacles light green with white flecks; distal portion of tentacles dark brown with white tip. Side of foot white with many green dots; sole of foot light green with white specks. Minute accessory boring organ with long duct dorsal to long, thin pedal gland.

Osphradial length slightly more than one-half ctenidial length; osphradium and ctenidium about equal in width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium bending below osphradium. Anterior ctenidial lamellae wider than deep; posterior lamellae almost as wide as deep. Lateral edge of ctenidial lamellae concave; ventral edge straight.

Vaginal opening small, elliptical, situated on dorsal side of rodlike, tubular, partially detached extension of pallial gonoduct and located directly below anal opening. Bursa copulatrix consisting of main channel and connecting chamber on right side, the latter continuous with capsule gland. Ventral channel initially located under ventral lobe, farther posterior under right lobe, and formed by large, complex flange with longitudinal ridges. Ventral flange emanating from ventral epithelium. Ingesting gland dark brown, consisting of several small chambers filled with flocculent brown material; located on left side and partially ventral to capsule gland, extending to left side of albumen gland. Seminal receptacles white, located on dorsal periphery of omega-shaped albumen gland.

Penis large, strongly recurved, with small papilla-like tip. Penial vas deferens as duct-within-a-duct system occupying one-fourth of penial width. Cephalic vas deferens a well-developed duct-within-a-duct system. Prostate white, C-shaped in cross section (anteroposterior view), with large C-shaped lumen separating left and right lobes; folded over and under rectum, thus enveloping it. Seminal vesicles yellowish white.

Proboscis long, unpigmented, narrower than gland of Leiblein. Esophagus attached to ventral surface of proboscis by numerous, thin muscle threads. Accessory salivary glands absent. Large paired salivary gland lobes separate; right gland under proboscis; left one dorsal, extending between left side of proboscis and gland of Leiblein. Valve of Leiblein short, separate from salivary glands. Caplike structure present on anterior portion of valve of Leiblein. Salivary ducts attached to esophagus a short distance from valve of Leiblein. Valve of Leiblein adjacent to nerve ring. Glandular folds on mid-esophagus indiscernible. Esophagus directly attached to caramel brown gland of Leiblein. Posterior esophagus embedded along left side of gland of Leiblein. Gland of Leiblein spiral, forming two folds (three "lobes"). Posterior blind duct shorter than gland itself, but larger than one-half of gland length.

Stomach tubular, very elongate; distinct lines or small folds on posterior mixing area, and one diverticulum present. Stomach typhlosole and intestinal typhlosole well developed. Anal opening conspicuous. Rectal gland appearing integrated with hypobranchial gland and separated from rectum by epithelial layer.

Radula: Ribbon length about 30% of shell height (Fig. 10C). Central cusp of rachidian constricted at base; inner lateral denticle on base of lateral cusp attached almost along its entire side; outer edge of lateral cusp straight, lateral denticles absent; six to seven elongate marginal denticles on slightly sloping, narrow marginal edge, with one or two fused with base of lateral cusp; marginal cusp thicker and longer than marginal denticles. Lateral teeth curved, longer than one-half of rachidian width.

Egg Capsules: Unknown.

Ecology: Much information is available on the ecology of several species of *Drupa.* J. D. Taylor (1983) has extensively studied the ecology and in particular the feeding habits of *Drupa* species. Besides general information on feeding habits, species and sizes of prey from different geographic region were listed and discussed (J. D. Taylor, 1983). *Drupa morum* feeds mainly on eunicid polychaetes, such as *Lysidice* sp. (Bernstein, 1970), but occasionally also on *Lepidonotus* sp., *Perinereis* sp. and *Eurythoe complanata* (Pallas) (J. D. Taylor, 1984; Thomas & Kohn, 1985). *Drupa ricinus* feeds on *Dendropoma gregaria* (Thomas & Kohn, 1985).

J. D. Taylor (1971) reported finding *Drupa morum* on the outside of cobbles and boulders, and stated that *Drupa* species tend to live on vertical surfaces. I have found *Drupa morum* living on intertidal limestone benches, where wave action can be very high. Thomas & Kohn (1985) reported three species of *Drupa* living on a windward, seaward platform. *Drupa morum* lives subtidally as well, with individuals reaching a large size in this habitat. Emerson & Cernohorsky (1973) reported *Drupa morum* living at a depth of 40 m. I have collected *Drupa grossularia* at 10 m depth on Niue Island (central South Pacific).

Distribution: Indo-Pacific (between 35°N and 35°S), from Red Sea to Easter Island, Pitcairn Island, and Clipperton Island (Emerson & Cernohorsky, 1973).

Genus *Haustrum* Perry, 1811
(Fig. 11A–D)

Haustrum Perry, 1811, pl. 44.

Lepsia Hutton, 1884: 222 [type: *Buccinum haustrum* Martyn, 1784 [non-binomial], by subsequent designation, D. H. Graham, 1941: 155, = *Haustrum haustorium* (Gmelin, 1791)].

Type Species: Haustrum zealandicum Perry, 1811, by subsequent designation, Iredale, 1915: 474, = *Haustrum haustorium* (Gmelin, 1791); synonyms: *Buccinum haustrum* Martyn, 1784 (non-binominal); *Buccinum haustorium* Gmelin, 1791.

Remarks: Haustrum haustrum is a rejected name (ICZN, Opinion 479, 1957: 407), because it was published in a non-binominal work. Thiele (1929: 296) and Wenz (1941: 1117) both recognized *Haustrum* as a genus.

Shell: Protoconch not seen, but reported as having ". . . about 2 smooth whorls, . . ." (Suter, 1913: 422). Teleoconch (Fig. 11A, B) light, ovate, of 5–7 whorls, and with impressed suture, low spire, and high whorl expansion rate. Adult shell about 65 mm in height, 45 mm in width. Body whorl dome-shaped, about 85% of shell height, smooth, with 40–50 incised fine, spiral lines. Aperture very large, about 80% of shell height; apertural lip thin, without denticles, but showing grooved pattern at edge of lip. Columella flattened to concave, with heavy callus layer and axial fold. Anterior siphonal canal moderately short; posterior siphonal canal absent. Siphonal fasciole slightly curved, covered with callus. Shell brown grey, grooves white; columella white, with brown smudge on upper region; aperture white, with thin brown rim on edge.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (45–50%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–7%); calcitic layer (15–20%) (Fig. 11C).

Operculum: D-shaped, upper end rounded, with lateral nucleus in lower right (compare Fig. 1D). Free surface with staff-shaped growth lines; attached surface with about 1–3 arch-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot and tentacles unpigmented to faint yellowish. Kidney light cream brown. Digestive gland dark green. Cephalic tentacles short and stubby. Mantle edge follows contour of aperture. Incurrent siphon very short, not extending beyond mantle edge. Small accessory boring organ dorsal to wide pedal gland with folds (Fig. 4B).

Osphradial length less than one-half ctenidial length; osphradium and ctenidium equal in width or osphradial width slightly less than ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamella attached along one-half of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae wider than deep; posterior lamellae about as wide as deep. Lateral edge of ctenidial lamellae convex; ventral edges concave. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections (more pronounced in posterior lamellae).

Vaginal opening round, with diameter one-half that of capsule gland, situated on end of short tube, and located directly below anal opening. Bursa copulatrix running dorso-ventrally, splitting into capsule gland on right, and blind sac on lower left. Ventral channel minute, present only for short distance beneath ventral and left lobe, then present as few, thin ridges emanating from ventral epithelium; posteriorly, ventral channel formed

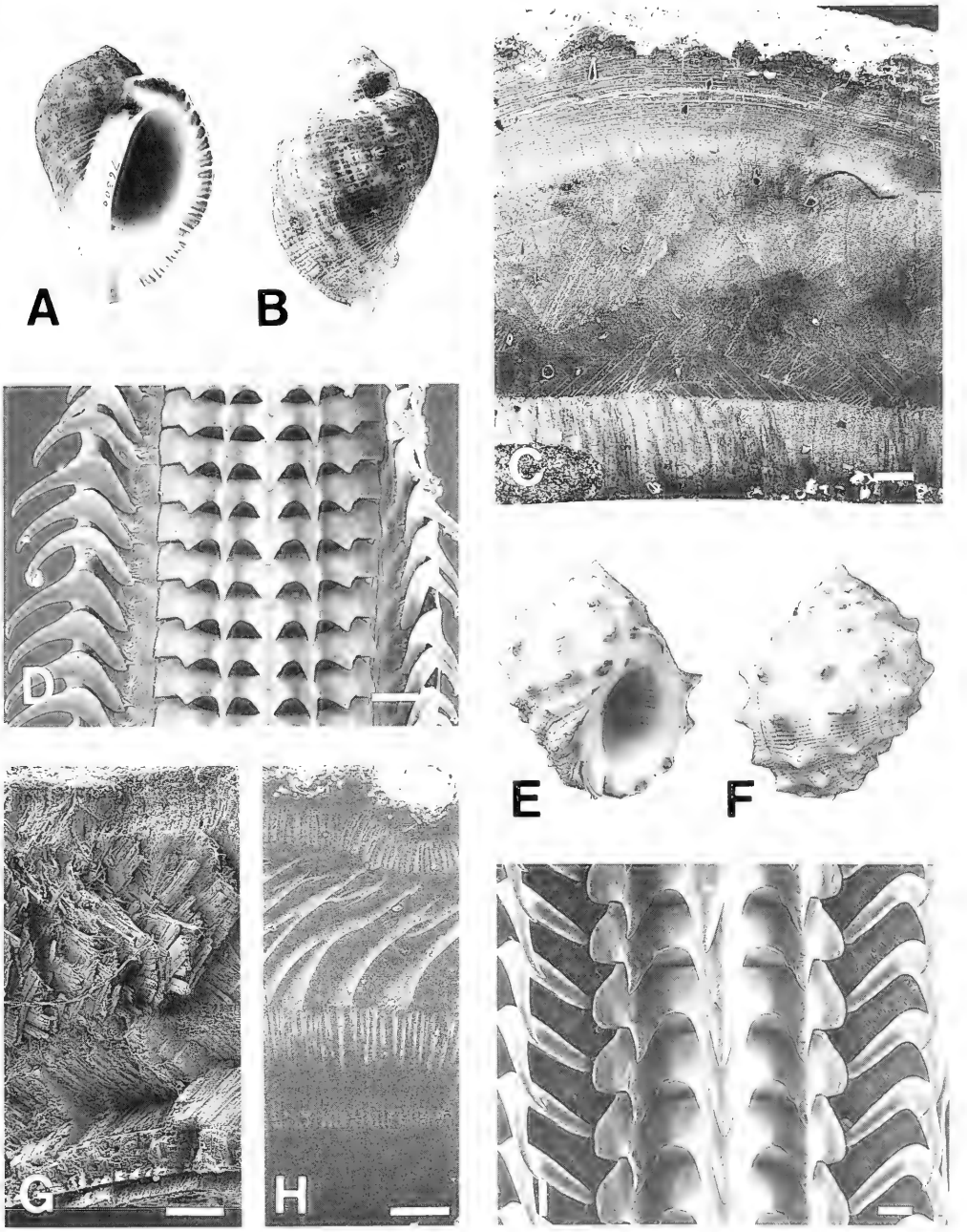

FIG. 11. A–D, *Haustrum haustorium.* A, shell (48 mm), apertural view. B, shell (48 mm), abapertural view. C, shell ultrastructure, SEM (bar = 0.10 mm). D, radula, SEM (bar = 25 μm). E–I, *Mancinella alouina.* E, shell (44 mm), apertural view. F, shell (44 mm), abapertural view. G, shell ultrastructure, SEM (bar = 0.20 mm). H, shell ultrastructure, polished surface, SEM (bar = 0.20 mm). I, radula, SEM (bar = 40 μm).

by flange originating from ventral epithelium, with minute longitudinal ridges (inward projections in cross section). Albumen gland arch-shaped, very elongate. Ovary olive green.

Penis small, lightly curved, smooth, and dorso-ventrally flattened. Penial duct open (perhaps due to poor preservation), very narrow, dorsal and along posterior margin of penis. Cephalic vas deferens closed, visible externally as thin, clear white line directly below surface. Duct continuing posteriorly on interior of mantle as open canal before entering prostate. Prostate small, solid, grey, opaque with dorso-ventral slit, adjacent to rectal wall. Seminal vesicles convoluted, poorly developed, dirty white.

Proboscis large, unpigmented, narrower than gland of Leiblein. Right accessory salivary gland long, thin, nearly one-half of shell height, located in right upper anterior corner of buccal mass, extending posteriorly and ventrally, adjacent to right side of salivary glands. Left accessory salivary gland absent. Yellow salivary gland mass consisting of elongate portions of glandular material with multitude of small threads. Well-developed left part of salivary mass about equal in size to right accessory salivary gland. Valve of Leiblein elongate, partially attached to salivary glands. Salivary ducts attached at varying distances from valve of Leiblein, which lies at least one length away from nerve ring. Portion of mid-esophagus with glandular folds long; folds poorly developed. Well-developed, long duct between esophagus and gland of Leiblein, nearly or about as thick as posterior esophagus. Posterior esophagus attached by minute threads of connective tissue to lower left portion of gland of Leiblein. Gland of Leiblein large, spiral, forming two folds, of hard consistency, light brown, with external strawlike membrane thickest in older specimens. Posterior duct very short (few mm), terminating with ampulla.

Stomach U-shaped, with large posterior mixing area. About 20 distinct folds, oriented towards center, on stomach wall, with minute lines crossing over. Yellow layer overlays grey, opaque folds. Two digestive diverticula present. Intestinal typhlosole well developed, with small, small parallel folds in intestinal groove. Intestine with many small lateral folds of varying sizes. Rectum very large in diameter. Rectal gland undetectable from outside due to dark brown to black hypobranchial gland. Anal opening large, well defined, with upward-pointing anal papilla.

Radula: Ribbon length approximately 20–25% of shell height (Fig. 11D). Short central cusp of rachidian wide at base; elongate, needle-shaped, well-developed, cusplike inner denticles separate from lateral cusps, and nearly as long as central cusp; outer edge of short and wide lateral cusps straight, devoid of denticles, sloping towards rachidian base. Lateral teeth thin, smooth, slightly longer than one-half of rachidian width.

Egg Capsules: Oval to circular, about 6 mm in height, with large, central, ovate exit hole. All capsules attached at common basal membrane (D. H. Graham, 1941).

Ecology: This species lives in the intertidal on rocks (Powell, 1979).

Distribution: New Zealand (Powell, 1979) and southern Australia (W. F. Ponder, personal communication).

Genus *Mancinella* Link, 1807
(Fig. 11E–I)

Mancinella Link, 1807: 115.

Type Species: Mancinella aculeata Link, 1807, by absolute tautonymy through its cited synonym, *Murex mancinella* Linnaeus, 1758 (ICZN, Opinion 911, 1970: 20), = *Mancinella alouina* (Röding, 1798); synonyms: *Mancinella mancinella* (Linnaeus, 1758), *species dubium,* rejected name (ICZN, Opinion 911, 1970: 21); *Volema alouina* Röding, 1798; ?*Volema glacialis* Röding, 1798; *Purpura gemmulata* Lamarck, 1816.

Remarks: Cossmann (1903: 71) placed *Mancinella* in the synonymy of *Purpura* Bruguière. Thiele (1929: 297), Clench (1947: 83), Keen (1971b: 549) and Abbott (1974: 1118) used *Mancinella* as a subgenus of *Thais.* Wenz (1941: 1118) used *Mancinella* as a full genus.

Cernohorsky (1969: 296–297) stated that *Mancinella mancinella* Linnaeus, 1758, is the type of the genus by tautonymy, although the Linnaean taxon is a composite species. Cernohorsky points out that it is clear that Linnaeus only described one of the specimens (*Mancinella mancinella* of authors) in the "*Murex mancinella*" box in the Linnaean collection. However, Vokes (1970) noted that Linnaeus' description does not fit any of the specimens in the box. Vokes followed F. A. Smith (1913: 287) and considered *Murex mancinella* a *nomen dubium.* Keen (1964) petitioned the ICZN that *Mancinella gemmulata*

(Lamarck, 1816) (= *M. aculeata* Link) be designated as the type of *Mancinella.* The ICZN ruled (Opinion 911, 1970: 20) that *Mancinella aculeata* be the type species of the genus *Mancinella.* An available earlier name for *Mancinella aculeata* is Röding's *Volema alouina.*

Shell: Protoconch unknown. Teleoconch (Fig. 11E, F) strong, oval, squat, of about five adpressed whorls. Adult shell up to about 60 mm in height, 40 mm in width. Globose body whorl about 95% of shell height and sculptured with five spiral rows of 9–10 occasionally spinelike, axially arranged knobs. Largest knobs on second and third row, knobs on fifth row weakest. About ten narrow minute ridges between rows. Aperture large, about 75% of shell height. Apertural lip with 10–12 spiral striae beginning about 1 cm from apertural edge. Siphonal canal moderately developed, deep, semi-closed. Columella flat to slightly concave, with angular curve in lower portion forming part of short, open anterior siphonal canal; posterior siphonal canal absent. Siphonal fasciole with 5–6 knobs. Shell cream brown, knobs rusty brown, especially when worn; aperture and columella light to dark orange, with apertural striae dark orange.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (15–20%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (7–9%); calcitic layer (4–6%) (Fig. 11G, H).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 4–7 bracket-shaped growth lines and with callused, glazed rim (about 35–45% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot and tentacles rusty, light to dark brown. Kidney olive green. Hypobranchial gland bright light green. Digestive gland grey brown. Mantle edge smooth; incurrent siphon extending far from mantle edge. Accessory boring organ dorsal to pedal gland (Fig. 4B).

Osphradial length slightly more than one-half ctenidial length; osphradial width nearly equal to ctenidial width. Osphradium symmetrical in shape along lateral axis; right pectin wider than left. Osphradial lamellae attached along very small portion of their base.

Anteriormost portion of ctenidium straight, extending slightly farther anteriorly than osphradium. Anterior and posterior ctenidial lamellae as deep as wide. Lateral edges of ctenidial lamellae faintly S-shaped; ventral edges concave.

Vaginal opening central, slightly protruded on short tubular oviduct and located below and posterior to anal opening. Bursa copulatrix short, as part of vagina and anterior to capsule gland. Ventral channel formed by small flange originating from ventral epithelium. Ventral flange with few longitudinal ridges and located under ventral lobe. Ingesting gland a single chamber (not visible from outside). Albumen gland of the omega- or arch-shaped type, with many long, white seminal receptacles on dorsal periphery. Ovary yellow (in preserved specimens).

Penis strongly recurved, with flagelliform tip, dorso-ventrally flattened. Penial vas deferens as central, minute duct-within-a-duct system occupying about one-sixth of penial width. Cephalic vas deferens thin, running along mantle prior to entering prostate. Prostate small, yellow, with central duct, smaller in diameter than adjacent rectum.

Proboscis large, unpigmented, nearly equal in width to gland of Leiblein. Paired accessory salivary glands very small, short, thin; left gland located in left anterior portion of buccal mass adjacent to salivary gland mass; right accessory salivary gland located in right anterior portion of buccal mass, adjacent to proboscis. Salivary glands small, yellowish, located to left of proboscis, and anterior to gland of Leiblein. Salivary ducts attached to anterior portion of esophagus directly anterior of valve of Leiblein. Valve of Leiblein elongate, adjacent to nerve ring. Folds on mid-esophagus nearly indiscernible. Duct between mid-esophagus and gland of Leiblein short and much thinner than posterior esophagus. Posterior esophagus adjacent to lower left portion of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, yellowish, with thin external membrane. Posterior duct about one-half of length of gland of Leiblein and with terminal ampulla.

Stomach nearly rectangular, with large posterior mixing area. About 12–15 folds on stomach wall, oriented towards center of stomach. Two digestive diverticula present. Stomach typhlosole only moderately developed. Intestinal typhlosole thin. Intestinal wall

with many minute lateral lines and small folds. Intestinal groove with few thin longitudinal folds. Rectum with moderate diameter. Anal opening well defined, with anal papilla.

Radula: Ribbon length about 25% of shell height (Fig. 11I). Rachidian with thick, needle-shaped central cusp; short, wide lateral cusps smooth, with outside edge sloping to rachidian edge. Lateral teeth smooth, about three-fourths of rachidian width.

Egg Capsules: Unknown.

Ecology: Mancinella alouina lives from the intertidal to subtidal zones on sheltered rocks, whereas *Mancinella echinulata* occurs in crevices on exposed reefs (Kilburn & Rippey, 1982). Remains of small crustaceans were present in the rectum of several animals examined.

Distribution: Red Sea and throughout Indo-Pacific (Cernohorsky, 1969).

Genus *Morula* Schumacher, 1817
(Fig. 12A–G)

Morula Schumacher, 1817: 68, 227.
Tenguella Arakawa, 1965: 123 [type: *Purpura granulata* Duclos, 1832, by original designation, = *Morula granulata* (Duclos, 1832)].

Type Species: Morula papillosa Schumacher, 1817 (*non* Philippi, 1849), by monotypy, = *Morula uva* (Röding, 1798); synonyms: *Drupa uva* Röding, 1798; *Ricinula nodus* Lamarck, 1816; *Ricinula aspera* Lamarck, 1816; *Ricinula morus* Lamarck, 1822; *Purpura sphaeridia* Duclos, 1832; *Ricinula alba* Mörch, 1852; ?*Sistrum striatum* Pease, 1868; ?*Morula nodilifera* Habe & Kosuge, 1966.

Remarks: Thiele (1929: 295) and Wenz (1941: 1114) considered *Morula* a section of the subgenus *Drupa* in the genus *Drupa. Morula granulata* was designated as type species of *Tenguella* Arakawa, 1965, based on radular characters (presence and number of marginal denticles). However, the number of marginal denticles is variable in both species and overlap occurs. *Tenguella* is herein considered synonymous with *Morula.*

Shell: Protoconch (Fig. 12C, D) tall, conical, of at least 4.25 adpressed whorls [exact count could not be made from available specimen], sculptured with 3 spiral cords of small bead-like pustules directly below suture, but otherwise smooth, and with outward-flaring lip; sinusigeral notch covered by teleoconch. Teleoconch (Fig. 12A, B) ovate, of 5–6 adpressed whorls, with moderately high spire. Adult shell up to about 27 mm in height, 17 mm in width. Body whorl about 80% of shell height, sculptured with five spiral rows of 12 short but well-developed knobs. One spiral, faintly lamellose ridge between rows with deep groove on each side. Elongate aperture about 68% of shell height. Apertural opening narrow, due to pair of heavy denticles pointing inward. Two smaller denticles located on lower end. Anterior siphonal canal very short, semi-closed; posterior siphonal canal absent. Columella concave; lower part with several faint denticles. Siphonal fasciole strongly curved, previous edges still visible, not knob-like. Shell white, knobs black; aperture and columella pink to violet purple.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (15–25%); aragonitic layer with crystal planes oriented parallel to growing edge (75–85%) (Fig. 12F).

Operculum: D-shaped, with S-shaped left edge, tapered at lower end, with lateral nucleus in lower right (Fig. 1F). Free surface with bracket-shaped growth lines; attached surface with about 4–6 bracket-shaped growth lines and with callused, dull rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals): Head with long cephalic tentacles emanating from common base. Lower part of head-foot mottled black and white to uniform black on lower portion; upper part with white and orange flecks. Tentacles uniform black at bases, white distally, or white with small black lateral band at eye levels. Mantle edge crenate, folded; underside of mantle with black and white patches. Incurrent siphon uniform black, or with white flecks. Kidney caramel brown. Digestive gland dark brown. Sole white with central, opaque, white speckled band, oriented antero-posteriorly. Accessory boring organ large, with short duct opening close to anteriorly located pedal groove. Hypobranchial gland very large, divided into red brown, white, and green portions, and with black rods of unknown composition pointing towards mantle cavity. Ventral pedal gland combined with accessory boring organ.

Osphradial length slightly greater than one-half ctenidial length (Fig. 3D); osphradial

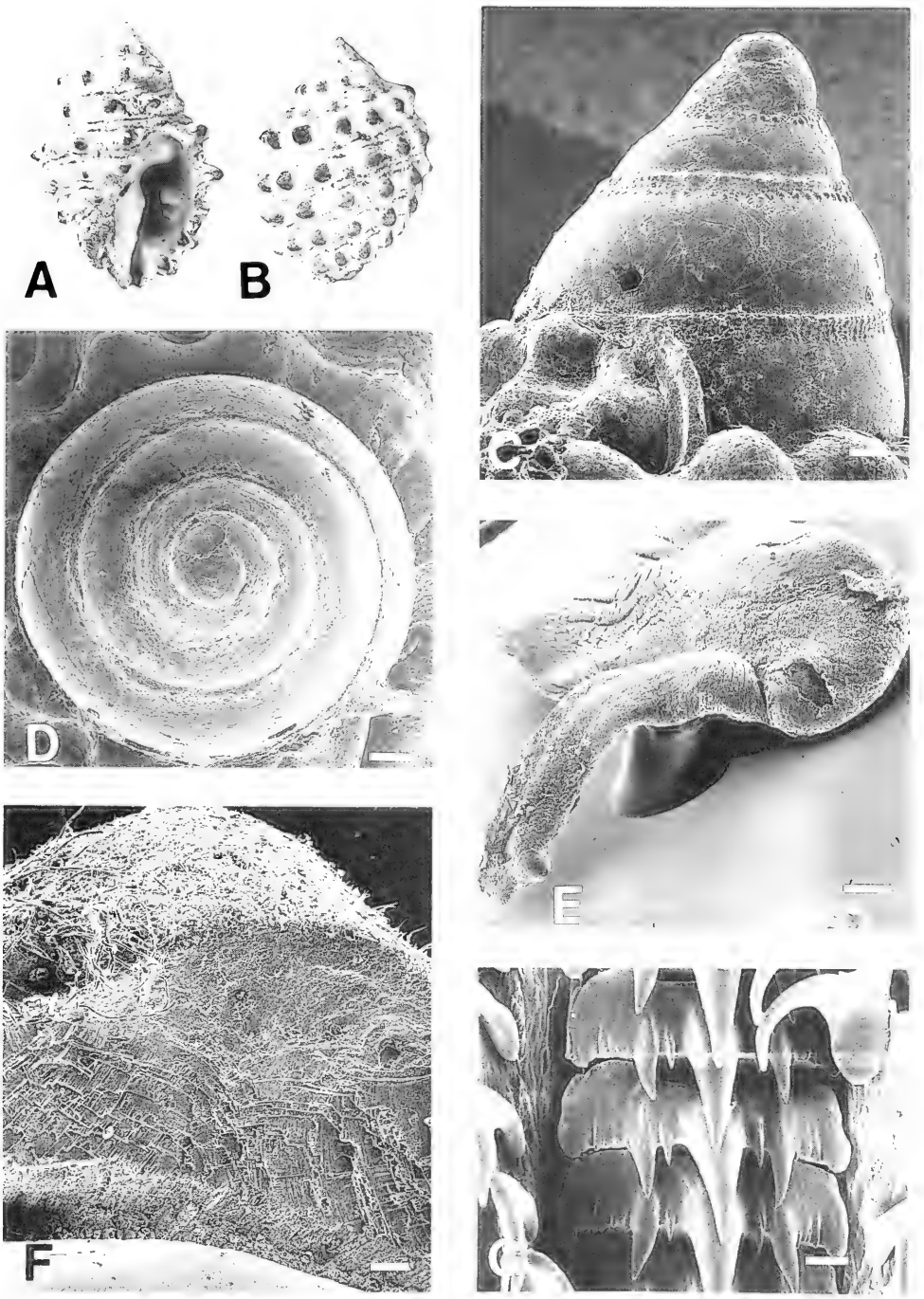

FIG. 12. *Morula uva*. A, shell (25 mm), apertural view. B, shell (25 mm), abapertural view. C, protoconch, side view, SEM (bar = 60 μm). D, protoconch, apical view, SEM (bar = 60 μm). E, penis, viewed postero-anteriorly, SEM (bar = 0.20 mm). F, shell ultrastructure, SEM (bar = 0.10 mm). G, radula, SEM (bar = 10 μm).

width equal to or slightly greater than ctenidial width. Osphradium more tapered at posterior end; right pectin slightly wider than left. Osphradial lamellae attached along most of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae deeper than wide; posterior lamellae as deep as wide. Lateral edges (Fig. 3D, le) of ctenidial lamellae concave; ventral edges straight. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening a short slit (more rounded in juveniles) situated on distal end of tubular extension of pallial gonoduct and located beneath anal opening. Bursa copulatrix as dorso-ventral slit open to vagina and continuous with capsule gland. Vagina continuing as ventral channel with large, circular ventral flange with many longitudinal and well-developed ridges; flange positioned below left lobe of capsule gland anteriorly, smaller, flattened, and below both lobes posteriorly. Ventral channel branching away from capsule gland, forming large posterior bursa. Branch of bursa continuing as oviduct, larger portion as blind sac. Bursa connected to single-chambered ingesting gland with short duct. Ingesting gland larger than albumen gland and black when viewed from outside. Albumen gland staff-shaped, with anterior portion being much shorter and less developed. Few seminal receptacles (3–5) at dorsal side branching from ovi-sperm duct prior to it connecting to albumen gland. Ovary white to yellow. [The female reproductive system of *Morula granulata* was described in detail by Srilakshmi (1991)].

Penis (Fig. 5E, 12E) very large, strongly recurved, round in cross section, V-shaped, with flattened, large side lobe; distal end of penis varying in length and attached by small connection to proximal part of penis. Penial vas deferens as duct-within-a-duct system occupying about one-fifth of penial width. Cephalic vas deferens minute, describing "Z" pattern. Prostate solid, glandular, opaque, white opaque or dark brown, with closed duct; prostate much larger than rectum and not separated from it by layer of epithelium. Seminal vesicles well developed, white to dark orange brown.

Proboscis large, equal in width to gland of Leiblein, occasionally folded and horseshoe-shaped, laying against left side of gland of Leiblein. Paired accessory salivary glands club-shaped, small, equal in length, much smaller than one-half of shell height; left accessory salivary gland embedded in left salivary gland; right gland separate. Salivary glands very large, much larger than accessory salivary glands and almost as large as gland of Leiblein, located dorsally either as separate lobes or solid mass. Salivary ducts attached close to valve of Leiblein. Valve of Leiblein short, with caplike structure on anterior end, and lying adjacent to nerve ring, separate from salivary glands. Glandular folds of mid-esophagus nearly indiscernible. Duct between mid-esophagus and gland of Leiblein very thin. Posterior esophagus separate from gland of Leiblein. Gland of Leiblein spiral, forming two folds, of soft consistency, consisting of small cavities, dark brown, lacking strawlike membrane.

Stomach as wide tube with few very large folds and many minute folds on stomach wall of posterior mixing area. Small unciliated area between posterior mixing area and intestine. Stomach and intestinal typhlosoles very well developed. One diverticulum present directly anterior to esophagus. Anal opening inconspicuous but with very large papilla. Thin rectal gland along entire capsule gland.

Radula: Ribbon length about 15% of shell height (Fig. 12G). Central cusp on rachidian tooth needle-shaped, with moderately wide base; lateral denticle separate from lateral cusp; outer and inner edge of lateral cusp straight, smooth; several stubby marginal denticles present on wide, horizontal edge of rachidian; wide, short marginal cusp. Lateral teeth strongly curved, smooth, with wide base; about one-half of rachidian width.

Egg Capsules: Unknown.

Ecology: Common on intertidal limestone benches, where it feeds almost exclusively on vermetid gastropods (Kay, 1971; Miller, 1970; J. D. Taylor, 1976, 1984).

Distribution: Indo-Pacific, from Red Sea to Isla Guadalupe and Clipperton Island (Cernohorsky, 1969; Keen, 1971b).

Genus *Nassa* Röding, 1798
(Fig. 13A–G)

Nassa Röding, 1798: 132 (*non* Lamarck, 1799, = *Nassarius* Duméril, 1806).
Iopas H. & A. Adams, 1853: 128 [type: *Buccinum sertum* Bruguière, 1789, by sub-

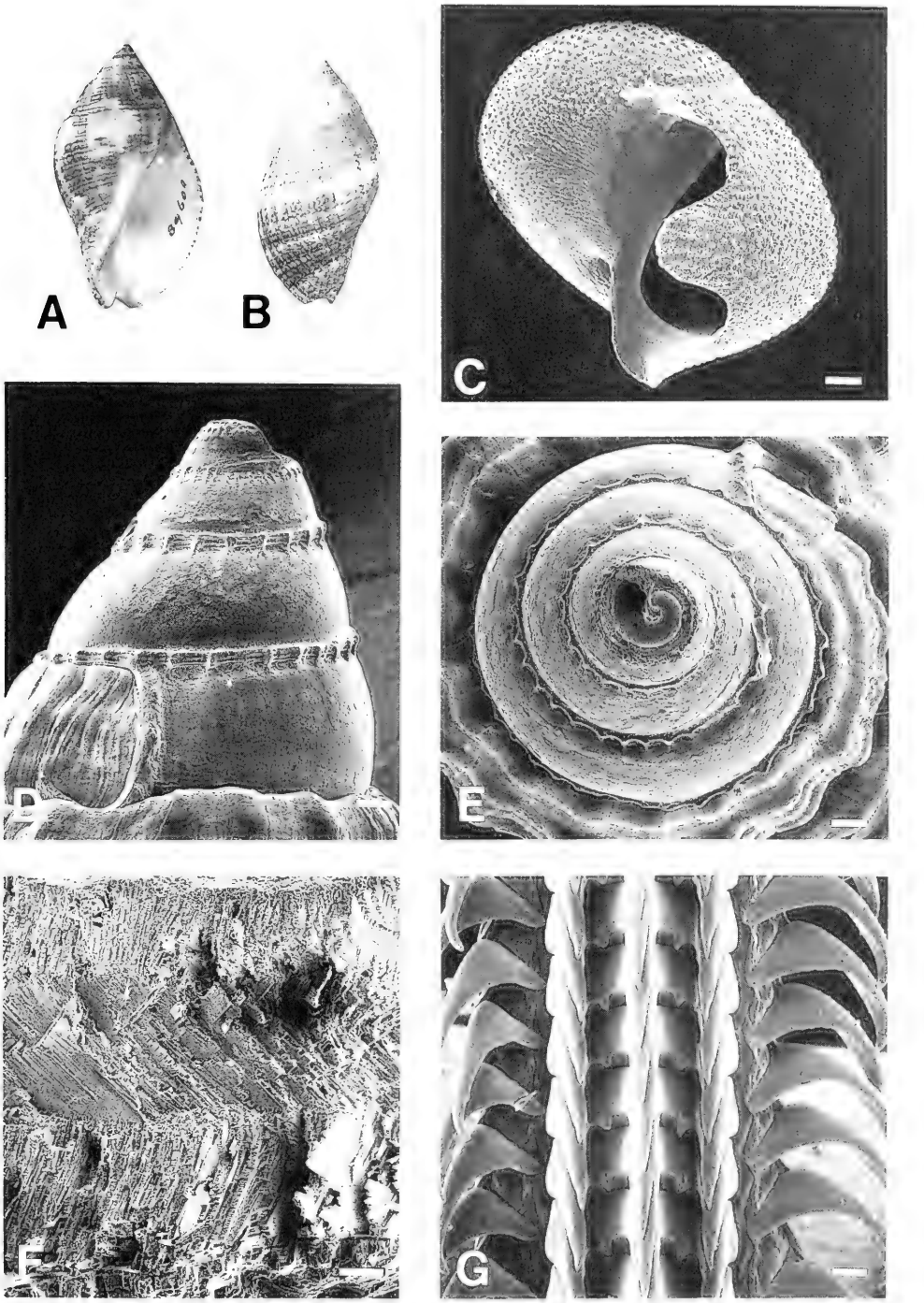

FIG. 13. A–C, F–G, *Nassa serta:* A, shell (40 mm), apertural view. B, shell (44 mm), abapertural view. C, larval shell, side view, SEM (bar = 25 μm). F, shell ultrastructure, SEM (bar = 0.10 mm). G, radula, SEM, (bar = 25 μm). D–E, *Nassa* "*francolina*" D, protoconch, side view, SEM (bar = 80 μm). E, protoconch, apical view, SEM (bar = 80 μm).

sequent designation, Baker, 1895: 185, = *Nassa serta* (Bruguière, 1789)].
Jopus Schaufuss, 1869 (error for *Iopas*).
Jopas Baker, 1895: 185 (unjustified emendation of *Iopas*).

Type Species: According to a number of authors (Winckworth, 1945; Iredale & McMichael, 1962; Cernohorsky, 1969), Dall (1909) subsequently designated *Nassa picta* Röding, 1798, as the type species of *Nassa.* However, Dall (p. 47) does not list the name *picta,* but rather "*Purpura sertum* Lam" as type of *Nassa,* which was not one of the species included by Röding and is therefore unavailable. I can find no valid subsequent designation and here designate the type species as *Nassa picta* Röding, 1798, = *Nassa serta* (Bruguière, 1789); synonyms: *Buccinum sertum* Bruguière, 1789; *Buccinum coronatum* Gmelin, 1791; ?*Stramonita hederacea* Schumacher, 1817; ?*Buccinum francolinus* Bruguière, 1789; *Buccinum situla* Reeve, 1846.

Remarks: Cossmann (1903: 68) considered *Nassa* a full genus (as *Iopas*), and included, besides *Iopas s.s, Taurasia* Bellardi, 1882. Thiele (1929: 296) used *Jopas* and included the subgenera *Jopas* (= *Nassa*) and *Vexilla.* Wenz (1941: 1116) used *Nassa* and included the subgenera *Nassa, Vexilla,* and *Taurasia.*

Controversy exists about whether the genus *Nassa* contains one or two species. The nominal species *serta* and *francolina* can be separated on the basis of shell sculpture and geographic distribution (see "Distribution"). Individuals from the Pacific Ocean, traditionally grouped under *N. serta,* have shells with relatively coarse spiral ribs, whereas the shells of Indian Ocean specimens have very fine spiral lines and appear nearly smooth. I suspect, however, that future research will show that these taxa are conspecific, considering the range of variation in sculptural patterns in many other rapanine species.

Shell: Embryonic shell (Fig. 13C) with well-developed beak and pattern of spiral rows of microscopic volcanolike pustules. Protoconch (Fig. 13D, E; typical *N. francolina*) tall, conical, of at least 4.25 adpressed whorls [exact count could not be made from available specimen], with subsutural plicae interconnected by three thin spiral ridges, but otherwise smooth, and with outward-flaring lip; sinusigeral notch covered by teleoconch. Teleoconch (Fig. 13A, B) elongate, slender, fusiform, of 6–7 adpressed whorls. Adult shell up to about 70 mm in height, 35 mm in width. Body whorl rounded, about 85–90% of shell height. Body whorl sculptured with about 30 small, spiral cords of minute pustules, nearly smooth in typical *N. francolina.* Aperture elongate, large, about 75% of shell height, curved angularly at base to form part of siphonal canal. Apertural lip smooth interiorly, but crenate at edge, corresponding to external pattern of small ridges. Siphonal notch wide and open. Columella lightly callused and rounded. Posterior siphonal canal absent, but protrusion of columellar callus directly across from similar protrusion on inside of apertural lip forming canal in posteriormost end of aperture. Siphonal ridge with similar pattern as on body whorl, slightly curved, adjacent to columellar callus. Shell with varying color patterns comprising combinations of cream (usually as median band running around body whorl), light and dark brown spiral bands which may consist of blotches; aperture white with some yellow tinges towards edge, and dark brown crenulations on edge, corresponding with dark brown spiral ridges; top of columella yellow white, caramel brown at base.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (45–50%); aragonitic layer with crystal planes oriented parallel to growing edge (30–35%); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–20%) (Fig. 13F).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface without distinct growth lines and with callused, glazed rim (about 45–55% of opercular width) on left.

Anatomy (based on living and preserved animals): Cephalic tentacles long, uniform black, with distal halves of tips white. Head-foot uniform black, lightly spotted with white. Mantle edge simple and straight. Incurrent siphon long, uniform black. Hypobranchial gland brown to yellow. Kidney brown. Nephridial gland S-shaped, wide, opaque. Digestive gland dark brown. Sole of foot yellow, with pattern of thin ridges. Accessory boring organ with long duct. Pedal gland large, located under accessory boring organ (Fig. 4B).

Osphradial length equal to or greater than ctenidial length; osphradium and ctenidium

about equal in width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae of right pectin attached along one-half of their base; those of left pectin attached along entire base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior and posterior ctenidial lamellae much deeper than wide. Lateral and ventral edges of ctenidial lamellae variable in shape. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening slit-shaped, with two longitudinal flanges in opening and located below and posterior to anal opening. Bursa copulatrix as large storage area with fine horizontal lines, continuous with capsule gland. Small, circular flange originating from ventral epithelium, under small ventral lobe of anterior portion of capsule gland; flange minute, hooklike posteriorly, perpendicular to capsule gland lobes. Flange split at base in central portion of capsule gland. Ingesting gland as large thin-walled chamber containing granular, caramel brown material. Seminal receptacles on dorsal periphery of omega-shaped albumen gland elongate to club-shaped, white, nearly reaching oviduct. Ovary orange.

Penis long, thin, slightly recurved, flagelliform, oval in cross section (Fig. 5C). Penial vas deferens as duct-within-a-duct system occupying one-fourth of penial width. Cephalic vas deferens thin, inconspicuous. Prostate small, white, with central duct, separated from very large rectum by epithelial layer. Seminal vesicles well developed, white.

Proboscis very large, equal in width to gland of Leiblein, white. Paired accessory salivary glands thin, equally long, about one-third of shell height. Left accessory gland adjacent to salivary gland mass; right gland in anterior right area of buccal cavity separate from salivary gland mass. Paired accessory salivary glands equal in size to salivary gland mass. Salivary glands inseparable, oriented dorso-ventrally. Valve of Leiblein elongate, not embedded in salivary glands. Salivary ducts attached to anterior portion of valve of Leiblein. Valve of Leiblein adjacent to nerve ring. Portion of mid-esophagus with glandular folds short, well developed. Duct between mid-esophagus and gland of Leiblein distinct, but thinner than esophagus. Posterior esophagus attached to lower left portion of gland of Leiblein. Gland of Leiblein spiral, forming one fold, light brown, with strawlike membrane. Posterior blind duct of gland of Leiblein longer than one-half of length of gland itself and opening into dorsal branch of renal afferent vein, extending beyond kidney opening.

Stomach as wide tube with large posterior mixing area. Large number of folds on stomach wall of posterior mixing area; folds oriented towards stomach center; each one containing many lateral folds, directing small particles laterally. Stomach typhlosole well developed with two digestive diverticula at base; intestinal typhlosole narrow but distinct. Several small elongate folds in intestinal groove. Large bulbous papilla extending from dorsal rectal wall, lying over very small anal opening. Large thick orange gland over pallial gonoduct. Rectal gland dark green, thin, along entire capsule or prostate.

Radula: Ribbon length about 25% of shell height (Fig. 13G). Rachidian with thin central cusp; inner lateral cusp denticle separate from lateral cusp in males; denticle may be absent, especially in narrower rachidian tooth of females (see Maes, 1966); lateral cusps smooth, less developed in female specimens relative to central cusp; outer edge of lateral cusps sloping nearly straight down to edge of rachidian. Lateral teeth very wide at base and as long as rachidian width.

Egg Capsules: Cylindrical, 6–8 mm in height; base wide, 1–2 mm in length. Some appearing to consist of four sides, base constricted lengthwise along axes. All capsules attached to basal membrane. Exit hole on circular apical plate, usually slightly off center.

Ecology: Nassa serta lives under boulders and coral rubble on limestone benches and reef flats of the Pacific Ocean. Analysis of stomach contents revealed rachidian teeth of *Nassa* radula, suggesting cannibalism. Some specimens were found laying egg capsules under a large piece of coral rubble at low tide.

Distribution: Indian Ocean, from Cocos-Keeling Islands (Maes, 1967: 132) throughout tropical Pacific Ocean (Abbott & Dance, 1982) (typical *Nassa serta*); in remainder of Indian Ocean (Cernohorsky, 1969) usually referred to as *Nassa francolina.*

Genus *Neorapana* Cooke, 1918
(Fig. 14A–F)

Neorapana Cooke, 1918: 7 (as a subgenus of *Acanthina* Fischer von Waldheim, 1807).

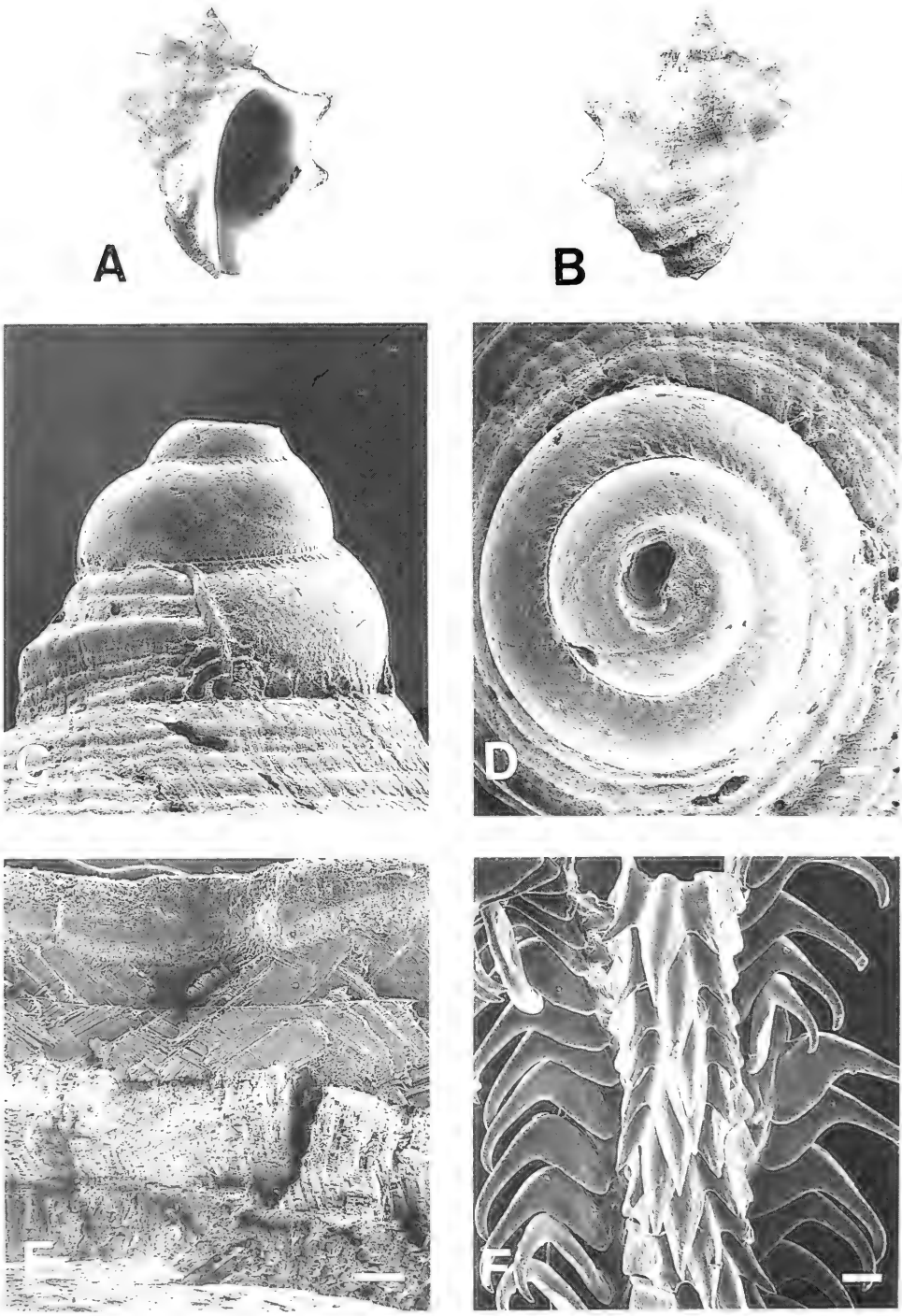

FIG. 14. *Neorapana muricata.* A, shell (45 mm), apertural view. B, shell (45 mm), abapertural view. C, protoconch, side view, SEM, (bar = 0.20 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, SEM (bar = 0.20 mm). F, radula, SEM (bar = 35 μm).

Type Species: Purpura muricata Broderip, 1832, by original designation, = *Neorapana muricata* [Broderip, 1832]; synonyms: *Purpura truncata* Duclos, 1832; *Monoceros tuberculatum* Sowerby, 1835, *ex* Gray Ms.

Remarks: Cooke based his separation of *Neorapana* from *Acanthina s.s.* on radular characters. The shell of *N. muricata* resembles that of species of *Acanthina* in having a labial tooth. This single character was the primary criterion for inclusion of this species in the genus *Acanthina* by several authors. Thiele (1929: 297) allotted *Neorapana* section status under the subgenus *Mancinella* of the genus *Thais.* Wenz (1941: 1118) considered *Neorapana* a subgenus of *Thais.* Keen (1971b: 554) considered *Neorapana* a full genus in the Rapaninae.

Specimens of *Neorapana muricata* used in this study are representatives of typical *Neorapana tuberculata* (Sowerby, 1835); *N. muricata* has a greater distribution, ranging from Guaymas, Mexico, to Ecuador, whereas typical *N. tuberculata* ranges from Cabo San Lucas, Mexico, throughout the Gulf of California to Mazatlán, Mexico (Keen, 1971b), thus partially overlapping in range with *N. muricata.* I regard the latter as merely a form or variant of the former; intergrading shell forms suggest conspecificity. Detailed anatomical and molecular studies, however, could show these forms to be different species. But until such a study has been performed, I will continue considering these two names to be synonyms, with *muricata* having priority over *tuberculata.*

Shell: Protoconch (Fig. 14C, D) tall, conical, of at least 3.25 adpressed whorls [exact count could not be made from available specimen], with faint, small subsutural plicae and microscopic pustules (last whorl), and with outward-flaring lip; sinusigeral notch covered by teleoconch. Because the descriptions of *N. muricata* beyond the shell morphology are based on "tuberculate" specimens, a description of the tuberculate shell morph follows. Teleoconch (Fig. 13A, B) large, heavy, conical, of 5–6 adpressed whorls. Adult up to about 60 mm (80 mm in typical *N. muricata*) in height, 45 mm (70 mm in typical *N. muricata*) in width. Body whorl about 85–90% of shell height, somewhat dome-shaped, sculptured with well-developed shoulder, and bearing four rows of spiral bands of 6–7 knobs. Suture lying adjacent to and following lower contours of second row of knobs on penultimate whorl. First row of knobs on angular shoulder, highly developed and with discontinuous ridge on knobs. Second, third and fourth rows consecutively less developed. Knobs of two uppermost rows lying directly under and above each other, as do third and fourth row, but knobs on latter pair not axially aligned with knobs on first two rows. Five to eight narrow, delicately lamellose spiral ridges between pairs of rows of knobs. Aperture large, about 80–90% of shell height. Apertural lip with 12–16 ridges on inside surface, most pronounced on last growth increment. Edge of lip crenate and thin. Anterior siphonal canal short, well developed in some specimens, but only a notch in others; posterior siphonal canal poorly developed. Columella lightly to heavily callused, rounded to concave. Siphonal fasciole strongly curved, bending outward and free of callus margin. Shell cream to yellow orange brown; columella white to yellow; interior apertural lip white to yellow orange.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45°-angle to growing edge (15–20%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–8%); calcitic layer (8–15%) (Fig. 14E).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 3–6 bracket-shaped growth lines and with callused, glazed rim (about 45–50% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot mottled black on white base. Mantle edge crenate, following aperture contour. Siphon long, black and white, extending some distance beyond mantle edge. Hypobranchial gland with cottonlike appearance. Digesting gland caramel brown (one male examined) or dark olive green (one female examined). Accessory boring organ relatively small, dorsal to narrow ventral pedal gland in females (Fig. 4B), with small transverse folds on transition zone.

Osphradial length about one-half ctenidial length; osphradial width less than one-half ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Os-

phradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior and posterior ctenidial lamellae wider than deep. Lateral edge of ctenidial lamellae strongly concave; ventral edge moderately concave or S-shaped. Distal tips of ctenidial support rods extending beyond lateral edge as papillate projections.

Vaginal opening slit-shaped, situated on distal end of short, attached, tubular extension of pallial gonoduct, and located below and slightly posterior to anus. Bursa copulatrix small, with large inner ridges; bursa in open connection with vagina and located on right side of it, continuous with capsule gland. Large, complex ventral flange located under right lobe of capsule gland. Ingesting gland very large, dark brown, filled with dark brown granular chunks; single chambered, with small tubes connecting walls; extending from dorsal left posterior portion of capsule gland to left of albumen gland. Albumen gland omega-shaped, tilted strongly backwards. Seminal receptacles on dorsal periphery of albumen gland white.

Penis strongly recurved, elongate, thick, muscular gradually tapering, and oval in cross section. Penial vas deferens as minute duct-within-a-duct system occupying one-eighth of penial width. Prostate white, with large longitudinal central opening closed, directly adjacent to rectum. Seminal vesicles well developed, orange or white.

Proboscis black and white, much thinner than gland of Leiblein. Paired accessory salivary glands thin, equally long, about one-third of shell height; left gland adjacent to salivary gland, right one largely separate from salivary gland. Paired salivary glands as joined mass, each lobe consisting of many worm-shaped strands connected by small ducts. Valve of Leiblein elongate, separate from salivary gland mass, a considerable distance from nerve ring. Salivary ducts attached to anterior portion of esophagus directly anterior of valve of Leiblein. Glandular folds on mid-esophagus inconspicuous. Duct between gland of Leiblein and esophagus poorly developed. Posterior esophagus attached to posterior lower left side of gland of Leiblein. Gland of Leiblein large, spiral, forming one fold with hole in center for passage of anterior aorta, of hard consistency, yellow to cream, and with thin strawlike membrane. Posterior blind duct of gland of Leiblein about one-half of length of gland of Leiblein and entering dorsal branch of afferent renal vein.

Stomach tubular, with large posterior mixing area, with 6–15 folds on stomach wall oriented towards center of stomach. Stomach typhlosole very large, sometimes continuing up left portion of stomach wall. Intestinal typhlosole thin, flat. Several small folds in intestinal groove. Wide, thick fold demarcating entrance of intestine in older female specimens. Smooth area adjacent to thick fold. Two large digestive diverticula present. Rectum of moderate diameter, embedded in spongy connective tissue. Long papilla lying over distinct but small anal opening. Wide rectal gland adjacent to most of prostate and capsule gland.

Radula: Rachidian with thick, wide central cusp, nearly one-third of rachidian width (Fig. 14F); inner edge of lateral cusps convex, outer edge slightly concave; outer edge of lateral cusp sloping steeply towards marginal edge of rachidian, and with faint minute folds on lower base. Lateral teeth with wide bases and curving "hooked" tips; length of lateral teeth greater than rachidian width.

Egg Capsules: Unknown.

Ecology: Neorapana muricata lives on boulders in the intertidal zone but may occur in the sublittoral. I found many specimens partially buried in sand at the sand-rock interface; it is not clear whether this resulted from burrowing behavior or from sediment accumulation. Small crabs were present in the mantle of two specimens of *Neorapana muricata.* The diet of this species is not known.

Distribution: Eastern Pacific, from eastern Baja California, Mexico, to Ecuador (Keen, 1971b).

Genus *Nucella* Röding, 1798
(Fig. 15A–G)

Nucella Röding, 1798: 130.

Polytropa Swainson, 1840: 80, 305 [type: *Buccinum lapillus* Linnaeus, 1758, by subsequent designation, Gray, 1847: 138, = *Nucella lapillus* (Linnaeus, 1758)].

Polytropalicus Rovereto, 1899: 105 (unnecessary replacement name for *Polytropa* Swainson; section of *Purpura*) (*nomen dubium*).

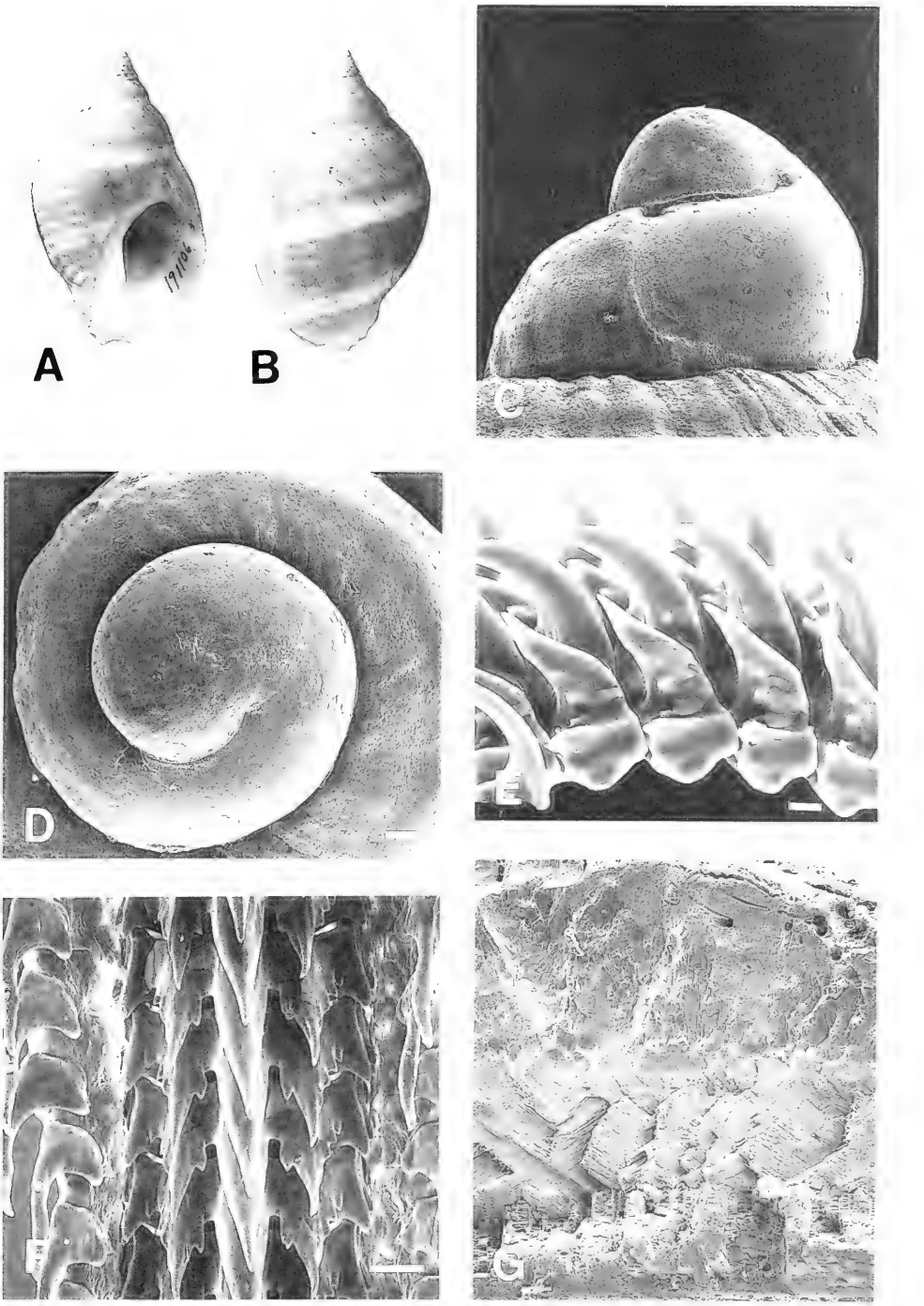

FIG. 15. *Nucella lapillus.* A, shell (32 mm), apertural view. B, shell (32 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, SEM (×55). F, radula, SEM (bar = 20 μm). G, radula, side view, SEM (bar = 10 μm).

Type Species: Buccinum filosum Gmelin, 1791, by subsequent designation, Stewart, 1927: 386 (footnote 260), = *Nucella lapillus* (Linnaeus, 1758); synonyms: *Buccinum lapillus* Linnaeus, 1758: 739; *Nucella theobroma* Röding, 1798; *Purpura imbricata* Lamarck, 1822; *Purpura bizonalis* Lamarck, 1822; *Purpura buccinoidea* Blainville, 1829; *Purpura celtica* Locard, 1886; *Coralliophila rolani* Bogi & Nofroni, 1984.

Remarks: Cossmann (1903: 68) recognized Rovereto's subgenus *Polytropalicus,* not realizing that it was an unnecessary replacement name for *Polytropa.* Thiele (1929: 298) included the sections *Nucella, Acanthina, Acanthinucella* Cooke, 1918, and *Neothias* (as *Neothais;* unjustified emendation) in the genus *Nucella.* Wenz (1941: 1123) raised these sections to subgeneric status under *Nucella. Nucella* species have often been placed in *Thais* and *Purpura.* For detailed information on the taxonomic history of the type species designation for *Nucella,* see Rehder (1962) and Kool & Boss (1992).

Shell: Protoconch (Fig. 15C, D) short, conical, of about 1.25 smooth whorls, and with impressed suture; transition with teleoconch smooth. Teleoconch (Fig. 15A, B) highly polymorphic, but usually elongate, oval, of 6–7 adpressed whorls. Adult shell up to about 55 mm in height, 30 mm in width. Body whorl rounded, about 80% of shell height, smooth or sculptured with pattern of 15 spiral, occasionally lamellose ridges. Aperture oval, about 65% of shell height; apertural lip wide, inside smooth, occasionally with 3–4 denticles on edge of thickened lip. Anterior siphonal canal short, open or semi-closed; posterior siphonal canal absent. Columella with moderate amount of callus, flat to concave, with angular curve in lower portion to form part of siphonal canal. Siphonal fasciole poorly developed, adjacent to callus layer. Shell color variable: white, grey, yellow, brown, orange-red; often with banding patterns of these colors; aperture and columella white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (15–25%) (not always present); aragonitic layer with crystal planes oriented parallel to growing edge, occasionally colored reddish brown (15–35%); calcitic layer (40–85%) (Fig. 15G).

Operculum: D-shaped, upper end rounded, with lateral nucleus in lower right (compare Fig. 1D). Free surface with staff-shaped growth lines; attached surface with about 3–5 arch-shaped growth lines and with callused, glazed rim (about 35–40% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot light yellow to white, with elongate, thin cephalic tentacles and short anterior siphon. Mantle edge smooth, straight. Sole of foot with ridges. Small nephridial gland arching over pericardium. Large accessory boring organ separated from adjacent, equally large pedal gland present in females (Fig. 4A).

Osphradial length slightly more than one-third ctenidial length; osphradial width less than one-half ctenidial width. Osphradium symmetrical in shape along lateral axis; right pectin usually wider than left. Osphradial lamellae attached along one-half of their base.

Anteriormost portion of ctenidium straight, extending slightly farther anteriorly than osphradium. Anterior ctenidial lamellae wider than deep or as wide as deep; posterior lamellae as wide as deep. Lateral edge of ctenidial lamellae varying from strongly convex to straight; ventral edge straight. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening round with slightly swollen surrounding edges and located below and posterior to anus. Bursa copulatrix a large diverticulum, connected to vagina by wide ventral passage. Ventral channel formed by two small interlocking flanges located under ventral lobe of capsule gland, one arising from left lobe, the other from ventral epithelium. Albumen gland arch-shaped, elongate. Single-chambered ingesting gland extending between capsule gland and albumen gland. Ovary yellow to light golden in living specimens. Pseudo-penis usually present in females.

Penis dorso-ventrally flattened, straight or lightly curved, and with abruptly tapering, papillalike end. Penial vas deferens as minute, simple duct, semi-closed by overlapping ventral and dorsal sides of penis. Cephalic vas deferens well developed. Prostate gland bilobed, white, with dorso-ventral slit partially open to mantle cavity. Vas deferens poorly developed, whitish, separated from rectum by epithelial layer. Testis light brown to golden in living specimens.

Paired accessory salivary glands extremely long, usually longer than one-half of shell height; left gland intertwined with salivary gland mass, right one separate from salivary gland mass and located in right anterior corner of buccal cavity. Salivary gland mass in center of dorsal buccal cavity between gland of Leiblein and short, pear-shaped valve of Leiblein. Salivary ducts attached to anterior portion of esophagus at some distance from valve of Leiblein. Glandular folds on mid-esophagus indiscernible. Duct between mid-esophagus and gland of Leiblein short, thick. Esophagus attached to left side of gland of Leiblein in horseshoe-shape. Gland of Leiblein spiral, of hard consistency, yellowish. Posterior blind duct very short, with terminal ampulla.

Stomach tubular, with 8–12 large folds on stomach wall oriented toward center of stomach. Stomach typhlosole extending upwards on left portion of posterior mixing area. Intestinal typhlosole thick, wide. Two digestive diverticula present. Large papilla lying over equally large anal opening. Rectal gland sometimes not apparent.

Radula: About 30–35% of shell height (Fig. 15E, F). Rachidian widening dramatically from cusp bases toward base of rachidian; central cusp of rachidian thin, somewhat constricted at base; inner lateral denticle low on base of lateral cusp, and occasionally bifurcate; straight outer edge of lateral cusp with several short denticles at base; base of lateral cusp adjacent to base of large marginal cusp; marginal cusps in different plane than lateral cusps (about 75° angle) and parallel to elongate lateral extension at base of rachidian tooth, resulting in bifid rachidian edge. Lateral teeth shorter than rachidian width.

Egg Capsules: Oval-elongate, vase-shaped, up to about 9 mm in height, 3 mm in width, each attached with short, thin base about 1 mm long. Apex tapered with central exit hole. Capsules deposited some distance from other capsules but interconnected by base. Each capsule contains up to 600 embryos, 94% of them being nurse eggs (Crothers, 1985).

Ecology: Probably more is known about *Nucella* ecology than that of any other muricid. *Nucella lapillus* and its western American congeners have been the topic of many comprehensive studies (Kincaid, 1957; Crothers, 1985) and Ph.D. dissertations (Emlen, 1966; Spight, 1972; Etter, 1987). *Nucella* feeds on barnacles and mussels (Largen, 1967; Murdoch, 1969; Connell, 1970; Crothers, 1973; Spight, 1982) in the rocky intertidal zone and is eaten by crabs and birds (Spight, 1976). Moore (1938) reported winter and spring to be the main spawning period.

Studies show that environmental factors (wave action, food availability, etc.) drastically influence shell morphology (Cooke, 1895; Agersborg, 1929; Colton, 1922; Moore, 1936).

Distribution: North Atlantic Ocean from southern Portugal to Novaya Zemblya [records from the western Mediterranean (Nordsieck, 1968, 1982), Azores, Morocco, Senegal, and Canary Islands (Adanson, 1757) are highly suspect (Cooke, 1915) and need confirmation]; Great Britain; Ireland; Iceland; Greenland; New Jersey, U.S.A., to northern Canada (Abbott, 1974) (For extensive list of geographical range and localities, see Cooke, 1915.)

Genus *Pinaxia* H. & A. Adams, 1853
(Fig. 16A–E)

Pinaxia H. & A. Adams, 1853: 132.
Conothais Kuroda, 1930: 1 [type: *Conothais citrina* Kuroda, 1930, by monotypy].

Type Species: Pinaxia coronata H. & A. Adams, *ex* A. Adams MS, 1853, by monotypy, = *Pinaxia versicolor* (Gray, 1839); synonyms: *Pyrula versicolor* Gray, 1839; ?*Conothais citrina* Kuroda, 1930.

Remarks: Cossmann (1903: 68) allocated section status to *Pinaxia* under *Iopas* (*Iopas*) [= *Nassa*], whereas Thiele (1929: 297) used *Pinaxia* as a section of *Thais* (*Thais*). Wenz (1941: 1121) allotted subgeneric status to *Pinaxia* under *Thais.* Fujioka (1985a: 242) considered *Conothais* congeneric with *Pinaxia.* I agree with Fujioka based on intergrades between *Conothais citrina* and *Pinaxia versicolor.*

Shell: Protoconch (Fig. 16C, D) tall, conical, of about four adpressed whorls, with small subsutural plicae and several microscopic pustules (last whorl), and with outward-flaring lip and sinusigeral notch. Teleoconch (Fig. 16A, B) small, conical to bulbous, smooth, of 4–6 adpressed whorls. Adult shell up to about 25 mm in height, 15 mm in width, with thin,

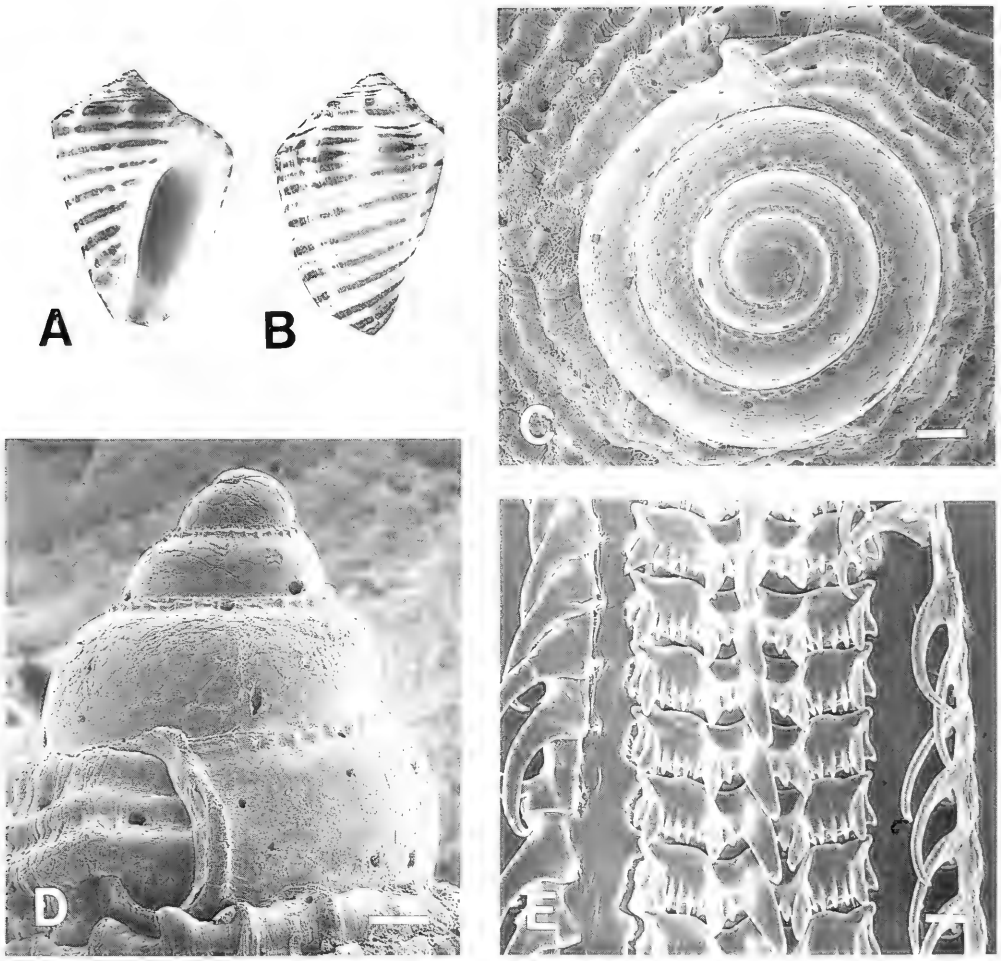

FIG. 16. *Pinaxia versicolor.* A, shell (17 mm), apertural view. B, shell (17 mm), abapertural view. C, protoconch, apical view, SEM (bar = 0.10 mm). D, protoconch, side view, SEM (bar = 0.10 mm). E, radula, SEM (bar = 10 μm).

cream brown periostracum. Body whorl about 90% of shell height, smooth, usually with heavy shoulder with 6–7 inconspicuous wide swellings or knobs. Aperture about 80% of shell height, elongate, narrow. Upper part of thin apertural lip nearly straight, lower end curved. Apertural lip with elongate (4–6 mm) riblets starting about one mm from edge. Anterior siphonal canal a poorly developed notch; posterior siphonal canal absent. Columella nearly straight, margin rounded, with little callus. Siphonal fasciole forming thin, slightly elevated ridge adjacent to callus on lower columella. Shell yellow to orange with 10–11 thin, continuous or discontinuous, spiral, dark brown bands (although banding pattern may be absent); apertural lip and columella yellow to orange brown.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (10–15%); aragonitic layer with crystal planes oriented parallel to growing edge (70–75%); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–25%).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free side with bracket-shaped growth rings; attached side without or with 1–2 bracket-shaped growth

lines and with callused, glazed rim (about 30–45% of opercular width) on left.

Anatomy (based on poorly preserved animals only): Head-foot predominantly brown, uniform black at periphery. Cephalic tentacles elongate, brown dorso-centrally, black on periphery, and with white tips. Mantle edge simple, smooth, following contour of aperture, and brown on inside. Siphon long, brown with white specks, extending substantial distance beyond mantle edge. Large accessory boring organ dorsal to ventral pedal gland in females (Fig. 4B).

Osphradium and ctenidium about equal in length; both about equal in width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamella attached along small portion of their base.

Anteriormost portion of ctenidium bending towards anterior portion of osphradium; both equidistant from mantle edge. Anterior ctenidial lamellae wider than deep; posterior lamellae as deep as wide. Lateral and ventral edges concave.

Vaginal opening below and posterior to anal opening. Ventral channel located near left side of capsule gland, consisting of single, hooked flange which originates from ventral epithelium. Large ventral lobe in anterior portion of capsule gland. Ingesting gland between capsule gland and albumen gland. Albumen gland omega-shaped, large, tilted backwards. Low number of white seminal receptacles on dorsal side of albumen gland.

Penis large, slightly recurved, dorsoventrally flattened, elongate, with flagelliform tip. Penial vas deferens as central duct-within-a-duct system occupying about one-third of penis width. Cephalic vas deferens a well-developed duct-within-a-duct system, inconspicuous from outside. Prostate small, closed, solid, yellow, lacking prominent duct, adjacent to narrow, white-walled rectum. Seminal vesicles well developed, golden, orange or white.

Proboscis thinner than gland of Leiblein, unpigmented. Paired accessory salivary glands stubby, club-shaped, short, of equal length, much less than one-half of shell height; left gland completely loose from salivary gland mass; right accessory salivary gland adpressed to salivary gland mass. Salivary glands soft, cottonlike, located dorsally in buccal cavity, larger than accessory salivary glands. Valve of Leiblein elongate, adjacent to salivary gland mass and nerve ring, and with cap structure on anterior end. Salivary ducts attached to anterior portion of esophagus at base of valve of Leiblein. Portion of mid-esophagus with glandular folds long; folds poorly developed. Duct between gland of Leiblein and esophagus as thick as or thicker than posterior esophagus. Esophagus free from gland of Leiblein. Gland of Leiblein spiral, forming one fold between two attached lobes, with central hole for passage of anterior aorta, of hard consistency, yellow, with strawlike outer membrane. Posterior blind duct of gland of Leiblein nearly equal in length to gland itself.

Tubular stomach with about ten folds. Rectal gland not apparent. Small anal opening on tubular extension of rectum. Anal papilla absent.

Radula: Ribbon length about 20–25% of shell height (Fig. 16E). Central cusp on rachidian tooth thin, needle-shaped, straight or bent to either side (artifact?); small backward extension present at central cusp base close to rachidian base; inner lateral denticle on lower half of lateral cusp; outer edge of lateral cusp straight, with one outer denticle on base of lateral cusp, three more well-developed denticles on wide, horizontal marginal edge; lateral cusps nearly equal in length to central cusp; large marginal cusp more than one-half of lateral cusp length; laterally extending lobe on rachidian edge and rachidian base somewhat widened anteroposteriorly. Lateral teeth slender with wide bases, hooked at distal ends, and longer than one-half of rachidian width.

Egg Capsules: Unknown.

Ecology: Pinaxia versicolor lives on intertidal sandflats with rocks and algae. Rehder & Ladd (1973) reported this species from the subtidal zone.

Distribution: Indo-Pacific, from Mauritius (Drivas & Jay, 1987) to Japan (Abbott & Dance, 1982).

Genus *Plicopurpura* Cossmann, 1903 (Fig. 17A–F)

Plicopurpura Cossmann, 1903: 69 (as section of *Purpura*).

Microtoma Swainson, 1840: 72 (*non* Laporte, 1832) [type: *Buccinum patulum* Linnaeus, 1785, by subsequent designation, Herrmannsen, 1847: 42, = *Plicopurpura patula* (Linnaeus, 1758)].

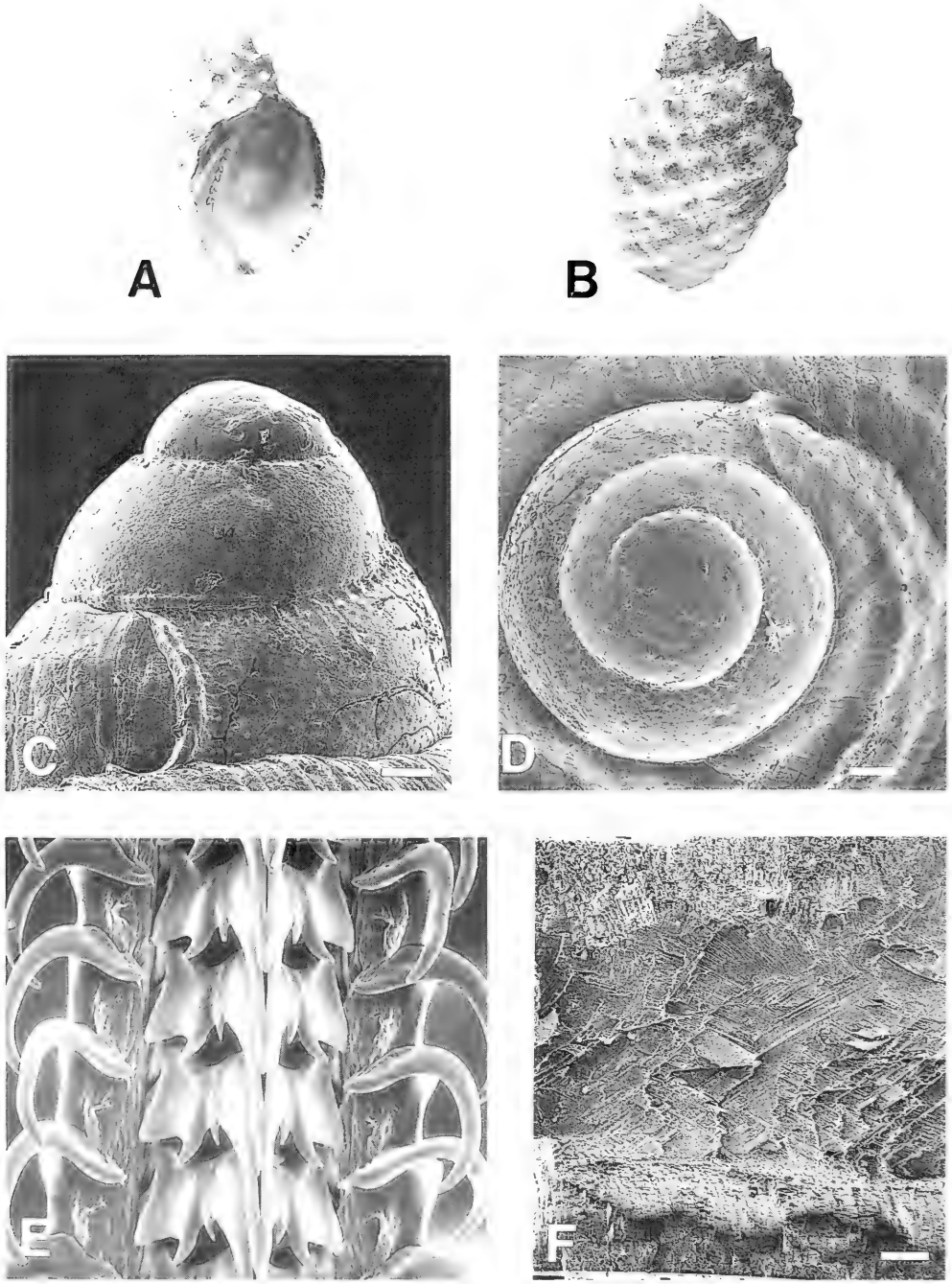

FIG. 17. *Plicopurpura patula*. A, shell (53 mm), apertural view. B, shell (53 mm), abapertural view. C, protoconch, side view, SEM (bar = 70 μm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, radula, SEM (bar = 20 μm). F, shell ultrastructure, SEM (bar = 0.15 mm).

Purpurella Dall, 1871: 110 (*non* Robineau-Desvoidy, 1853, *nec* Bellardi, 1883; as subgenus of *Purpura*) [type: *Purpura columellaris* Lamarck, 1816, by original designation, = *Plicopurpura columellaris* (Lamarck, 1816)].

Microstoma Paetel, 1875: 126 (error for *Microtoma* Swainson).

Patellipurpura Dall, 1909: 50 [type: *Buccinum patulum* Linnaeus, 1758, by monotypy, = *Plicopurpura patula* (Linnaeus, 1758); as section of *Thais*].

Patellapurpura Abbott, 1974: 180 (error for *Patellipurpura* Dall).

Type Species: Purpura columellaris Lamarck, 1816, by original designation, = *Plicopurpura columellaris* (Lamarck, 1816); synonyms: ?*Buccinum patulum* Linnaeus, 1758; *Haustrum dentex* Perry, 1811 [*nomen oblitum;* ICZN, Opinion 886, 1969: 129]; *Purpura pansa* A. A. Gould, 1853.

Remarks: Cossmann (1903: 69) introduced *Plicopurpura,* because the earlier name, *Purpurella* Dall, was preoccupied. Dall (1909: 50) erected *Patellipurpura* for the Caribbean species *patula,* which lacks a columellar fold as found in *Plicopurpura* and placed both *Patellipurpura* and *Plicopurpura* as sections under *Thais.* Thiele (1929: 296) followed Cossmann in recognizing *Plicopurpura* and *Purpura s.s.* as sections of the genus *Purpura,* and synonymized *Patellipurpura* with *Purpura s.s.* (see below). Wenz (1941: 1115) accorded full generic status to *Plicopurpura* and included *Plicopurpura* and *Patellipurpura* as subgenera. Keen (1971b: 552) indicated that *Plicopurpura* is perhaps a nodose subgenus of *Purpura.* Kool (1988b) showed that *Plicopurpura* is sufficiently different from *Purpura* to warrant separate generic status.

Traditionally three species/subspecies were included in this genus: *Plicopurpura columellaris, P. patula,* and *P. patula pansa. Plicopurpura patula* occurs in the Caribbean Province and has been separated from populations in the eastern Pacific since the closure of the Isthmus of Panama; based on the fact that *P. patula* no longer interbreeds with *P. columellaris* in nature, I consider these two taxa separate species on the basis of interrupted gene flow. Keen (1971b: 552) allotted full species status to the two eastern Pacific species: *P. columellaris* and *P. pansa.* However, Wellington & Kuris (1983) provided evidence for conspecificity of these two nominal species. I suspect this species complex to consist of two species: one in the Caribbean, the other in the eastern Pacific (see "Remarks" under treatment of *Stramonita*). Molecular data may demonstrate the actual degree of divergence.

Shell: Protoconch (Fig. 17C, D) moderately tall, conical, of about 2.25 adpressed whorls, with numerous faint subsutural plicae and microscopic pustules (last whorl), with outward-flaring lip and sinusigeral notch. Teleoconch (Fig. 17A, B) large, oval, of 5–6 adpressed whorls, and with high whorl-expansion rate. Adult shell up to about 85 mm in height, 55 mm in width. Body whorl dome-shaped, about 90% of shell height. Body whorl sculptured with 7–8 spiral rows of nodules (most pronounced and nearly spinelike on many juvenile specimens) with four small striae between rows. Aperture wide, oval, about 80% of shell height. Apertural lip smooth on inside, crenate on edge, corresponding to pattern of striae on outside. Anterior siphonal canal a poorly developed notch; posterior siphonal canal well developed in older specimens. Columella flattened, wide, with acute angle of 135° in lower portion. Siphonal fasciole a slightly elevated uneven ridge. Shell grey white to light brown; apertural lip white, with darker areas indicating dark pattern on outside surface; edge of lip caramel brown, with blotched dark brown crenulations; columella caramel brown (sometimes partially white) frequently with sizable dark brown upper parietal blotch.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (30–35%); aragonitic layer with crystal planes oriented parallel to growing edge (10–15%); aragonitic layer with crystal planes oriented perpendicular to growing edge (60–70%) (Fig. 17F). Presence of calcitic layer questionable; scored with "?" in cladistic analysis.

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 4–6 arch- and bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals; Fig. 3A): Head-foot nearly uniform black. Elongate cephalic tentacles black except for white distal tips. Grooved sole of foot yellowish. Mantle edge slightly crenate, following aperture contours. Incurrent siphon

black, extending beyond mantle edge. Pedal gland combined with well-developed accessory boring organ (Fig. 4B).

Osphradial length about one-half ctenidial length; osphradial width about one-fifth ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae much wider than deep; posterior lamellae about as deep as wide. Lateral and ventral edge of ctenidial lamellae varying from concave to convex. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening situated on distal end of loose, tubular extension of pallial gonoduct, curled towards mantle or toward buccal mass, and located below and posterior to anal opening. Bursa copulatrix a dorso-ventral chamber connecting with vagina, continuous with capsule gland. Small ventral lobe in anterior portion of capsule gland, lying over ventral channel, which is formed by small, heavily ciliated, circular flange with longitudinal folds and grooves. Capsule gland embedded in spongy connective tissue. Posteriorly, ventral sperm channel divided into two branches: one unciliated, leading into ingesting gland; the other ciliated, leading to albumen gland. Albumen gland omega-shaped. Ingesting gland single- or double-chambered, extending from posterior lower left part of capsule gland to left of anterior part of albumen gland. Seminal receptacles located at dorsal periphery of anterior portion of albumen gland. Females occasionally with minute pseudo-penis.

Penis large, strongly recurved, oval in cross section, tapering distally or with extended, flagelliform tip. Penial vas deferens as duct-within-a-duct system occupying about one-seventh of penial width. Cephalic vas deferens thin, inconspicuous, in straight line from penis to prostate. Prostate closed, directly adjacent to rectum, both embedded in opaque spongy connective tissue. Seminal vesicles well developed, brown.

Proboscis moderately muscular, one-half of gland of Leiblein width, semi-transparent, with pink odontophores (visible in living specimens). Paired salivary glands usually equal in length (but right accessory salivary gland occasionally shorter); both glands elongate, thin, adjacent to salivary glands, about one-third of shell height. Salivary glands often joined, globular in appearance, larger than accessory salivary glands. Salivary ducts attached to anterior portion of esophagus at some distance from valve of Leiblein. Anterior portion of esophagus widened, forming elongate valve of Leiblein, adjacent to salivary glands. Portion of mid-esophagus with glandular folds short, swollen; folds poorly developed. Duct between mid-esophagus and gland of Leiblein well-developed, about equal to posterior esophagus width. Posterior esophagus adjacent to gland of Leiblein, connected to it by connective tissue, or separate. Gland of Leiblein spiral, forming two lobes with dorso-ventral opening for anterior aorta, caramel brown, covered with thick, strawlike outer membrane. Posterior blind duct of gland of Leiblein narrow, elongate, longer than gland itself, and entering dorsal branch of afferent renal vein.

Stomach tubular, with small posterior mixing area with about ten large folds on right two-thirds of interior stomach; left portion smooth. Two digestive diverticula present. Stomach typhlosole and intestinal typhlosole thin. Rectal gland long, thin, dark green, adjacent to entire length of capsule gland. Rectum large in diameter, embedded in spongy connective tissue without separation from capsule gland or rectum by epithelial layer. Anal opening small, well defined, with distinct anal papilla.

Radula: Ribbon length about 45% of shell height (Fig. 17E). Central cusp of rachidian tooth elongate, needle-shaped, with slightly widened base and elongate median slit in central cusp extending from base of rachidian to slightly below tip; small inner lateral denticle separate from but directly adjacent to central and lateral cusps; lateral cusps smooth, with concave outer edge and convex inner edge; outer edge of lateral cusp sloping steeply down to rachidian base. Lateral teeth thin, strongly curved, equal in length to rachidian width.

Egg Capsules: Flat and rounded, up to about 4 mm in width; flat, round top of capsule with central, circular exit hole. Each capsule containing 50–100 eggs measuring about 0.24 mm in diameter (Lewis, 1960). These data are very different from descriptions given by Kool (1989) of *Plicopurpura columellaris.* Because the descriptions of Kool are based on specimens that were collected without the animal that laid them (ANSP 324406), they are probably based on eggs of a different spe-

cies. The explanation that the egg capsule morphology of the two species is very different appears less likely.

Ecology: Plicopurpura patula occurs from the splash zone and low intertidal to shallow subtidal, on hard substrates (often limestone platforms) in high-energy environments. It feeds on such mollusks as chitons (Clench, 1947; Lewis, 1960; Bandel, 1987; Kool, 1987) and nerites (Britton & Morton, 1989), and also on barnacles (Lewis, 1960; Kool, 1987). As described by Bandel (1987), *Plicopurpura* paralyzes a chiton with a purple staining secretion, pulls it off the substrate, and, while holding it with its foot, eats it. Bandel noted that *Plicopurpura* feeds in the splash zone because the paralyzing secretion would lose much of its effect by dilution when the animal is submerged. However, many rapanines are known to paralyze their prey, yet feed when submerged (Kool, personal observation). Breeding occurs in August and September (Lewis, 1960).

Distribution: Western Atlantic, from central east Florida throughout West Indies to Brazil and Bermuda (Abbott, 1974). Occurrence of a *Plicopurpura*-like shell on Mauritius (Drivas & Jay, 1987) needs further investigation.

Genus *Purpura* Bruguière, 1789
(Fig. 18A–G)

Purpura Bruguière, 1789: 15 (*non* Röding, 1798, *nec* Lamarck, 1799).

Type Species: Buccinum persicum Linnaeus, 1758, by subsequent designation, ICZN, Opinion 886, 1969: 128, = *Purpura persica* (Linnaeus, 1758); synonym: ?*Purpura inerma* Reeve, 1846.

Remarks: The generic name "*Purpura*" was first used by Martini (1777) and subsequently by Martyn (1784) and Meuschen (1787), all of which are non-binominal works. Bruguière formally introduced *Purpura* as a genus in 1789, but did not mention any species. Three years later, Bruguière (1792) included the nominal species *Purpura tubifer* Bruguière, 1792, which would make this the type species by subsequent monotypy. Unfortunately, this taxon is now regarded as a species of *Typhis* Montfort, 1810 (Muricidae: Typhinae). Later, Lamarck (1799, 1801) cited *P. persica* as the sole species in the genus, which did not result in *P. persica* being the type species by monotypy, as Bradley & Palmer (1963: 252) incorrectly stated it to be. To resolve this matter, Bradley & Palmer (1963) and Keen (1964) proposed, by petition to the International Committee of Zoological Nomenclature, that *Purpura persica* be designated type species of *Purpura. Purpura persica* officially became the type of *Purpura* after publication of ICZN, Opinion 886 (1969). Detailed nomenclatural history on this genus is given by Dall (1905), Winckworth (1945), Dodge (1956), Bradley and Palmer (1963), and Keen (1964).

Cossmann listed *Purpura persica* as the sole example of the genus *Purpura.* Thiele (1929: 296) incorrectly cited *Purpura patula* as type of *Purpura,* and synonymized *Patellipurpura* with this genus. He recognized the sections *Purpura* and *Plicopurpura* (type species *Purpura columellaris* Lamarck, 1816). Wenz (1941: 1125), and later Pchelintsev & Korobkov (1960: 207), used *Plicopurpura* Cossmann for *Purpura s.l.,* and *Purpura* Martyn for the muricine "*Purpura*" *foliata.* Keen (1971b: 552) synonymized the genera *Plicopurpura* and *Patellipurpura* with *Purpura.* Kool (1988b) argued for separation of *Plicopurpura* and *Purpura.*

Shell: Protoconch (Fig. 18C, E) tall, conical, of about three adpressed whorls [exact count could not be made from available specimen] with outward-flaring lip and sinusigeral notch. Sculptural pattern unknown (due to erosion). Teleoconch (Fig. 18A, B) with high whorl expansion rate, large, heavy, oval, of about six adpressed whorls. Adult shell up to about 115 mm in height, 90 mm in width. Body whorl dome-shaped, about 95% of shell height, sculptured with minute spiral grooves and 7–15 slightly elevated spiral ridges, with one to several less elevated, thinner ridges in between these; surface shiny, appearing smooth. Aperture very wide, oval, about 85% of shell height. Anterior siphonal canal short, wide, open; posterior siphonal canal deep, well developed. Apertural lip smooth, crenate towards edge, corresponding with outside groove pattern. Columella flat to concave, wide with moderate callus layer, with angular curve in lower portion of columella bordering wide, shallow anterior siphonal canal. Siphonal fasciole a slightly elevated ridge, adjacent to columellar callus. Shell grey brown; spiral ridges with color pattern of alternating dark brown and white; dark brown portions of upper two ridges often elevated to form spiral cords of small beads; apertural lip bluish white, with about 30 spiral, dark brown lines

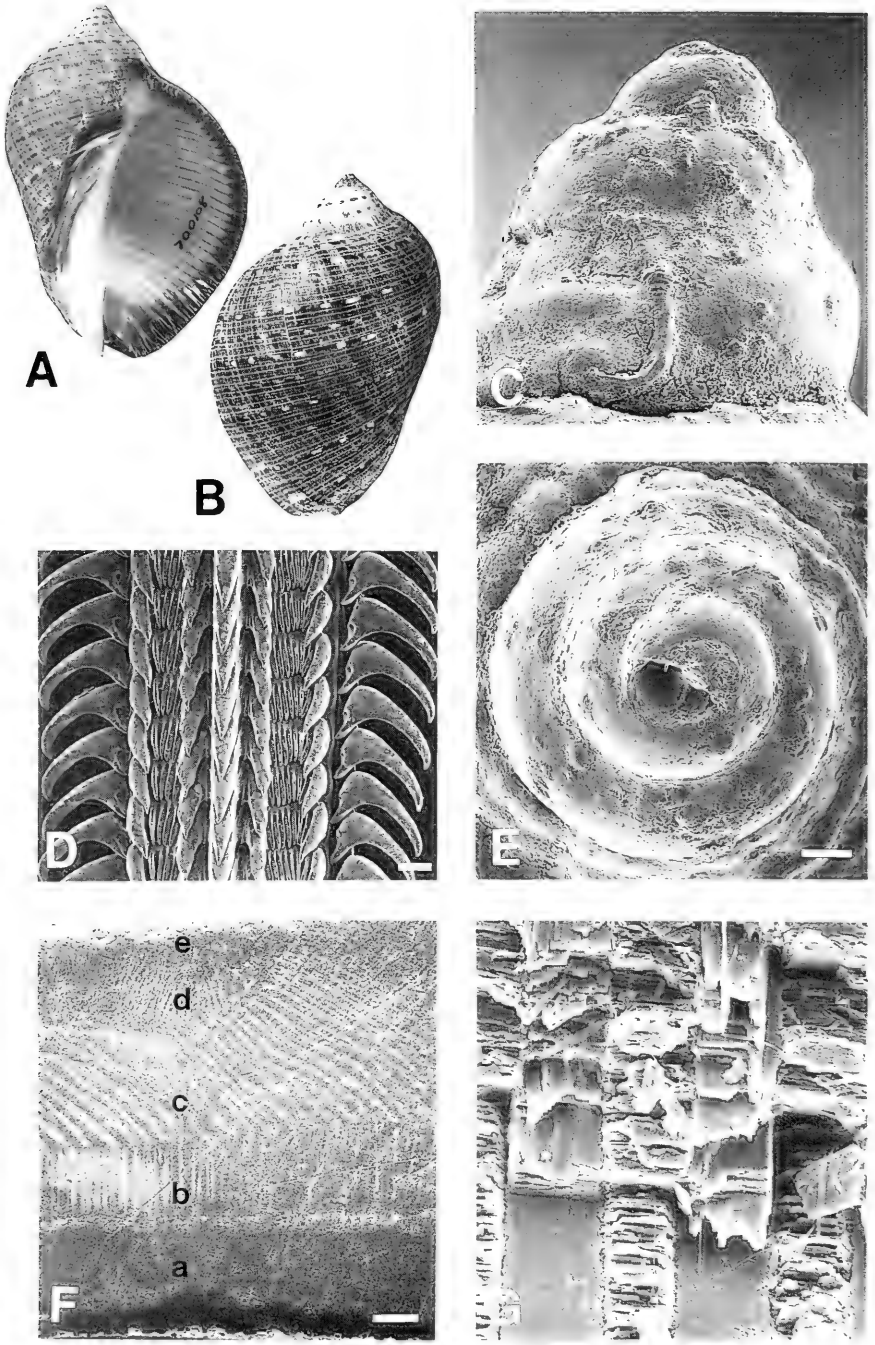

FIG. 18. *Purpura persica*. A, shell (61 mm), apertural view. B, shell (61 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, radula, SEM (bar = 50 μm). E, protoconch, apical view, SEM (bar = 0.10 mm). F, shell ultrastructure, sawed surface, SEM (bar = 0.25 mm); a, aragonite (crystal planes oriented in 45° angle to growing edge); b, aragonite (crystal planes oriented perpendicular to growing edge); c, aragonite (crystal planes oriented parallel to growing edge); d, aragonite (crystal planes oriented perpendicular to growing edge); e, calcite. G, detail of fracture zone of layer b (Figure 18F), SEM (×700).

continuing far into the aperture, with almost uniform, narrow (5–10 mm), black band along edge; columella orange on inside, with blotches of dark brown, cream and blue grey on upper parietal region.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (Fig. 18F, a) (15–25%); aragonitic layer with crystal planes oriented perpendicular to growing edge (Fig. 18F, b, G) (20–25%); aragonitic layer with crystal planes oriented parallel to growing edge (Fig. 18F, c) (35–55%); aragonitic layer with crystal planes oriented perpendicular to growing edge (Fig. 18F, d) (5–15%); calcitic layer (5–10%) (Fig. 18F, e).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 1–2 bracket-shaped growth lines and with callused, glazed rim (about 35–40% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot region flecked with dark brown to black (often in vertical striae) on light yellow background. Elongate tentacles dark brown with light yellow tips. Mantle edge straight, smooth, unpigmented. Incurrent siphon brown black, extending some distance beyond mantle edge. Anterior lobes of foot light brown. Kidney yellowish, not distinct. Accessory boring organ minute, dorsal to pedal gland and located in anteriormost portion of foot.

Osphradial length about one-half ctenidial length; osphradial width between one-fourth and one-third ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes, occasionally more tapered anteriorly. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae much wider than deep; posterior lamellae deeper than wide. Lateral edge of ctenidial lamellae variable; ventral edge concave.

Vaginal opening on tubular extension of pallial gonoduct and located directly below anal opening. Small bursa copulatrix a horizontal slit open to vagina and continuous with capsule gland. Minute ventral sperm channel formed by semi-circular flange originating from the ventral epithelium, located under ventral lobe. Ventral lobe initially small, becoming larger posteriorly, finally disappearing. Posterior ventral channel with one minute flange below larger flange. Lower half of capsule gland opaque; upper portion yellow orange, flocculent. Ingesting gland with several to many sizable chambers surrounded by loose, white connective tissue, extending from left side of capsule gland to albumen gland. Albumen gland omega-shaped, tilted onto posterior half. Seminal receptacles on dorsal periphery of albumen gland. Ovary light brown.

Penis large, strongly recurved, and flattened dorsoventrally at distal end, with large flagellar papilla curved along shaft. Penial duct as duct-within-a-duct system occupying one-third of penial width. Cephalic vas deferens meandering towards prostate. Prostate closed, large, similar to capsule gland in females; embedded in spongy tissue, not distinctly separated from rectum. Small, dark brown seminal vesicles.

Proboscis very large, larger than gland of Leiblein, connected to dorsal wall of buccal cavity with small muscle bundles. Paired accessory salivary glands elongate, thin, equal in length, less than one-half of shell height; right accessory salivary gland loose in right anterior buccal cavity; left gland partially adjacent to salivary gland. Very large salivary glands nearly equal in size to gland of Leiblein and partially located below proboscis. Salivary ducts attached to anterior portion of esophagus close to anterior part of valve of Leiblein. Salivary gland mass partially ventral to proboscis. Valve of Leiblein thin, elongate, adjacent to salivary glands. Portion of mid-esophagus with glandular folds long. Duct between mid-esophagus and gland of Leiblein nearly equal in diameter to posterior esophagus. Posterior esophagus embedded in lower left portion of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, thick, light caramel brown, with strawlike outer membrane. Blind posterior duct of gland of Leiblein much longer than gland itself.

Stomach with large, deep posterior mixing area. Three-fourths of whole posterior mixing area occupied by 25 small folds; anterior one-fourth (adjacent to intestine) smooth, probably non-ciliated. Two large digestive diverticula present. Stomach typhlosole thin. Intestinal typhlosole absent. Rectum thick-walled dorsally, with small internal longitudinal folds; rectum embedded in spongy tissue, separated from capsule gland by distinct layer of epithelium. Anal opening distinct, with up-

ward-pointing papilla at anal opening. Rectal gland moderately wide, extending along entire length of capsule or prostate gland; gland green in females, but usually pink with traces of green in males.

Radula: Ribbon length about 30–35% of shell height (Fig. 18D). Rachidian wide, with needle-shaped central cusp; straight lateral cusps nearly equal in width to central cusp; with or without (can vary within same specimen) single minute denticle on base of inner edge of lateral cusp; outer edge of lateral cusp with one denticle on base; 4–7 well-developed, long, thin denticles on horizontal marginal area; very well-developed marginal cusp nearly equal in size to lateral cusps. Lateral teeth smooth, slightly curved, about three-fourths of rachidian width.

Egg Capsules: Short, dirty yellow, up to 6 mm in height, 5 mm in width, each with flat, widened base; bases usually confluent, capsules occasionally deposited on top of one another; flat, oval top of capsule with central, circular exit hole. Each capsule containing approximately 160–200 eggs measuring about 0.2 mm in diameter (Tirmizi & Zehra, 1983).

Ecology: This species occurs in the rocky subtidal zone (Tirmizi & Zehra, 1983), often in high energy environments (B. Smith, personal communication), where it feeds, among other items, on limpets, as determined from docoglossate rachidian teeth found in gut-content analysis.

Distribution: Indo-Pacific, from Mauritius (Drivas & Jay, 1987) to Marquesas Islands (Salvat & Rives, 1975).

Genus *Stramonita* Schumacher, 1817
(Fig. 19A–F)

Stramonita Schumacher, 1817: 68, 226.

Type Species: Buccinum haemastoma Linnaeus, 1767, by subsequent designation, Gray, 1847: 138, = *Stramonita haemastoma* (Linnaeus, 1767); synonyms: *Thais grisea* Röding, 1798; *Thais metallica* Röding, 1798; *Thais nebulosa* Röding, 1798; *Thais stellata Röding, 1798; Purpura floridana* Conrad, 1837; *Purpura consul* Reeve, 1846; *Purpura forbesii* Dunker, 1853; *Thais floridana haysae* Clench, 1927; *Thais (Stramonita) hidalgoi* Coen, 1946; ?*Thais (Stramonita) langi* Clench, 1948.

Remarks: Most authors have considered *Stramonita* to be a subgenus of *Thais* Röding, 1798 (Cossmann, 1903: 68; Wenz, 1941: 1120; Woodring, 1959: 222; Keen, 1971b: 549). Thiele (1929: 297) placed *Stramonita* as a section of *Thais s.s.,* genus *Thais.* Korobkov (1955: 299) considered *Stramonita* a subgenus of *Thais.* (Kool, 1987: 118) accorded *Stramonita* full generic status. Subspecific status may be accorded to several of the taxa placed in synonymy with *Stramonita haemastoma* ("*Thais*" *haemastoma haysae* Clench, 1927; "*Purpura*" *floridana* Conrad, 1837), but further anatomical, genetic (see Liu et al., 1991), and molecular studies are necessary prior to separation. Based on experiments in the laboratory, Bandel (1976: 118) concluded that *S. floridana* is only an ecological form of *S. haemastoma.*

The tropical eastern Pacific species *Stramonita biserialis* (Blainville, 1832) deserves separate species status because it occurs on the west side of the Isthmus of Panama and has thus been genetically isolated from western Atlantic populations for 2–3 million years (see "Remarks" under treatment of *Plicopurpura*).

Shell: Embryonic shell with pattern of spiral rows of microscopic, volcanolike, cone-shaped pustules. Protoconch (Fig. 19C, D) tall, conical of at least 3.5 adpressed whorls (exact count could not be made from available specimen), with outward-flaring lip; sinusigeral notch covered by teleoconch. First three whorls with faint shoulder with thin ridge sculptured with small plicae; last whorl with shoulder more pronounced and bearing numerous microscopic pustules; numerous small subsutural plicae on each whorl. Teleoconch (Fig. 19A, B) highly variable, fusiform to more oval-shaped, of 7–8 whorls, with varying degree of prominence of suture. Adult shell up to about 90 mm in height, 55 mm in width. Body whorl about 75–85% of shell height, rounded or with distinct shoulder, sculptured with one or two spiral cords with faint knobs and with dense pattern of 30–40 narrow but distinct ridges. Aperture moderately wide, about 60% of shell height. Apertural lip with crenulations continuing into aperture as narrow, tall ridges. Anterior siphonal canal a short, wide notch; posterior siphonal canal present in many adult specimens, but poorly developed, flanked on left by small protrusion of columellar callus. Columella rounded, slightly curved, with little or no cal-

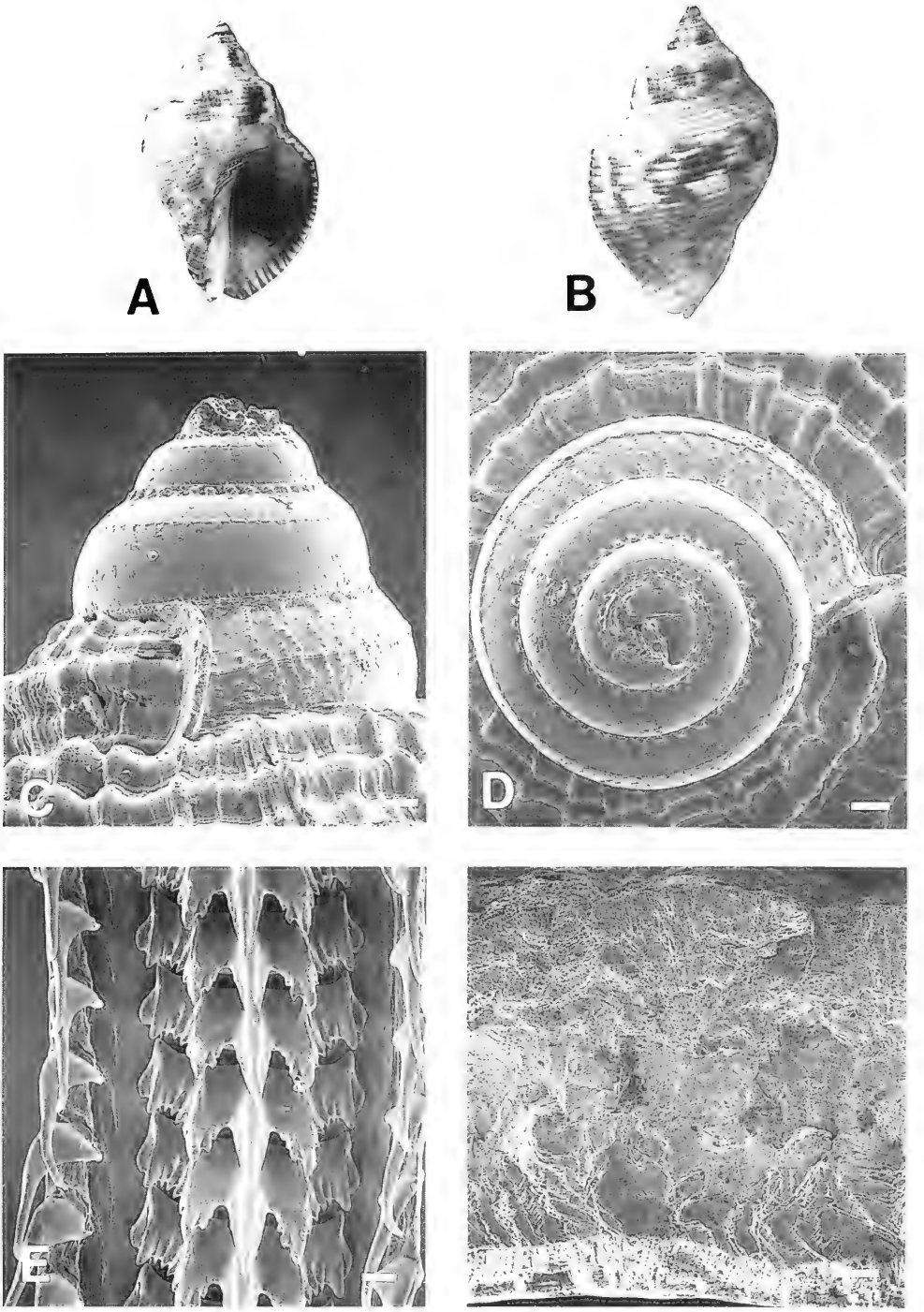

FIG. 19. *Stramonita haemastoma*. A, shell (33 mm), apertural view. B, shell (33 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, radula, SEM (bar = 25 μm). F, Shell ultrastructure, fracture surface, SEM (bar = 0.15 mm).

lus. Siphonal fasciole directly adjacent to callus, with spiral ridge as on rest of whorls. Shell flecked with dark brown, grey, and white, usually forming semi-axial patterns; lower columella white to orange on callused region; upper columella with color pattern similar to that on outside of shell; apertural lip white to orange, with dark brown between distal ends of internal ridges and crenulations.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (10–20%) (lacking in some specimens); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); calcitic layer (40–60%) (Fig. 19F).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 3–5 bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot mottled and blotched with grey black on white background. Cephalic tentacles uniform grey, with black tips. Large mantle covering total head-foot, crenate, with a few, caramel-brown antero-posterior elongate flecks on edge. Incurrent siphon very thick, short, mottled with grey black. Hypobranchial gland pink. Accessory boring organ oval, 2 mm long, with duct (about 4 mm), located dorsal to pedal gland in females (Fig. 4B).

Osphradial length about one-third ctenidial length; osphradial width one-half ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes, or slightly more tapered posteriorly. Osphradial lamella attached along small portion of their base.

Anteriormost portion of ctenidium straight, extending farther anteriorly than osphradium. Anterior and posterior ctenidial lamellae wider than deep. Lateral edges of ctenidial lamellae varying from convex (anterior) to concave (posterior); ventral edges straight.

Vaginal opening a simple hole situated on end of attached tubular extension of pallial gonoduct (in typical *S. haemastoma* morphs; in rounded morphs, vagina more elongate) and located below and slightly anterior to anal opening. Bursa copulatrix extending along entire capsule gland and measuring one-half of gland height. Anterior part of bursa narrow, oriented dorso-ventrally, but circular posteriorly, with intricately branching ridges. Well-developed ventral flange perpendicular to capsule gland lobes, originating from spongy, epithelial tissue on left side of capsule gland or from left lobe of capsule gland. Ingesting gland large, usually black, solid, with material similar to that found in rectal gland. Albumen gland arch-shaped, occasionally with anterior and posterior lobes disjunct to form arch, and with black or white seminal receptacles at periphery. Small, pseudo-penis occasionally present in females.

Penis in males thick, strongly recurved, blunt, dorso-ventrally flattened. Penial vas deferens as duct-within-a-duct system occupying about one-sixth of penial width. Cephalic vas deferens simple, running directly below epithelium. Prostate small, yellow, with wide central duct, adjacent to much larger rectum.

Proboscis thin, long. Paired accessory salivary glands elongate, of equal length, thin, one-third of shell height. Left accessory salivary gland adpressed to salivary gland mass, partially intertwined with it; right accessory salivary gland loose in anterior right buccal cavity, ventral to proboscis. Salivary gland mass equal in size to one accessory salivary gland, located in dorsal buccal cavity between gland of Leiblein and proboscis. Salivary ducts adjacent to esophagus directly anterior to valve of Leiblein. Portion of mid-esophagus with glandular folds long. Mid-esophagus directly attached to gland of Leiblein. Gland of Leiblein of hard consistency, spiraled counterclockwise (forming two "folds" and three "lobes"), enveloped by thin strawlike membrane, varying in color from cream to light brown posteriorly to darker brown anteriorly. Posterior blind duct of gland of Leiblein long, about one-half of gland length, terminating in dorsal branch of afferent renal vein. Posterior esophagus loosely attached to left side of gland of Leiblein.

Stomach large, with several large folds oriented toward intestine. Single large vertical fold with several thin ridges on both sides, perpendicular to and continuous with well-developed stomach typhlosole. Two digestive diverticula present. Intestinal typhlosole well developed, continuing on stomach wall, demarcating intestine from stomach. Several small ridges in intestinal canal. Ciliary movement on stomach wall directed toward intestine. Rectum very wide. Rectal gland green. Anal opening well developed, with pronounced anal papilla.

Radula: Ribbon length about 25% of shell height (Fig. 19E). Rachidian with needle-shaped central cusp; lateral cusps with well-developed inner denticle high on cusp, occasionally with one or two additional denticle(s) below; outside edge of lateral cusp concave, with row of several well-developed denticles continuing up to large marginal cusp; rachidian base with lateral extension. Lateral teeth about equal in length to rachidian tooth.

Egg Capsules: Vase-shaped, large, each with concave and convex sides, up to about 13 mm in height, 2.5 mm in width. Apical plate usually flat or slightly concave, variable in contour, with round to oval, off-center exit hole. Two sutures extending from basal plate of each capsule to apical plate. Capsules arranged in clusters, with concave sides adjacent to convex sides and with confluent bases, each containing 150–800 embryos. Hatching occurs after about 15 days (D'Asaro, 1966). Boone (1984) reported a case of egg capsules attached to floating wood.

Ecology: This species occurs in low- and high-energy intertidal environments. It also lives in mangrove habitats and on *Phragmatopoma* reefs. It feeds on a variety of prey, such as mussels (Burkenroad, 1931), oysters (Bandel, 1976), barnacles (Cake, 1983), and polychaetes (*Phragmatopoma* sp.) (Kool, 1987). A variety of ecological topics was treated by Gunter (1979). I found this species usually to be relatively inactive during low tide, but feeding when submerged at high tide. Females often congregate prior to spawning, which usually occurs from April to May.

Distribution: Eastern Atlantic Ocean, from Mediterranean Sea to West Africa; western Atlantic Ocean, from North Carolina throughout the West Indies to Brazil (Abbott, 1974).

Genus *Thais* Röding, 1798
(Fig. 20A–F)

Thais Röding, 1798: 54.

?*Thalessa* H. & A. Adams, 1853: 127 [type: *Murex hippocastanum* Linnaeus, 1758, by subsequent designation, F. C. Baker, 1895: 183 (Suppressed by ICZN, Opinion 911, 1970: 20), = *Thais aculeata* (Deshayes, 1844)].

?*Menathais* Iredale, 1937: 256 [type: *Purpura pica* Blainville, 1832, by original designation, = *Thais tuberosa* (Röding, 1798)].

?*Thaisella* Clench, 1947: 69 [type: *Purpura trinitatensis* Guppy, 1869, by original designation, = *Thais trinitatensis* (Guppy, 1869)].

?*Reishia* Kuroda & Habe, 1971: 146 [type: *Purpura bronni* Dunker, 1861, by original designation, = *Thais bronni* (Dunker, 1861)].

Type Species: Murex fucus Gmelin 1791, by subsequent designation, Iredale, 1915: 472 (ICZN, Opinion 886, 1969: 128), = *Thais nodosa* (Linnaeus, 1758); synonyms: *Nerita nodosa* Linnaeus, 1758 [*in partem*]; *Murex neritoideus* Linnaeus, 1767 [*in partem*] [also cited as *neritoides* Linnaeus]; *Thais lena* Röding, 1798; *Thais meretricula* Röding, 1798; *Purpura ascensionis* Quoy & Gaimard, 1833.

Remarks: Troschel (1866–1893: 130) placed *Thais* as a subgenus in the genus *Stramonita.* Cossmann (1903) did not list *Thais.* Thiele (1929: 297) included the following subgenera under the genus *Thais: Mancinella,* with sections *Mancinella, Neorapana* and *Tribulus;* and *Thais,* with sections *Thais, Stramonita, Cymia, Pinaxia, Trochia,* and *Agnewia.* Wenz (1941: 1120) included the subgenera *Stramonita, Entacanthus, Cymia, Pinaxia, Trochia,* and *Agnewia* under the genus *Thais.* Fujioka (1985a: 243) recognized both *Reishia* and *Thaisella* as subgenera of *Thais.*

Iredale (1915: 472) provided a type species designation ("*Thais neritoides* = *Murex fucus* Gmel") in a synopsis of Dall's (1909) work. Stewart (1927: 386) listed *Thais fucus* as type species of *Thais* but recognized *Thais nodosa* as a valid name by explaining that *Murex neritoideus* was an unnecessary substitute for *Nerita nodosa* Linnaeus, both being based on the same figures. Stewart then synonymized the nominal species *fucus, neritoideus, lena,* and *nodosa.* In 1937 (p. 256) Iredale listed ". . . *Thais lena* Bolten [*sic*] = *Murex fucus* Gmelin, . . ." as the type species, with this type species fixed as *Murex fucus* Gmelin, 1791, by subsequent designation by Iredale (1915) (ICZN, Opinion 886, 1969: 128). Furthermore, the nominal species *nodosa,* the oldest available name, acquired official status in the same opinion.

Thais nodosa meretricula from Ascension Island is herein considered synonymous with *Thais nodosa nodosa.* The number of black dots on the columella, often cited as a distinctive character for separating the two forms, is

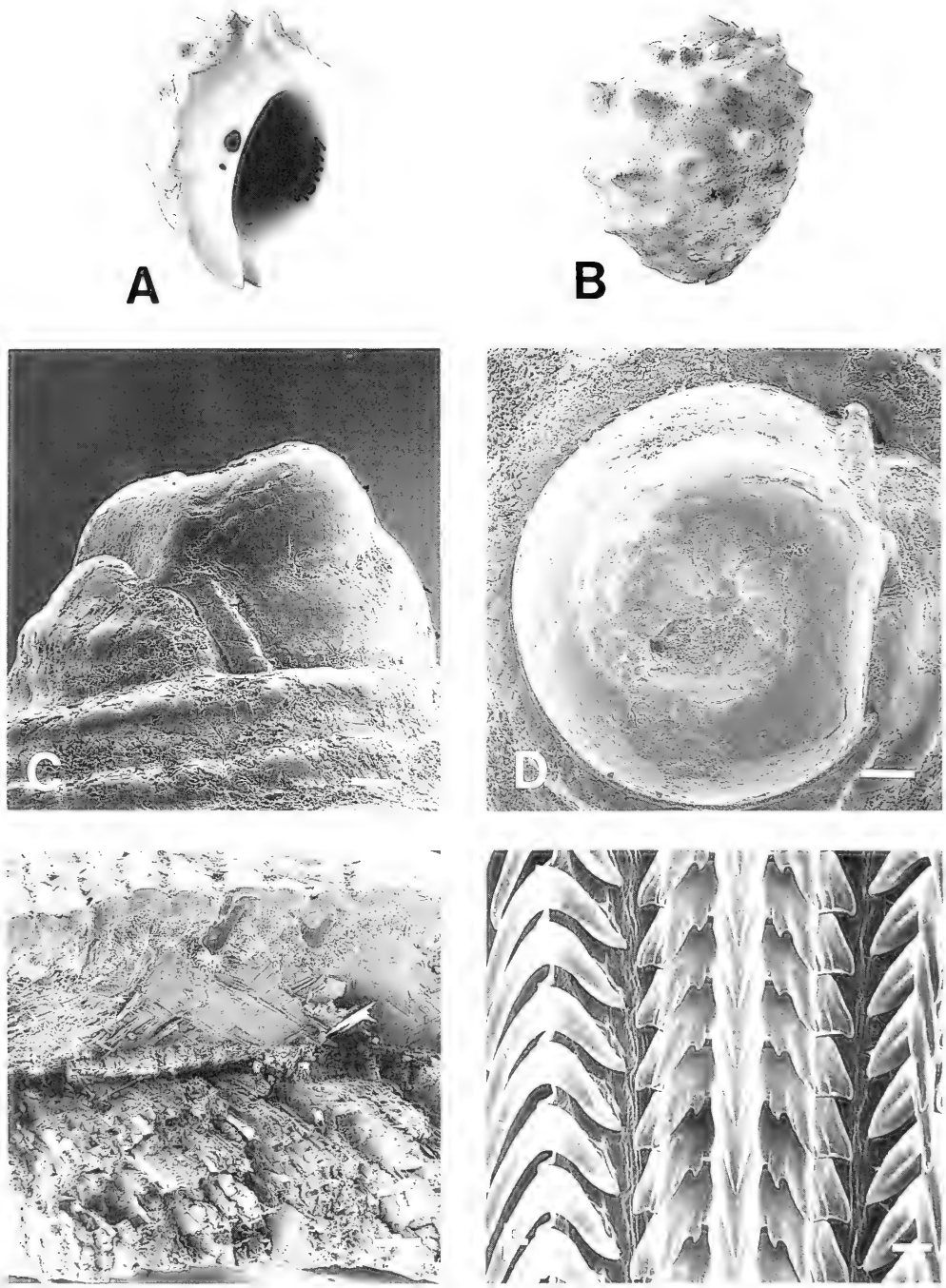

FIG. 20. *Thais nodosa.* A, shell (45 mm), apertural view. B, shell (25 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, fracture surface, SEM (bar = 0.50 mm). F, radula, SEM (bar = 25 μm).

variable in both and shows overlap. Specimens from the African mainland are usually nodose, whereas most, but not all, specimens from Ascension Island are smooth.

Shell: Protoconch (Fig. 20C, D) conical, of at least two adpressed whorls (exact count could not be made from available specimen), and with outward-flaring lip; sinusigeral notch covered by teleoconch. Sculptural pattern obscured by erosion, except for several microscopic pustules observed around lip region. Teleoconch (Fig. 20A, B) with high whorl expansion rate, large, ovate to nearly round, of 4–5 adpressed whorls. Adult shell up to about 70 mm in height, 55 mm in width (form *meretricula* has the largest representatives). Body whorl dome-shaped, usually exceeding 95% of shell height, occasionally with aperture reaching beyond apex. *Thais nodosa* form *nodosa* sculptured with five (sometimes four) spiral rows of 8–9 knobs (occasionally spinelike) and with about 35 narrow, low, spiral ridges, 4–6 of them between rows of knobs; knobs on second and third rows largest. *Thais nodosa* form *meretricula* with rounded body whorl sculptured with about 35 narrow, low spiral ridges. Both forms with wide, oval aperture usually exceeding 95% of shell height. Apertural lip thick, with crenulations on edge corresponding to ridge pattern on outer surface; inside smooth and polished. Anterior siphonal canal as poorly developed notch; posterior siphonal canal poorly developed in most specimens, well developed in others. Columella with wide, flat, heavily callused parietal region and with moderately angular curve in lower region. Siphonal fasciole a well-developed ridge lying behind callus on lower parietal region. Shell dirty white to brown, columella white, with 1–4 large brown black spots (although overlap occurs, usually 1–2 in *Thais nodosa* form *nodosa;* 3–4 in *T. nodosa* form *meretricula*) arranged in vertical row; aperture and apertural edge white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (30–50%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–15%); aragonitic layer with crystal planes oriented parallel to growing edge (20–25%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–10%); calcitic layer (5–10%) (Fig. 20E).

Operculum: D-shaped, with lateral nucleus in center right (Fig. 1C). Free side with bracket-shaped growth lines; attached side with about 4–6 bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot and long cephalic tentacles mottled with black. Mantle edge straight, simple, following contour of aperture. Anterior siphon extending substantial distance beyond mantle edge. Sole of foot a pattern of pustules and ridges. Nephridial gland yellow. Kidney grey brown. Accessory boring organ dorsal to pedal gland in females (Fig. 4B).

Osphradial length slightly more than one-half ctenidial length; osphradial width slightly less than ctenidial width. Osphradium symmetrical in shape along lateral axis; right pectin distinctly wider than left one. Osphradial lamellae deeper than wide, attached along very small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae wider than deep; posterior lamellae deeper than wide. Lateral edge of ctenidial lamellae varying from concave (anterior) to straight or convex (posterior); ventral edge varying from slightly concave (anterior) to distinctly concave (posterior).

Vaginal opening round, situated on posteriorly curved tubular extension of pallial gonoduct and located directly below anal opening. Ventral flange small, crescent-shaped, originating from ventral epithelium. Ventral channel under large ventral lobe. Ingesting gland on left and posterior sides of capsule gland. Several seminal receptacles on dorsal periphery of omega-shaped albumen gland.

Penis strongly recurved, dorso-ventrally flattened, with short thick flagelliform tip (Fig. 5D). Vas deferens as tube-within-a-tube system occupying about one-fifth of penial width. Prostate white yellow, embedded in spongy connective tissue, with closed duct, similar to capsule gland in females. Seminal vesicles pale yellow.

Proboscis very large, about equal in width to gland of Leiblein. Paired accessory salivary glands thin, long, less than one-half of shell height; right gland usually few millimeters longer than left; left gland intertwined with salivary gland mass, right gland free of salivary gland mass and located ventrally in anterior buccal cavity. Salivary gland mass in dorsal

buccal cavity. Valve of Leiblein small, elongate, adjacent to salivary gland mass. Salivary ducts attached to anterior portion of esophagus close to anterior part of valve of Leiblein. Duct between mid-esophagus and gland of Leiblein not pronounced. Posterior esophagus adjacent to lower left gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, dark brown with thin but distinct strawlike membrane. Posterior blind duct of gland of Leiblein more than one-half of gland length.

Tubular stomach smooth or with many small folds oriented toward center. Stomach with two digestive diverticula, but without intestinal typhlosoles (possibly not visible due to bad preservation). Rectal gland long, green. Anal opening small, indistinct, with anal papilla equal in size to opening.

Radula: Ribbon length about 30% of shell height (Fig. 20F). Rachidian with wide central cusp; inner edge of lateral cusp straight to convex, with large denticle at base; outer edge of lateral cusp straight or concave, with 1–2 small denticles on base; 1–2 more denticles on slightly sloping marginal edge; marginal cusp large. Lateral teeth about equal in length to rachidian width.

Egg Capsules: Unknown.

Ecology: Thais nodosa lives in the rocky intertidal zone (Rios, 1970; Abbott & Dance, 1982).

Distribution: Eastern Atlantic, from western Africa (Bernard, 1984), to Ascension Island (Rosewater, 1975) and Cape Verde Islands (Nordsieck, 1968); western Atlantic, Fernando de Noronha Island, off Brazil (Rios, 1970).

Genus *Tribulus* Sowerby, 1839
(Fig. 21A–E)

Tribulus (Klein) Sowerby, 1839: 107.
Planithais (Bayle) Fischer, 1884: 645 [type: *Purpura planospira* Lamarck, 1822: 240, by monotypy, = *Tribulus planospira* (Lamarck, 1822)].

Type Species: Purpura planospira Lamarck, 1822, by monotypy, = *Tribulus planospira* (Lamarck, 1822); synonyms: *Haustrum pictum* Perry, 1811 [rejected name; ICZN, Opinion 886, 1969: 129]; *Purpura lineata* Lamarck, 1816 [*nomen oblitum,* Old, 1964: 48].

Remarks: Sowerby (1839) formally introduced this name taken from an unpublished manuscript by Klein. H. & A. Adams (1853: 126) used *Tribulus* as a subgenus of *Purpura.* Cossmann (1903: 68) listed *Tribulus* (as *Planithais*) as a section of *Purpura s.s.;* Thiele (1929: 297) gave it section rank under *Mancinella s.s.;* Wenz (1941: 1118) included *Tribulus* as a subgenus of *Mancinella,* whereas Keen (1971b: 550) placed it under *Thais.* Old (1964: 47–48) pointed out that the nominal species *pictum* Perry, 1811 (see above), and *lineata* Lamarck, 1816, are *nomina oblita.* Therefore, Lamarck's taxon *Purpura planospira,* which he based on his own drawing of *P. lineata,* is the valid name and the type species of *Tribulus* by monotypy.

Shell: Protoconch (Fig. 21C, D) tall, conical, of 3.5–4 adpressed whorls and with outward-flaring lip; sinusigeral notch obscured by teleoconch. Sculptural pattern obscured by erosion. Teleoconch (Fig. 21A, B) large, oval to nearly round, of 3–4 adpressed whorls; dorsal sides of last whorls forming flat plateau. Adult shell up to about 75 mm in height, 60 mm in width. Body whorl and aperture reaching beyond apex. Body whorl dome-shaped, sculptured with 1–5 wide, low, spiral ridges between six lamellose, high ridges; first three adapical ridges most pronounced, top two most adjacent to each other. Apertural opening very wide, oval, usually reaching total shell height or extending beyond shell spire. Apertural lip thick, with elongate denticles on edge corresponding to ridge pattern on outside surface; inside smooth and polished, with traces of denticle pattern from previous growth stages. Anterior siphonal canal a wide, completely open notch; posterior siphonal canal absent. Columella concavely curved. Parietal region very wide, heavily callused, with large, deep, central indentation which partially excavates parietal region; several elongate denticles on lower portion of parietal region. Siphonal fasciole as ridge, resembling fifth and sixth body whorl ridges, lying behind callused lower portion of columella. Shell dirty white to uniform orange brown to dark brown; columella white, with orange brown blotches and black streak in white indentation of parietal region; denticles on columella and apertural lip orange brown, remainder of lip white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (10–15%) (lacking in many specimens);

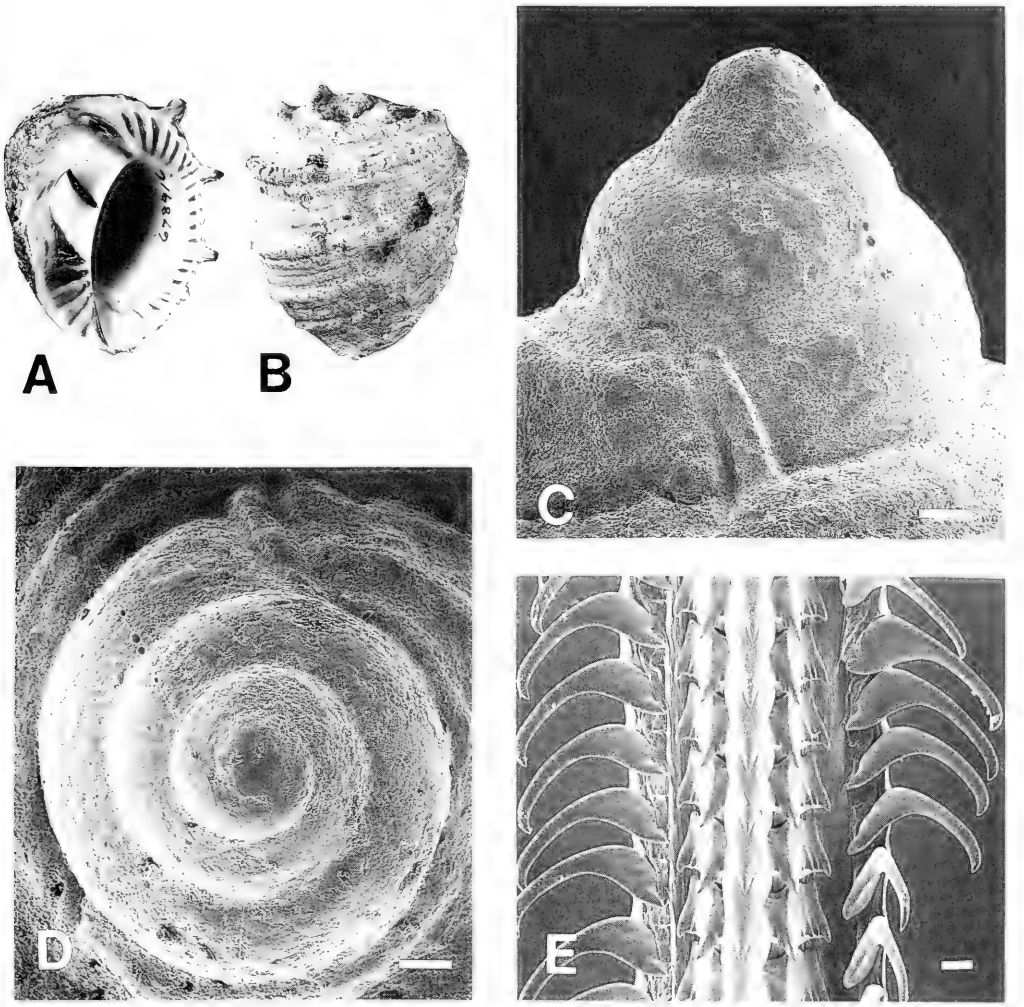

FIG. 21. *Tribulus planospira.* A, shell (50 mm), apertural view. B, shell (50 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, radula, SEM (bar = 35 μm).

aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (25–30%); aragonitic layer with crystal planes oriented perpendicular to growing edge (5–10%); calcitic layer (25–30%).

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with about 4–6 bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on poorly preserved male animals; no female specimens available): Head-foot red brown. Anterior siphon dark brown, extended some distance from mantle edge. Small accessory boring organ dorsal to small pedal gland (Fig. 4B).

Osphradial length about one-half ctenidial length; osphradial width less than one-half osphradial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along very small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphra-

dium. Anterior and posterior ctenidial lamellae wider than deep. Lateral edge of ctenidial lamellae varying from straight to concave; ventral edge straight.

Penis strongly recurved, with long flagellum recurved along penial shaft. Penial vas deferens as centrally located duct-within-a-duct system occupying about one-fifth of penis width. Seminal vesicles well developed, golden brown.

Proboscis unpigmented, narrower than gland of Leiblein. Accessory salivary glands thin, long. Salivary gland mass light brown, larger than accessory salivary glands. Gland of Leiblein spiral, caramel-brown, with straw-like external membrane. Mid-esophagus directly attached to gland of Leiblein over small portion. Posterior esophagus adjacent to left lower gland of Leiblein. Anal opening well developed, with anal papilla attached to wall.

Radula: Ribbon length about 30% of shell height (Fig. 21E). Rachidian with very wide central cusp, constricted at base; inner edge of lateral cusps straight to convex, with single denticle at base; outer edge of lateral cusps straight to concave, with several small denticles at base; base of outer edge of lateral cusp concavely sloping to large marginal denticle. Lateral teeth thin, smooth, longer than width of rachidian.

Egg Capsules (identification uncertain; deposited on valve of a pectinid, USNM 96840; egg capsule size corresponding with size of pedal gland): Small, laterally flattened, up to 4.5 mm in height, each capsule rectangular in cross section, consisting of four distinct plates: front and back plate 2–2.5 mm in width, side plates 0.5–1 mm in width; front plate vase-shaped, side plates of equal distance along total surface with central exit hole separating side plates. Capsule attached by all sides (stalk absent). Capsules deposited in row, with front plates adjacent to back plates.

Ecology: Tribulus planospira lives on vertical hard substrates in the high-energy intertidal zone (J. H. McLean, personal communication).

Distribution: Eastern Pacific, from Cabo San Lucas, Mexico, to Ecuador (Keen, 1971b) and Galápagos Islands (Sabelli & Tommasini, 1979).

Genus *Vasula* Mörch, 1860
(Fig. 22A–E)

Vasula Mörch, 1860: 99 (as a subgenus of *Purpura*).

Vascula Woodring, 1959: 223 (error for *Vasula* Mörch) (as a subgenus of *Thais*).

Type Species: Purpura melones Duclos, 1832, by monotypy, = *Vasula melones* (Duclos, 1832); synonym: *Purpura crassa* Blainville, 1832.

Remarks: Cossmann, Thiele and Wenz did not use this name. Keen (1971b: 550) allotted *Vasula* subgeneric status under *Thais,* following Woodring (1959: 223).

Shell: Protoconch of about 3.5 whorls, otherwise unknown. Teleoconch (Fig. 22A, B) solid, squat, elongate-ovate, of 6–7 appressed whorls. Adult shell up to about 50 mm in height, 35 mm in width. Body whorl about 90% of shell height, globose, but often with heavy shoulder and straight side, and sculptured with numerous (35–45) fine, nearly equidistant, spiral grooves; otherwise smooth. Apertural opening moderately wide, about 75–80% of shell height. Apertural lip rounded or J-shaped, depending on development of shoulder; inside smooth and polished, crenate on edge. Anterior siphonal canal a short, wide notch; posterior canal poorly developed. Columella rounded, nearly straight, with moderate callus layer. Siphonal fasciole forming slightly elevated ridge, slightly covered with callus on upper part. Shell dark brown with continuous or discontinuous spiral patterns of white blotches; columella pigmented with light brown, pink, white, yellow and/or orange; apertural lip whitish yellow, often with pinkish tint, and with narrow continuous or discontinuous black band along edge.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented in 45° angle to growing edge (10–15%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%); aragonitic layer with crystal planes oriented parallel to growing edge (55–60%) (Fig. 22C). Presence of calcitic layer questionable.

Operculum: D-shaped, with lateral nucleus in center right (compare Fig. 1C). Free surface with bracket-shaped growth lines; attached surface with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot mottled black; tentacles black on proximal half of distal tips. Mantle edge smooth. Long anterior siphon extending far beyond mantle edge. Digestive gland car-

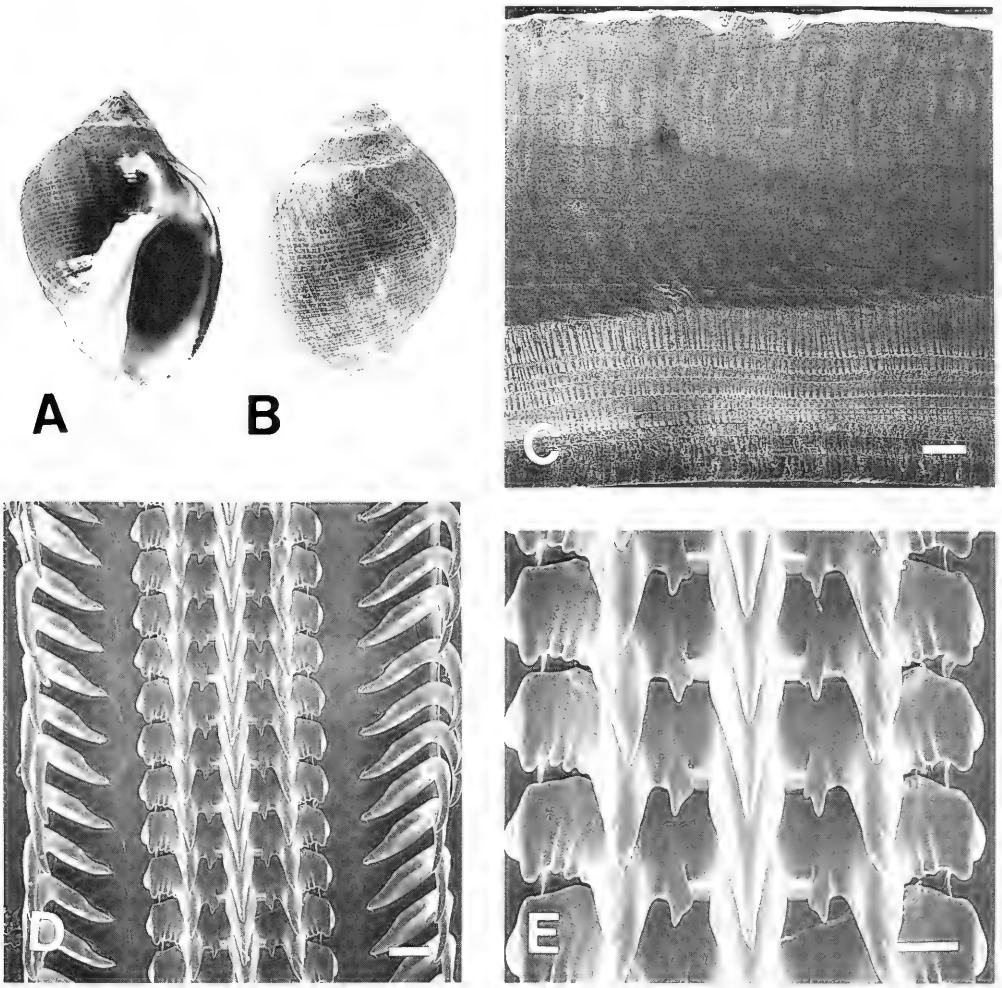

FIG. 22. *Vasula melones.* A, shell (45 mm), apertural view. B, shell (45 mm), abapertural view. C, shell ultrastructure, polished fracture surface, SEM (bar = 0.20 mm). D, radula, SEM (bar = 35 μm). E, radula, rachidian row, SEM (bar = 20 μm).

amel-brown. Well-developed, elongate accessory boring organ close to foot sole.

Osphradial length slightly more than one-half ctenidial length; osphradial width slightly more than ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae wider than deep; posterior lamellae deeper than wide. Lateral and ventral ctenidial lamellae concave.

Vaginal opening enlarged, protruding from short, tubular extension of pallial gonoduct, and located below and slightly posterior to anal opening. Bursa copulatrix as dorso-ventral slit connected to vagina, continuous with capsule gland. Large hook-shaped, ventral flange originating from ventral epithelium, located under ventral lobe of capsule gland, and minute posteriorly. Ingesting gland slightly dorsal to posterior portion of capsule gland, with many very small chambers filled with black granular material. Seminal receptacles on dorsal periphery of omega-shaped albumen gland.

Penis large, strongly recurved, with elongate flagelliform tip. Penial vas deferens as duct-within-a-duct system. Testis whitish.

Proboscis unpigmented, about as wide as gland of Leiblein. Paired accessory salivary glands long, thin, about one-half of shell height; left gland adjacent to proboscis and left salivary gland, right gland in anterior part of buccal cavity adjacent to proboscis and right salivary gland. Salivary glands separated by withdrawn proboscis. Duct between mid-esophagus and gland of Leiblein very short. Posterior esophagus adjacent to lower left side of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of soft consistency, light brown, without strawlike membrane.

Stomach thin-walled, with 20–30 thin, nearly parallel folds and small folds, each oriented towards stomach center. Several microscopic folds on small portion of posterior mixing area adjacent to intestine. Large stomach typhlosole as thin flange partially lying over small folds. Two digestive diverticula present. Intestine smooth-walled, with wide intestinal typhlosole and very thin folds in intestinal groove. Thin-walled, wide rectum with small crystals and black granular material. Rectal gland dark green to black, adjacent to most of capsule gland in females. Small papilla above small but distinct anal opening.

Radula: Central cusp on rachidian constricted at base (Fig. 22D, E); lateral cusps straight; inner denticle small (occasionally bicuspid) and nearly free from lateral cusp; several small marginal denticles at base of lateral cusp, on narrow, somewhat sloping marginal area; marginal cusp pronounced, larger than marginal denticles; rachidian base with lateral extension. Lateral teeth smooth, nearly total rachidian width.

Egg Capsules: Unknown.

Ecology: During low tide, animals were found in shady areas on groups of rocks and boulders overgrown with barnacles and different species of oysters.

Distribution: Eastern Pacific, from Mexico to Peru and Galápagos Islands (Keen, 1971b).

Genus *Vexilla* Swainson, 1840
(Fig. 23A–E)

Vexilla Swainson, 1840: 300.

Provexillum Hedley, 1918: 93 [type: *Strombus vexillum* Gmelin, 1791, by monotypy, = *Vexilla vexillum* (Gmelin, 1791)].

Type Species: Vexilla picta Swainson, 1840, by monotypy, = *Vexilla vexillum* (Gmelin, 1791); synonyms: *Strombus vexillum* Gmelin, 1791; *Purpura taeniata* Powys & Sowerby, 1835.

Remarks: Swainson (1840: 300) placed this genus in the subfamily Nassinae. Cossmann (1903: 68) considered *Vexilla* a valid genus; Thiele (1929: 296) placed it as a subgenus under *Nassa* (*Jopas*). Wenz (1941: 1117) followed Thiele's arrangement but used *Nassa* instead of *Jopas.* Most recent authors recognized this genus.

Shell: Protoconch (Fig. 23D, E) very short, domelike, of about two adpressed whorls, sculptured with small subsutural plicae on last whorl, and with outward-flaring lip; sinusigeral notch obscured by teleoconch. Teleoconch (Fig. 23A, B) elongate-oval, of 3–4 adpressed whorls. Adult shell up to about 25 mm in height, 15 mm in width. Body whorl rounded, elongate, smooth, up to about 95% of shell height. Apertural opening elongate, about 80% of shell height. Apertural lip slightly curved to J-shaped; inside of apertural lip smooth, polished, with crenulations on edge continuing inward as small ridges for short distance. Anterior siphonal canal a poorly developed notch. Posterior siphonal canal flanked on left by small protrusion of columellar callus. Columella rounded to flat, with little callus, curving inward at lower portion. Siphonal fasciole forming slightly elevated ridge. Shell usually colored with eight pairs of dark brown and cream, narrow, spiral bands; cream bands occasionally with reddish narrow line in center. Columella and parietal region white, sometimes with light or dark brown streak on lower end, occasionally continuing upward along inside of columella; interior apertural lip white, with faint, light brown lines (traces of color pattern on edges of previous growth stages); edge white with faint light brown blotches between crenulations and denticles corresponding to banding pattern on outside shell surface.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (30–35%); aragonitic layer with crystal planes oriented parallel to growing edge (40–45%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%).

Operculum: Ovate-elongate, tapered at lower end, with lateral nucleus in upper right (Fig. 1E). Free surface without distinct growth

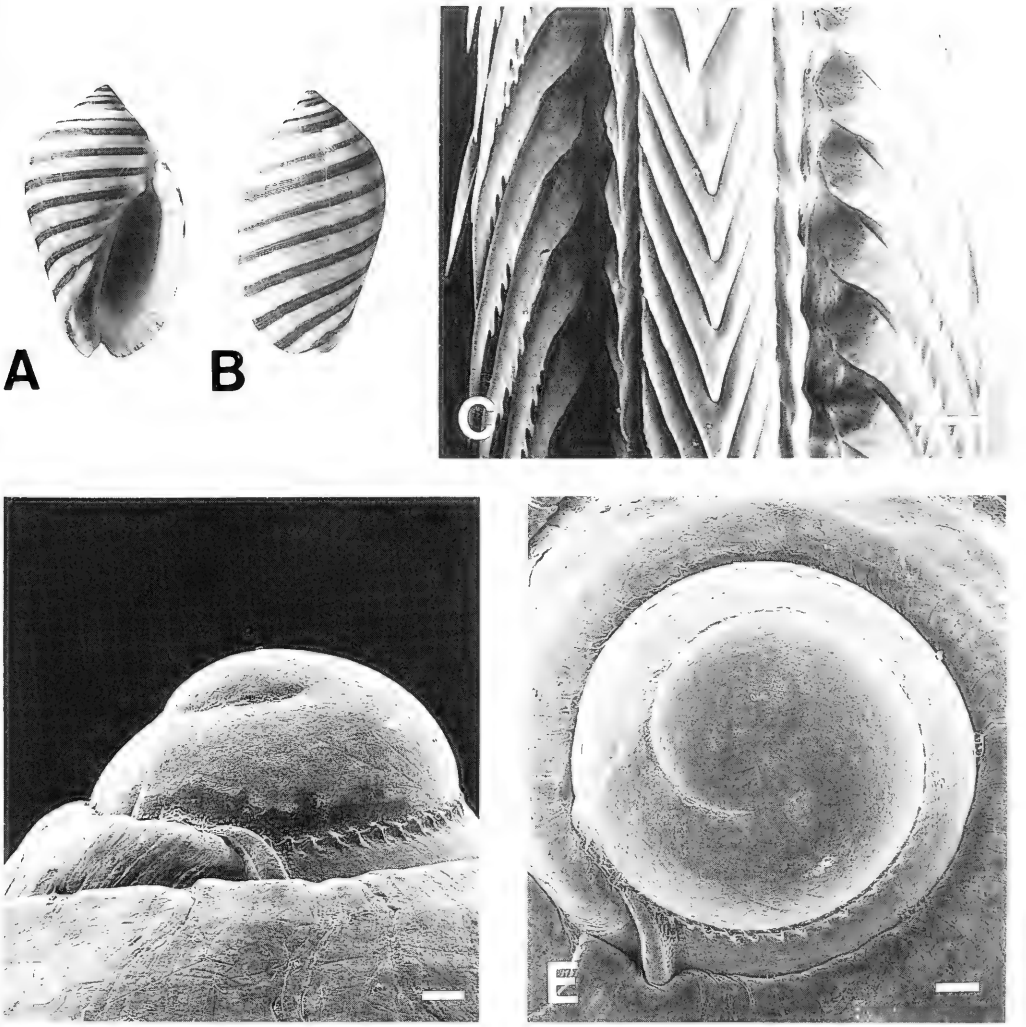

FIG. 23. *Vexilla vexillum.* A, shell (14 mm), apertural view. B, shell (14 mm), abapertural view. C, radula, SEM (bar = 20 μm). D, protoconch, apical view, SEM (bar = 50 μm). E, protoconch, side view, SEM (bar = 50 μm).

lines; attached surface also without distinct growth lines and with callused, glazed rim (about 45–50% of opercular width) on left.

Anatomy (based on living and preserved animals): Head-foot mottled dark brown on opaque grey. Cephalic tentacles long, mottled dark brown on grey, with many white dots, white at tips. Mantle edge simple, straight. Anterior siphon long, extending beyond mantle edge. Nephridial gland thin, short, dorsal to heart. Females with small, shallow ventral pedal gland close to anterior part of foot. Boring organ apparently absent. Sole of foot with small, shallow pustules.

Osphradial length slightly more than one-half ctenidial length; osphradium and ctenidium about equal in width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae triangular, attached along small portion of their base.

Anteriormost portion of ctenidium straight, equidistant from mantle edge with osphradium. Anterior ctenidial lamellae wider than

deep; posterior lamellae deeper than wide, or as deep as wide. Lateral edge of ctenidial lamellae concave; ventral edge straight.

Vaginal opening an elongated slit below and slightly posterior to anal opening. Semicircular ventral flange (originating from epithelium) located below right lobe. Albumen gland omega-shaped, with white, silvery seminal receptacles on dorsal periphery of albumen gland.

Penis flagelliform, slightly recurved, oval in cross section, folded at gradually tapering tip. Penial duct as minute duct-within-a-duct system occupying one-eight of penial width. Cephalic vas deferens minute, inconspicuous. Pallial vas deferens appearing open to mantle cavity (in specimens from USNM 718391) or closed (in specimens from Hawaii). Prostate solid, with ventral duct, adjacent to rectum. Seminal vesicles white.

Proboscis short and wide, equal in width to gland of Leiblein. Accessory salivary glands absent. Two large, orange (white in USNM 718391) distinctly separated salivary glands, one between proboscis and gland of Leiblein, other in right anterior part of buccal cavity; both glands in dorsal buccal cavity, multilobular. Valve of Leiblein short, with caplike structure on anterior end continuing smoothly into anterior portion of esophagus, some distance from nerve ring and adjacent to left salivary gland. Salivary ducts attached to anterior portion of esophagus at considerable distance from valve of Leiblein. Mid-esophageal folds inconspicuous (possibly due to overall poorly developed, thin esophagus). Duct between mid-esophagus and gland of Leiblein short, thinner than esophagus itself. Posterior esophagus loose from gland of Leiblein, occasionally looped at anteriormost fold of gland of Leiblein. Gland of Leiblein spiral, forming two folds, of hard consistency, brown (yellowish white and soft in specimens from USNM 718391), lacking strawlike outer membrane. Posterior duct of gland of Leiblein shorter than gland itself, terminating in dorsal branch of afferent renal vein.

Stomach as wide, U-shaped tube with several to many folds on stomach wall of posterior mixing area oriented toward center of stomach. Two digestive diverticula present. Stomach typhlosole lacking or poorly developed, located some distance from posterior mixing area edge, thus interrupting folds. Intestinal typhlosole distinct. Rectal gland thin, along entire capsule gland or prostate. Anal opening inconspicuous, with large anal papilla.

Radula: Ribbon length about 25% of shell height (Fig. 23C). Rachidian tooth with extremely wide central cusp extending along most of rachidian base; few small serrations at base of side of central cusp; lateral cusps smooth, one-third of central cusp length, sloping down toward edge of rachidian. Lateral teeth serrated along nearly entire length, much longer than rachidian width.

Egg Capsules: Unknown.

Ecology: This species occurs on high-energy rocky shores in the low intertidal zone on the sea urchins *Colobocentrotus* and *Echinometra* on which it feeds (Kay, 1979; Kool, 1987: 120).

Distribution: Indo-Pacific, from eastern Africa (Kilburn & Rippey, 1982) to Hawaii (Kay, 1979).

Descriptions of Taxa Traditionally Considered Belonging to Outgroups of Thaididae/nae of Authors

To evaluate taxonomic positions of the taxa described above at the subfamilial and familial levels, and to examine the boundaries of monophyletic groups, other muricid taxa, not believed to be in Thaididae/nae of authors, were studied and scored for the same characters. Choice of taxa depended on such criteria as availability and previous taxonomic placement. For example, *Muricanthus fulvescens* represents the Muricinae, *Rapana rapiformis* the Rapaninae of authors, and *Forreria belcheri* is a taxon *incertae sedis.*

Muricanthus fulvescens (Sowerby, 1841) (Fig. 24A–F)

Shell: Protoconch (Fig. 24C, F) very tall, conical, of 4.5–4.75 adpressed whorls, with outward-flaring lip and sinusigeral notch. First two whorls smooth, later whorls with microscopic pustules. Protoconch I nearly as wide as first whorl of Protoconch II. Teleoconch (Fig. 24A, B) very large, wide, fusiform, multispined, of about eight whorls, with impressed suture, and with long, well-developed siphonal canal. Adult shell up to about 185 mm in height, 105 mm in width. Body whorl about 85–90% of shell height, sculptured with 7–9 varices, each with about ten spiny knobs open on anterior side. Knobs on varices inter-

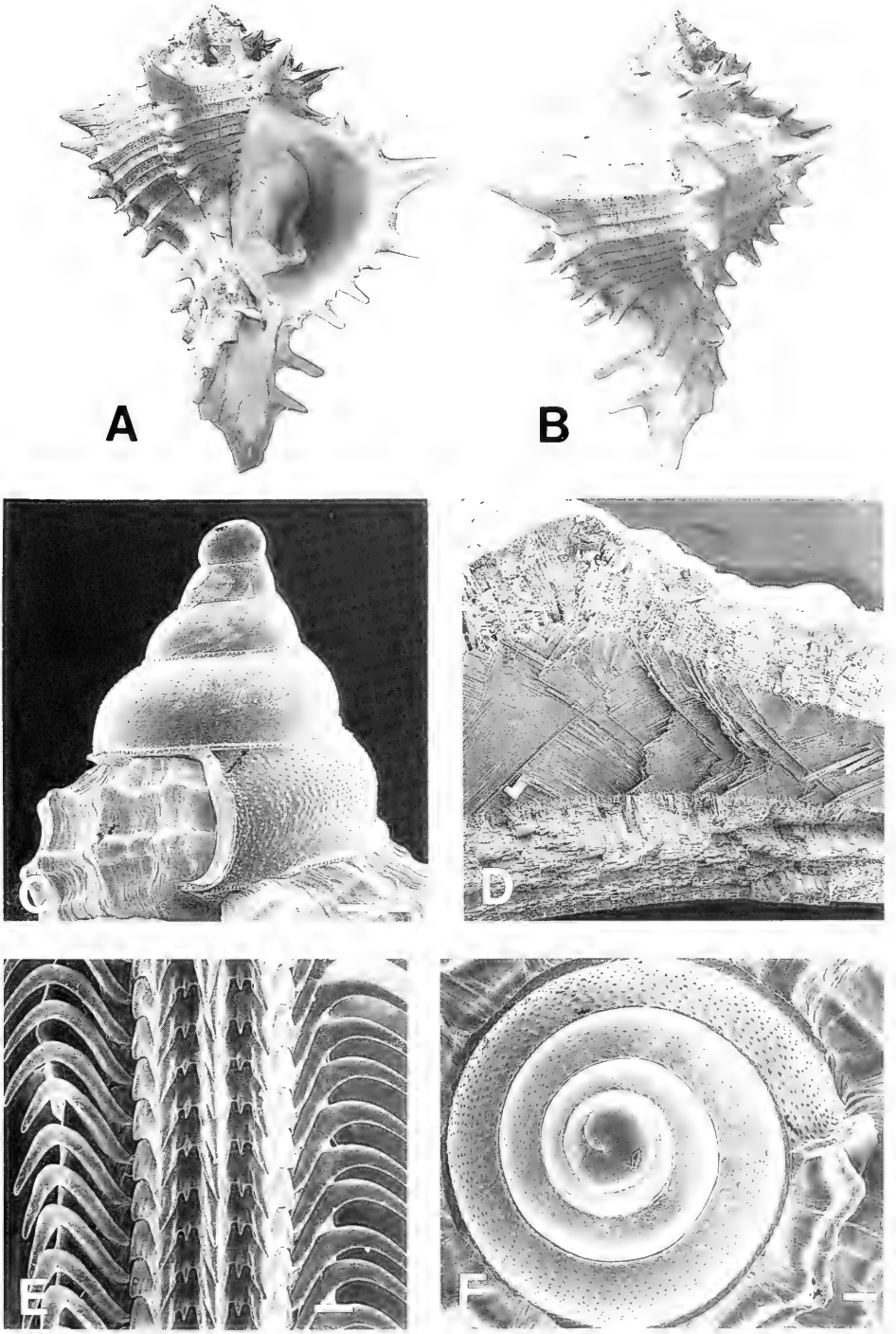

FIG. 24. *Muricanthus fulvescens.* A, shell (136 mm), apertural view. B, shell (136 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.25 mm). D, shell ultrastructure, fracture surface, SEM (×35). E, radula, SEM (bar = 50 μm). F, protoconch, apical view, SEM (bar = 0.10 mm).

connected by folds and ridges. Apertural opening round; aperture (including anterior siphonal canal) about 70% of shell height. Apertural lip semi-circular, thin, except when enforced with knobs on varix; inside smooth and shiny; crenulations on edge elongated, continuous with row of small denticles. Anterior siphonal canal long, wide, almost completely closed, straight, without callus, about 40–45% of shell height; posterior siphonal canal absent. Columella rounded, parietal region narrow, with moderate callus layer, occasionally partially detached at margin. Siphonal fasciole well developed, with former distal ends of siphonal canal forming angle with one another. Shell whitish yellow with light and dark brown spiral, continuous or discontinuous lines and blotches; columella and apertural lip white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (30–40%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (25–30%) (Fig. 24D).

Operculum: Ovate, with terminal nucleus in lower right (Fig. 1A). Free surface with concentric growth lines; new growth often partially overlapping previous growth, resulting in lamellose surface; attached surface with many (about 30–50) fine growth lines following contour of operculum and with very heavily callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on living and preserved animals): Anterior siphon not extending beyond mantle edge. Digestive gland and kidney green. Accessory boring organ well developed, short distance form sole of foot in males, combined with well-developed pedal gland in females (Fig. 4B).

Osphradial length slightly less than one-third ctenidial length; osphradial width one-third to one-half ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium straight, usually extending farther anteriorly than osphradium. Anterior and posterior ctenidial lamellae much wider than deep. Lateral and ventral edge of ctenidial lamellae varying from concave to convex. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vaginal opening a slit situated on distal portion of tubular extension of pallial gonoduct and located directly below anal opening. Bursa copulatrix as large diverticulum. Ventral flange long anteriorly, originating from left lobe of capsule gland, and minute posteriorly. Large ingesting gland on left side of posterior portion of capsule gland extending to albumen gland and consisting of many small chambers filled with black granular material. Albumen gland a large, single-chambered diverticulum.

Penis large, elongate, gradually tapering, occasionally lightly recurved, pigmented uniform black. Penial vas deferens as well-developed duct, semi-closed by epithelium with interlocking, lateral ridges (Fig. 5A). Cephalic vas deferens well developed. Prostate small, posteriorly open to mantle cavity. Seminal vesicles brown, well developed, occupying large surface area. Testis orange.

Right accessory salivary gland poorly developed, very small, somewhat club-shaped. Left accessory salivary gland absent. Paired salivary glands large, located on left and right sides of valve of Leiblein. Salivary ducts attached to anterior portion of esophagus at base of valve of Leiblein. Valve of Leiblein elongate, adjacent to nerve ring. Portion of mid-esophagus with glandular folds short; folds very well developed, wedged into most anterior fold of spiral gland of Leiblein. Gland of Leiblein long, spiral, forming two folds, long, of hard consistency, with thick strawlike external membrane. Duct between mid-esophagus and gland of Leiblein short, poorly developed. Posterior blind duct of gland of Leiblein long, more than half as long as gland of Leiblein, and with terminal ampulla located in dorsal branch of afferent renal vein.

Stomach with large, triangular posterior mixing area, with many small folds oriented towards stomach center. Stomach typhlosole poorly developed, intestinal typhlosole thin. Two digestive diverticula present. Rectum large, embedded in grey opaque connective tissue. Anal opening small but distinct with small papilla, about equal to size of opening and occasionally partially closing it.

Radula: Ribbon length about 20–25% of shell height (Fig. 24E). Rachidian with thin central cusp; small lateral denticle separate from base of lateral cusps; inner edge of lateral cusps smooth, convex; outer edge con-

cave, with faint, small folds at base, and deeply sloping towards edge of rachidian tooth. Lateral teeth long, curved, thin, smooth, simple, about equal in length to rachidian width.

Egg Capsules: Large, elongate, vase-shaped, about 16 mm in height, with concave and convex sides. One suture along lateral edges and continuing across flattened or concave apical plate but interrupted by small, oval, transparent exit hole in center. Between 1,300 and 1,500 embryos per capsule, hatching as veligers (D'Asaro, 1986).

Rapana rapiformis (Born, 1778)
(Fig. 25A–F)

Shell: Protoconch (Fig. 25B) tall, conical, of 3–3.25 adpressed whorls, with minute subsutural plicae and microscopic pustules on last whorls, and with outward-flaring lip and sinusigeral notch. Teleoconch (Fig. 25A) very wide, bulbous, of 7–8 whorls, with canaliculate suture, and with moderately long, wide siphonal canal. Adult shell up to about 125 mm in height, 100 mm in width. Body whorl bulbose, about 90% of shell height (siphonal canal included), sculptured with fine, spiral grooves and with three spiral rows of low, aligned, blunt, partially open knobs; lower two rows of knobs weaker than upper two or absent. Apertural opening very wide, oval, about 80–85% of shell height. Apertural lip semicircular, thin, with faint riblets extending inward, corresponding to external groove pattern. Anterior siphonal canal moderately long, wide, deep, open, about 20% of shell height; posterior siphonal canal poorly developed or absent. Columella rounded and slightly concave, with little callus deposition. Siphonal fasciole composed of partially overlapping distal ends of siphonal canals from previous growth stages. Shell with cream to brown spirally and/or axially continuous or discontinuous bands or blotches; columella and interior of aperture white to orange.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (20–25%); aragonitic layer with crystal planes oriented parallel to growing edge (30–40%); aragonitic layer with crystal planes oriented perpendicular to growing edge (15–25%); calcitic layer (10–15%) (Fig. 25D).

Operculum: Inverted tear-shaped, with lateral nucleus in lower right (Fig. 1B). Free surface with staff-shaped growth lines; attached surface with about 3–4 bracket-shaped growth lines and with callused, dull rim (about 35% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot, including long cephalic tentacles and anterior siphon, dark brown to black. Mantle edge simple, straight, following aperture contour, or irregular; anterior siphon extending slightly beyond mantle edge. Accessory boring organ (Fig. 25F, abo), large, dorsal to well-developed pedal gland in females (Fig. 25F, pg).

Osphradial length slightly less than one-half ctenidial length; osphradium and ctenidium equal in width or osphradial width slightly more than ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes, occasionally with posterior portion more tapered. Osphradial lamellae attached along small portion of their base.

Anteriormost portion of ctenidium bending slightly towards osphradium and extending slightly farther anteriorly than osphradium. Anterior ctenidial lamellae much wider than deep; posterior lamellae about as deep as wide. Lateral and ventral edges of lamellae varying from straight to slightly concave. Distal tips of ctenidial support rods extending beyond lateral edge as papillalike projections.

Vagina large, situated on distal end of partially detached tubular extension of pallial gonoduct and located below and slightly anterior to anal opening. Bursa copulatrix as dorso-ventral slit, continuous with ventral channel and capsule gland. Ventral flange in anterior portion of capsule gland large, curved, originating from ventral epithelium, located under small ventral lobe; flange becoming more reduced posteriorly, located under left and right lobe. Albumen gland omega-shaped with seminal receptacles on dorsal and anterior periphery.

Penis large, strongly recurved, with short, flagelliform tip. Penial vas deferens as duct-within-a-duct system occupying about one-fourth of penial width. Cephalic vas deferens poorly developed. Prostate small, orange, with no obvious duct. Seminal vesicles well developed, pale yellow to golden orange. Testis yellowish.

Proboscis large, brown, equal in width to gland of Leiblein. Paired accessory salivary glands about one-third to one-half of shell height; right gland located on right anterior side of buccal cavity separate from right salivary gland, left one sometimes much smaller

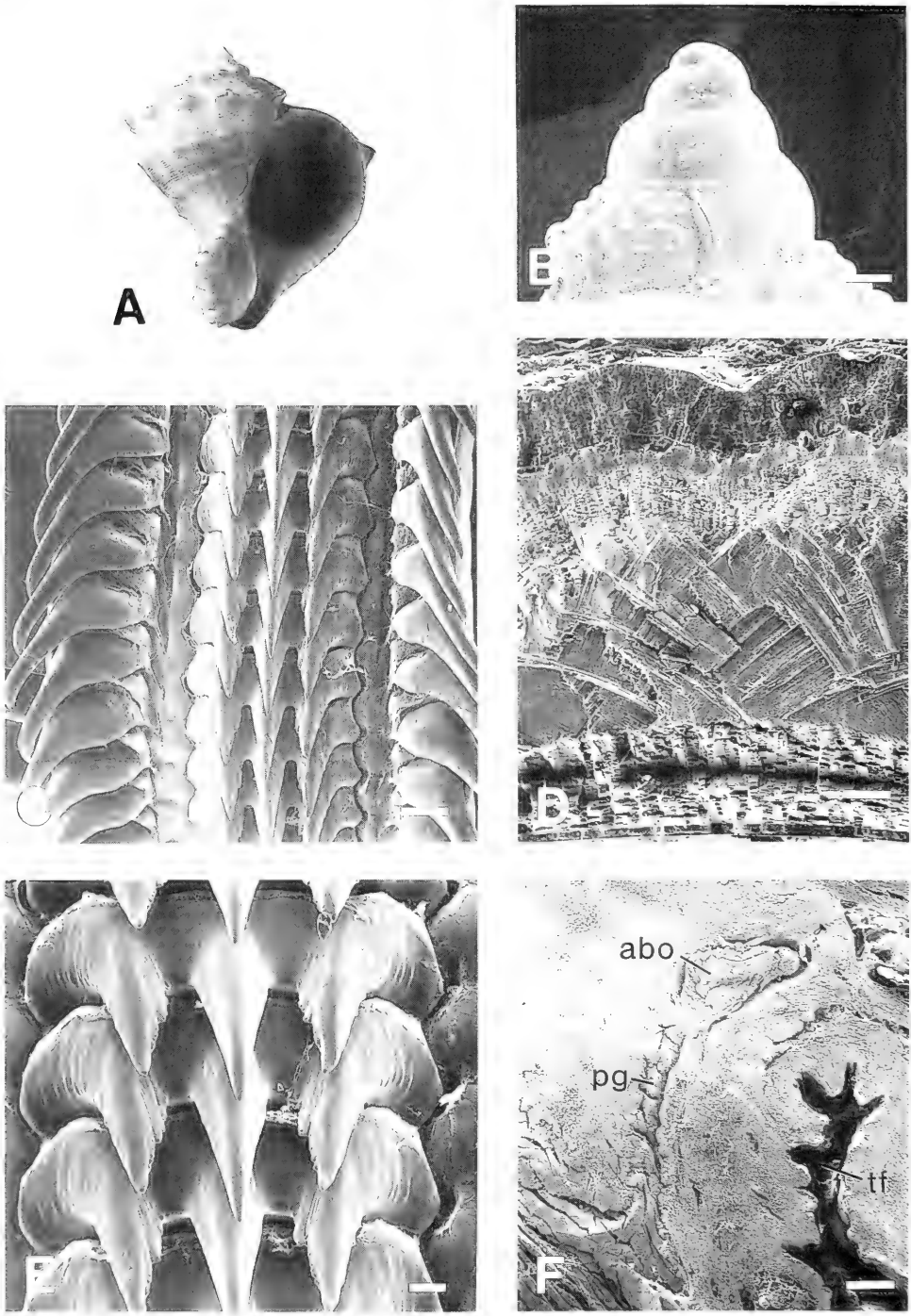

FIG. 25. *Rapana rapiformis*. A, shell (63 mm), apertural view. B, protoconch, side view, SEM (bar = 0.20 mm). C, radula, SEM (bar = 0.10 mm). D, shell ultrastructure, SEM (bar = 75 μm). E, radula, rachidian row, SEM (bar = 30 μm). F, sagittal cross section through anterior foot of female viewed from right side, showing accessory boring organ (abo), ventral pedal gland (pg), and transverse furrow (tf), SEM (bar = 0.50 mm).

than right and embedded in left salivary gland. Salivary glands separate, large; right gland ventral to right side of proboscis, left one adjacent to anterior side of gland of Leiblein and posterior proboscis. Salivary ducts attached at varying distance from valve of Leiblein. Valve of Leiblein short, surrounded by salivary glands, and adjacent to nerve ring. Portion of mid-esophagus with glandular folds long. Duct between esophagus and gland of Leiblein thin, poorly developed. Gland of Leiblein spiral, of hard consistency, large, usually with external strawlike membrane (thickest in older specimens). Posterior blind duct longer than gland of Leiblein itself.

Stomach with large posterior mixing area extending far posteriorly. Five to fifteen folds of different sizes on stomach wall. Stomach typhlosole very well developed, partially extending posteriorly. Intestinal typhlosole narrow and poorly developed. Several thin folds in intestinal groove. Two digestive diverticula present. Rectum large in diameter, thin-walled. Rectal gland not apparent. Anal opening wide.

Radula: Rachidian with thin central cusp (Fig. 25C, E); lateral cusps nearly equal in length to central cusp, with serrated edges; outside of lateral cusp steeply sloping down to edge of rachidian. Lateral teeth broad at base, simple, smooth, about as long as rachidian width.

Egg Capsules: Unknown.

Forreria belcheri (Hinds, 1844)
(Fig. 26A–F)

Shell: Protoconch (Fig. 26B, C) tall, conical, of about two smooth whorls, and with impressed suture; transition with teleoconch smooth. Teleoconch (Fig. 26A) very large, wide, elongate, fusiform, of 6–7 whorls, and with slightly impressed suture. Adult shell up to about 150 mm in height, 95 mm in width, and with long, well-developed siphonal canal. Body whorl (siphonal canal included) about 85% of shell height, with 10–11 varices overhanging new growth; body whorl sculptured with axial growth lines. Large, spinelike knobs on upper corner of square shoulder; moderately deep, wide canal below lower angle of shoulder. Apertural opening wide, oval, about 75% of shell height (siphonal canal included). Apertural lip semi-circular, or semi-hexagonal, thin (even where enforced by varix) to moderately thick; pronounced labial spine on lower lip; interior of aperture smooth and shiny. Anterior siphonal canal long (about 25% of shell height), wide, deep, straight, open; posterior siphonal canal absent. Columella round, moderately curved, with narrow parietal region; moderate callus layer partially detached at margin. Siphonal fasciole well developed, spiny in appearance due to earlier anterior siphonal canals. Wide, concave surface forming umbilicus between siphonal canal (opening) and margin of siphonal fasciole. Shell with faint bands of cream to light brown; columella, interior of aperture and anterior siphonal canal white.

Shell Ultrastructure: Aragonitic layer with crystal planes oriented perpendicular to growing edge (5–10%); aragonitic layer with crystal planes oriented parallel to growing edge (10–20%); calcitic layer (70–80%) (Figure 26F).

Operculum: D-shaped, upper end rounded, with lateral nucleus in lower right (Fig. 1D). Free surface with staff-shaped, growth lines; attached surface with about 7–10 arch- and bracket-shaped growth lines and with callused, glazed rim (about 30–35% of opercular width) on left.

Anatomy (based on preserved animals only): Head-foot, including sole, and short, cephalic tentacles greyish. Mantle edge folded. Anterior siphon not extending beyond mantle edge. Accessory boring organ adjacent to pedal gland in females (Fig. 4A). Digestive gland dark brown.

Osphradial length one-fourth to one-third ctenidial length; osphradial width less than one-third ctenidial width. Osphradium symmetrical in shape along lateral and longitudinal axes, occasionally wider anteriorly, and occasionally with right pectin occasionally slightly wider than left one. Osphradial lamellae attached along varying portions of their base.

Anteriormost portion of ctenidium straight, extending farther anteriorly than osphradium. Anterior and posterior lamellae more than twice as wide as deep (widest and shallowest lamellae located anteriorly). Lateral and ventral edge of ctenidial lamellae varying from straight to concave.

Vaginal opening large, simple, formed from mantle and tubular anterior portion of pallial gonoduct and located below and slightly posterior to anal opening. Bursa copulatrix as

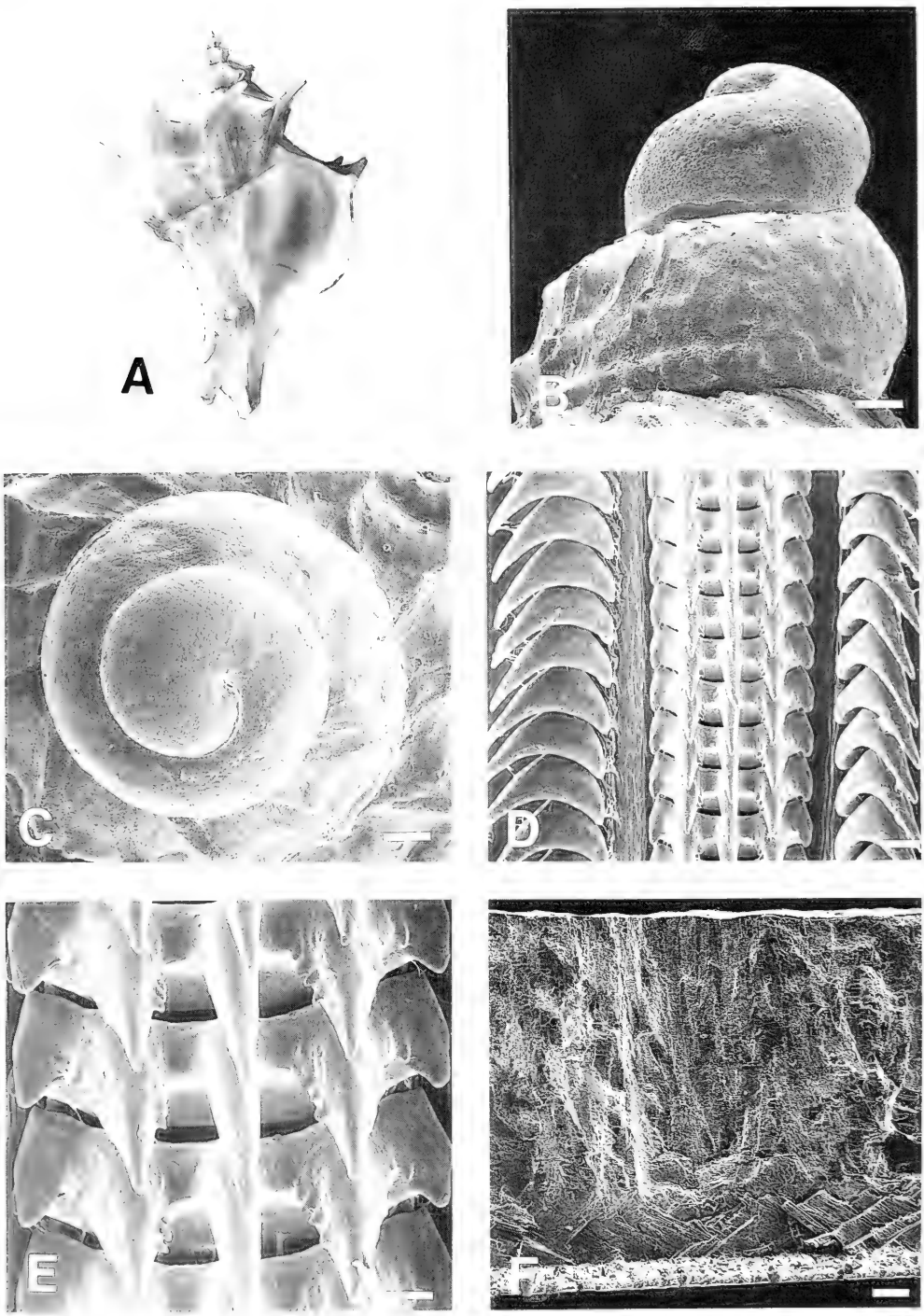

FIG. 26. *Forreria belcheri.* A, shell (114 mm), apertural view. B, protoconch, side view, SEM (bar = 80 μm). C, protoconch, apical view, SEM (bar = 80 μm). D, radula, SEM (bar = 50 μm). E, radula, rachidian row, SEM (bar = 25 μm). F, shell ultrastructure, SEM (bar = 0.10 mm).

large, separate diverticulum. Ventral channel formed by very small flange originating from left capsule gland lobe. Ventral lobe present only in anterior portion of capsule gland. Ingesting gland partially to right of posterior portion of capsule gland, consisting of one large and many smaller chambers, all filled with dark brown granular material. Albumen gland arch-shaped, nearly square in side view, lower ends slightly invaginated. Ovary beige to orange.

Penis elongate, gradually tapering, with microscopic pustules on dorsal side. Penial vas deferens as well-developed duct, semi-closed by epithelium with small, lateral interlocking ridges (Fig. 5A). Cephalic vas deferens well developed. Prostate large, grey to orange brown, composed of two lobes with yellowish longitudinal ridges, and with duct as dorsoventral slit, open ventrally to mantle cavity.

Paired accessory salivary glands extremely long, about one-half of shell height; right gland separate from salivary gland, left gland intertwined with salivary gland. Salivary glands adjacent to left side of proboscis and equal in size to accessory salivary glands. Salivary ducts attached to anterior portion of esophagus at short distance from valve of Leiblein. Valve of Leiblein elongate, with cap structure on anterior end, and surrounded by salivary gland lobes and lying adjacent to nerve ring. Portion of mid-esophagus with glandular folds short; folds very well developed, directly attached to gland of Leiblein. Gland of Leiblein large, spiral, elongate, of hard consistency, lacking strawlike membrane. Posterior esophagus horseshoe-shaped, lying against left side of gland of Leiblein. Posterior blind duct of gland of Leiblein short, less than one-half length of gland of Leiblein.

Stomach with large posterior mixing area and many fine folds oriented towards center of stomach. Small smooth area prior to intestinal area. Stomach typhlosole well developed, intestinal typhlosole thin. Two digestive diverticula present. Rectum moderately wide. Anal opening very small. Anal papilla occasionally formed from anteriorly extended dorsal wall of rectum.

Radula: Ribbon length about 15% of shell height (Fig. 26D, E). Rachidian with thin, needle-shaped central cusp; lateral cusps with 3–4 inner denticles and serrated outer edge with 1–2 faint outer denticles on base; base of outer edge of lateral cusps adjacent to base of inner edge of large marginal cusp; marginal cusps in different plane than lateral cusps (about 75° angle) and parallel to elongate lateral extension at base of rachidian tooth, resulting in bifid rachidian edge (compare Fig. 15E). Lateral teeth broad, smooth, simple, equal in length to rachidian width.

Descriptions of Taxa Used to Test Robustness of Synapomorphies

The species *Acanthina monodon* and *Trochia cingulata* were only examined on few features after initial cladistic analyses had revealed synapomorphies for a clade consisting of *Nucella* and *Forreria.* These two species, suspected of being closely allied to *Nucella* and *Forreria,* were tested for having the same synapomorphies as found for the *Nucella-Forreria* clade. The two taxa were usually included in Thaididae/nae of authors.

Acanthina monodon (Pallas, 1774) (Fig. 27A–D)

Anatomical data for *Acanthina monodon* were obtained from Wu (1985); this species has a bursa copulatrix that is separate from the lumen of the capsule gland, very long accessory salivary glands, a lightly curved penis with pseudo-papilla, an accessory boring organ separate from the ventral pedal gland (in females; Fig. 4A), and a D-shaped operculum with its upper end rounded and with a lateral nucleus in the lower right (compare Fig. 1D). Scanning electron micrographs of the shell ultrastructure were not available at the time of the cladistic analysis, but from light microscopy it was obvious that an inner aragonitic layer with the crystal planes oriented in a 45° angle to the growing edge is absent. The protoconch (Fig. 27C, D) is smooth, paucispiral (about 1.5 whorls), and lacks an outward-flaring lip.

Trochia cingulata (Linnaeus, 1758) (Fig. 28A–E)

Scanning electron micrographs of the protoconch and the shell ultrastructure revealed a smooth, paucispiral protoconch of about 1.5 whorls, lacking an outward-flaring lip (Fig. 28C, D), and a shell ultrastructure consisting of an aragonitic layer with crystal planes oriented perpendicular to growing edge (10–30%), an aragonitic layer with crystal planes oriented parallel to growing edge (25–

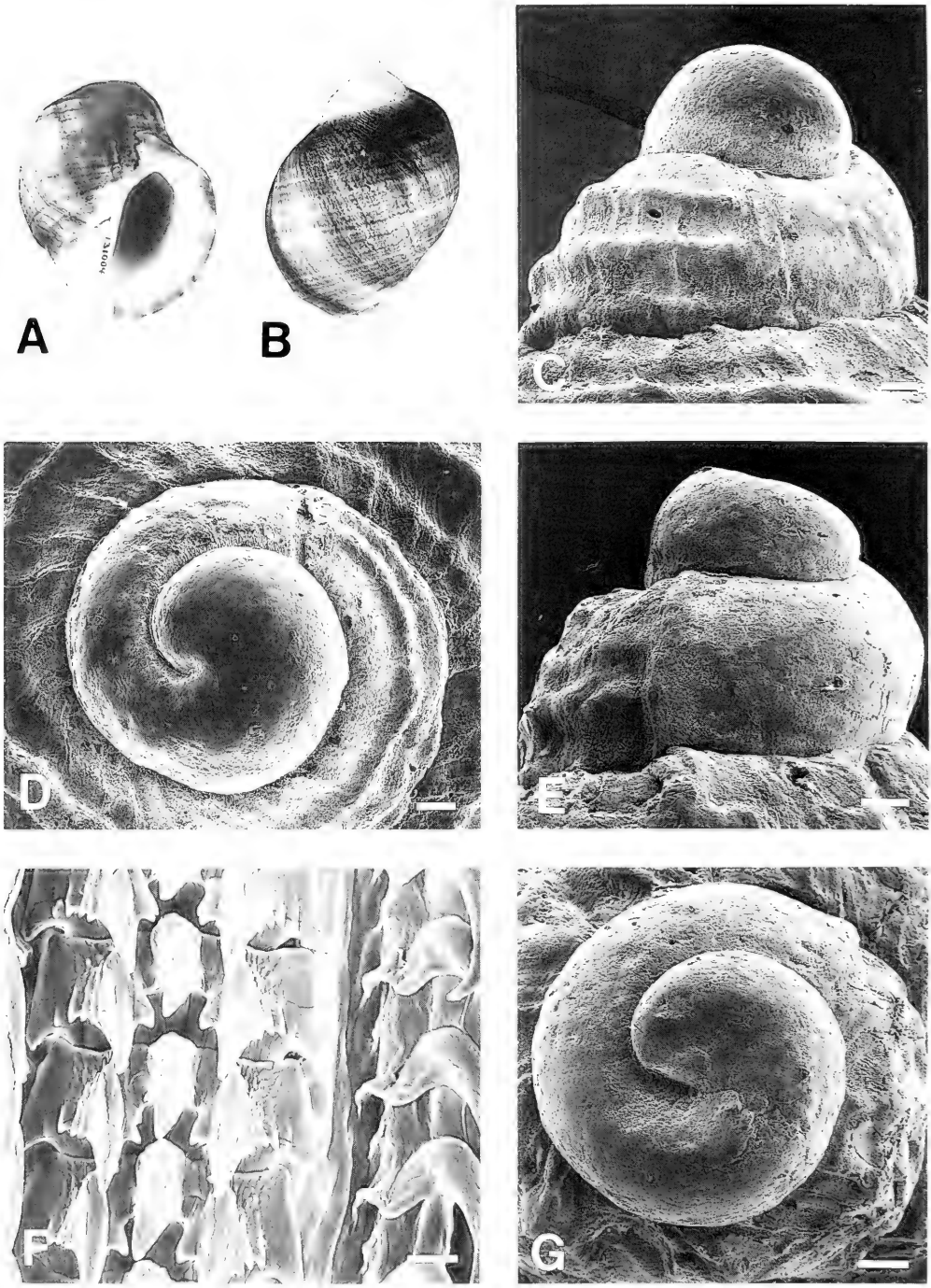

FIG. 27. A–D, *Acanthina monodon.* A, shell (46 mm), apertural view. B, shell (46 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E-G, *Urosalpinx cinerea.* E, protoconch, side view, SEM (bar = 0.10 mm). F, radula, SEM (bar = 10 μm). G, protoconch, apical view, SEM (bar = 0.10 mm).

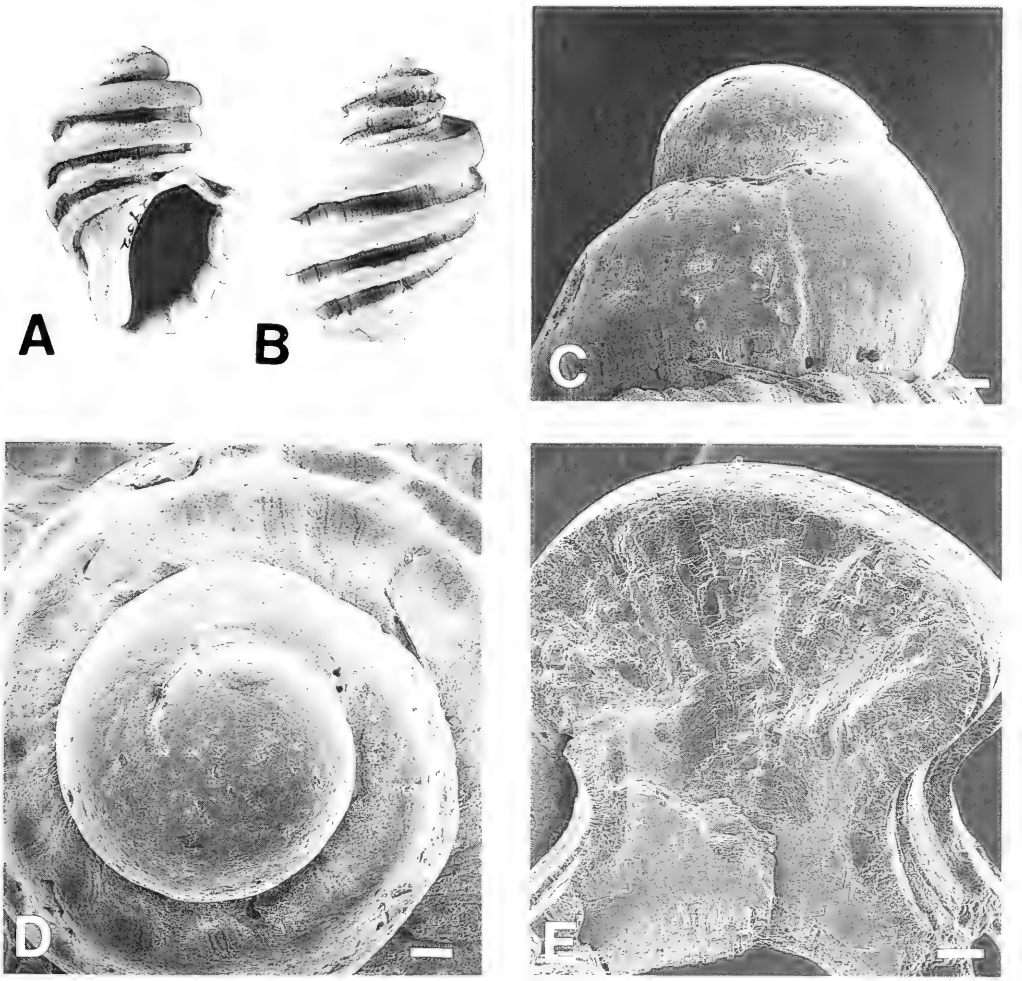

FIG. 28. *Trochia cingulata.* A, shell (40 mm), apertural view. B, shell (40 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.10 mm). D, protoconch, apical view, SEM (bar = 0.10 mm). E, shell ultrastructure, SEM (bar = 50 μm).

40%), and a calcitic layer (30–65%) (Fig. 28E).

Phylogenetic Analysis

Figure 30 shows a consensus tree of 6,288 trees obtained with all multistate characters (Table 3) scored as unordered and using the rigorous "mh* bb*" command. The consistency index of each of the trees is 0.86; the consistency index of the consensus tree is 0.77.

DISCUSSION AND CONCLUSIONS

Phylogenetic Analysis

It is obvious that the Thaididae/nae of authors, which prior to now usually included all taxa used in this study except *Muricanthus, Rapana,* and (usually) *Forreria,* can be divided into two monophyletic groups and that para- and polyphyly was present in previous taxonomic arrangements both at the generic and (sub)familial levels. For example, the type species of *Nucella* (often referred to in the literature as "*Thais*" *lapillus* or "*Purpura*"

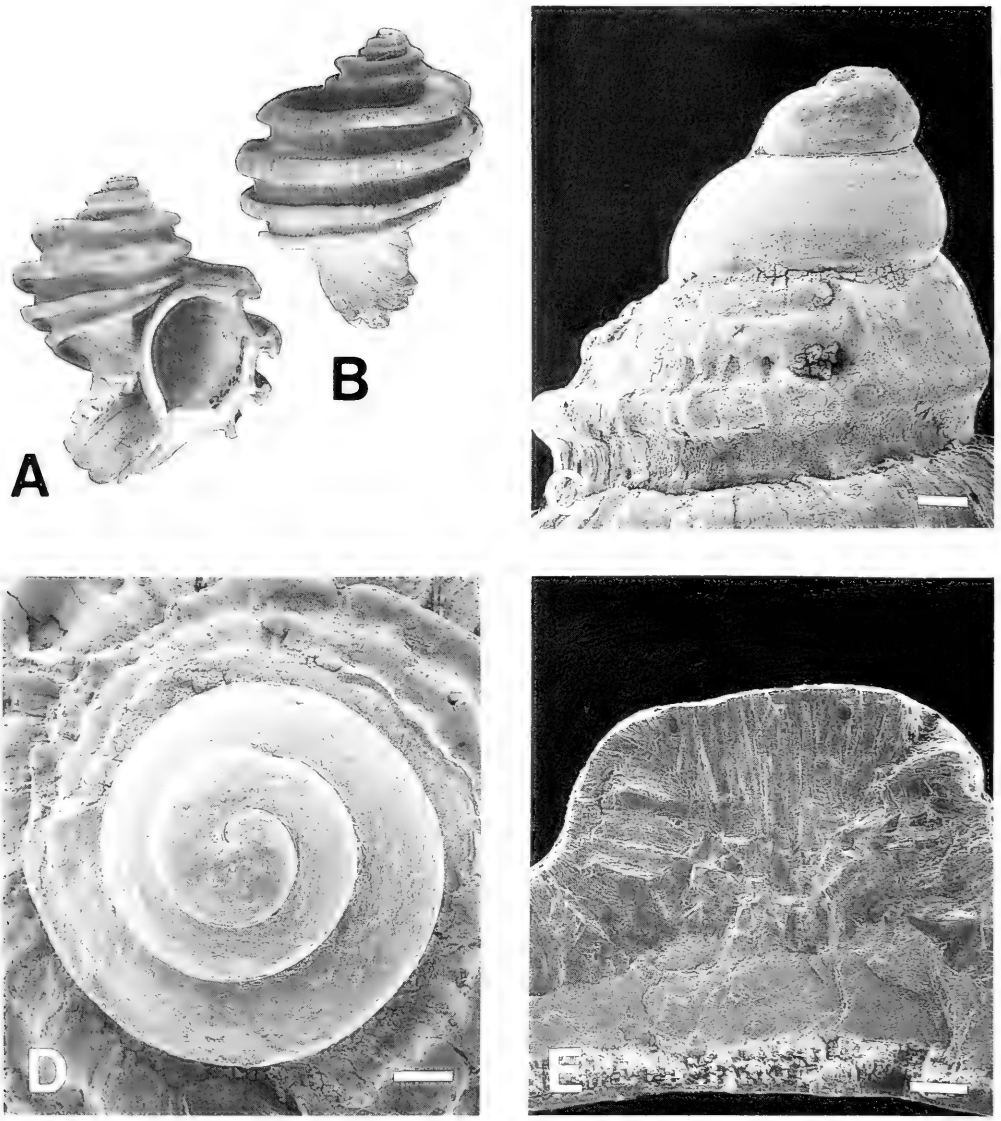

FIG. 29. *Ecphora* cf. *quadricostata.* A, shell (71 mm), apertural view. B, shell (71 mm), abapertural view. C, protoconch, side view, SEM (bar = 0.15 mm). D, protoconch, apical view, SEM (bar = 0.15 mm). E, shell ultrastructure, SEM (bar = 0.30 mm).

lapillus), is excluded from the taxon name to be used for Clade C (Fig. 30), based on a wide variety of characters, many of which it shares as synapomorphies with *Forreria belcheri,* the type species of *Forreria,* which was previously grouped within the Rapaninae as well as Thaidinae.

The high number of trees is partially due to the lack of data for two of the species of Clade B (*Acanthina monodon* and *Trochia cingulata*). This resulted in a multitude of resolutions for this clade and thus increased the total number of equally parsimonious trees.

The number of convergences and parallelisms among the two main clades (e.g. a separate pedal gland and accessory boring organ in *Nucella* and *Cymia*) and the outgroup, indicate that boundaries among these three

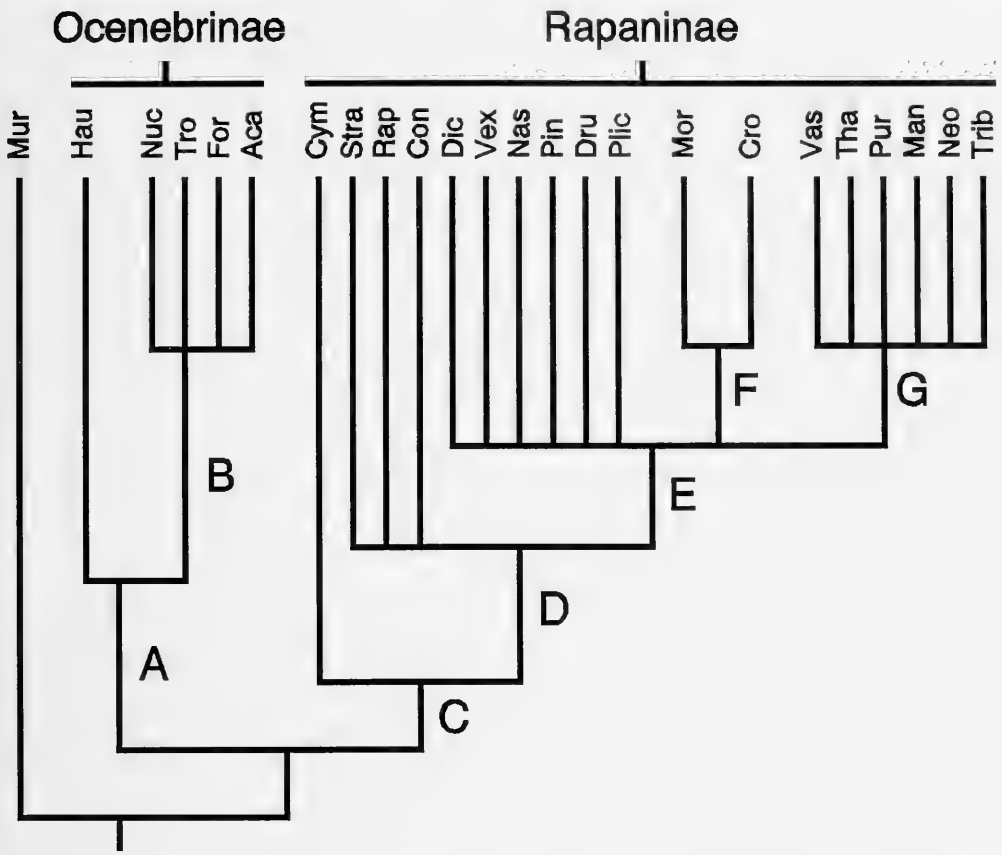

FIG. 30. Consensus cladogram with taxonomic groupings superimposed. Mur = *Muricanthus;* Hau = *Haustrum;* Nuc = *Nucella;* Tro = *Trochia;* For = *Forreria;* Aca = *Acanthina;* Cym = *Cymia;* Stra = *Stramonita;* Rap = *Rapana;* Con = *Concholepas;* Dic = *Dicathais;* Vex = *Vexilla;* Nas = *Nassa;* Pin = *Pinaxia;* Dru = *Drupa;* Plic = *Plicopurpura;* Mor = *Morula;* Cro = *Cronia;* Vas = *Vasula;* Tha = *Thais;* Pur = *Purpura;* Man = *Mancinella;* Neo = *Neorapana;* Trib = *Tribulus.*

groups are not sufficiently clear-cut to justify familial ranking for all three clades. I suggest that these clades merely be ranked as subfamilies.

The taxa on Clade A form a distinct, cohesive clade, despite the limited data available for two of its taxa. Previously, the genera *Haustrum, Acanthina, Nucella, Trochia,* and *Forreria,* had been included in Thaididae/nae of authors, although *Forreria* has also been allocated to Rapaninae of authors. However, the five species in Clade B show no more resemblance with members of Clade C than they do with *Muricanthus* (Muricinae). As stated earlier, studies of *Ocenebra s.s.* (Kool, 1993) revealed close phylogenetic relationship among Ocenebrinae and the taxa of Clade A.

The consensus tree shows that including only *Rapana* in Rapaninae would result in paraphyly. *Cymia* can be considered as an atypical member of Rapaninae (see below), but providing it with separate subfamilial status appears unjustified. All taxa of Clade C should be included in Rapaninae. Perhaps future studies will reveal that Rapaninae should be further subdivided into two or more subfamilies. For example, in some previous analyses *Cronia* and *Morula* grouped at the base of Clade C (Kool, 1989); either these two genera are very highly derived members of Clade C, or their placement in Clade C should be subjected to further examination, which may show that they are better placed in Ergalataxinae Kuroda & Habe, 1971. The present study, however, indicates that all taxa of

TABLE 3. Characters and character states. Numbers and letters correspond to those in text.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Taxon																		
Muricanthus	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Forreria	b	b	b	a	b	a	b	a	a	a	b	a	a	a	b	?	b	c
Nucella	b	b	b	a	b	a	b	a	a	a	b	b	c	a	b	b	b	c
Haustrum	b	?	c	a	b	a	a	a	a	a	b	b	b	a	e	b	a	b
Morula	a	a	a	a	c	b	a	b	b	b	c	c	d	b	c	a	a	e
Cronia	c	a	a	a	c	b	a	b	b	b	d	c	d	b	c	a	a	e
Rapana	a	a	c	a	d	a	a	a	b	c	d	e	d	b	b	a	a	f
Cymia	?	?	c	a	e	a	b	a	b	a	?	d	d	b	b	a	a	d
Stramonita	a	a	b	a	e	a	a	a	b	c	d	e	d	b	b	a	a	g
Concholepas	a	a	b	a	e	a	a	a	b	c	d	e	d	b	b	a	a	g
Dicathais	c	a	b	a	e	a	a	b	b	c	?	e	d	b	c	a	a	g
Vasula	?	?	?	b	e	a	a	b	b	c	d	e	d	b	c	?	a	j
Vexilla	d	a	a	a	f	a	c	b	b	c	d	f	d	b	d	a	a	?
Nassa	a	a	a	a	e	a	a	b	b	c	d	f	d	b	c	a	a	?
Pinaxia	a	a	a	a	e	a	a	b	b	c	d	f	d	b	c	a	a	h
Drupa	?	?	?	a	e	a	a	b	b	c	d	e	d	b	d	a	a	h
Plicopurpura	a	a	?	a	e	a	a	b	b	c	d	e	d	b	c	a	a	?
Thais	?	a	c	b	e	a	a	b	b	c	d	e	d	b	c	a	a	j
Purpura	?	a	c	b	e	a	a	b	b	c	d	e	d	b	c	a	a	h
Mancinella	?	?	c	b	e	a	a	b	b	c	?	e	d	b	c	a	a	i
Neorapana	?	a	c	b	e	a	a	b	b	c	d	e	d	b	c	a	a	j
Tribulus	?	a	c	b	e	?	a	b	?	?	?	e	d	?	?	?	a	j
Acanthina	b	b	?	a	b	?	b	?	a	?	?	b	?	?	?	?	?	?
Trochia	b	b	b	a	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Clade C are to be included in one subfamily, of which *Rapana* is the provider of the subfamilial name. Thaidinae becomes a subjective junior synonym of Rapaninae, by priority.

A discussion of the relationships among the taxa of the main clades of the consensus cladogram (Fig. 30) follows.

Clade A: Haustrum haustorium is more closely allied with the species of Clade B than it is with any of the species of Clade C. Two of the taxa of Clade B (*Acanthina* and *Trochia*) were not examined in detail for this study, but they grouped unambiguously with *Nucella* and *Forreria* based on the data available. Nevertheless, the hiatus of character states of these two taxa resulted in a large number of variations in the resolution of Clade B, contributing to the high number of trees obtained from the analysis.

Clade C (individual clades treated separately): Although *Cymia* is included in Clade C, it shares a synapomorphy with the species of Clade B (accessory boring organ and ventral pedal gland [females] with separate duct) and lacks, as do all members of Clade A, a synapomorphy found in all other members of Clade B (posterior seminal receptacles [females]). However, *Cymia* shares several synapomorphies with all other taxa of Clade B (bursa copulatrix continuous with capsule gland [females], strongly recurved penis, closed prostate, penial vas deferens a duct-within-a-duct [males]). Further detailed studies may determine whether the placement of this atypical, perhaps primitive, species in Rapaninae is justified.

The radular morphology of *Cymia tecta* reveals a possibly closer relationship with *Haustrum* than the tree topology indicates. To *a posteriori* test for homology (Patterson, 1982) in the radular morphology, the radular characters (17 and 18, Table 3) of *Cymia* were alternatively scored identical to those in *Haustrum,* because the superficial resemblance may be indicative of homology. However, this did not alter the tree topology; other characters overrode this "attempted" switch of *Cymia* to Clade A, and the original placement prevailed.

Clades D, E, F, G: Clades D and E have suffered significant loss of resolution compared to the individual trees from which the consensus tree was obtained. However, several distinct and stable clades can be found higher up the tree. Clade G consists of the taxa *Vasula, Thais, Purpura, Mancinella, Neorapana,* and

Tribulus. The similarity in radular morphology among the taxa *Thais, Tribulus, Neorapana,* and *Vasula* suggests that at these four genera are only distinct at the subgeneric level; I consider *Tribulus, Neorapana,* and *Vasula* subgenera of *Thais,* the oldest available name. *Mancinella* and *Purpura* are sufficiently different in radular morphology from one another and from the other four genera in Clade G to justify separate generic status for these two taxa. This separation at the generic level is further supported by the topologies of many of the obtained trees. Clade F, consisting of *Morula* and *Cronia,* is also very stable.

The low resolution among the taxa *Rapana, Stramonita,* and *Concholepas* of Clade D, and of *Dicathais, Vexilla, Nassa, Pinaxia, Drupa,* and *Plicopurpura* of Clade E, can be attributed to several factors. The characters and character states used are adequate to identify major groups, but are not sufficiently robust to yield only one most parsimonious, highly resolved tree. At the lower taxonomic levels, convergence and parallelism appear to be more common, thus increasing the number of equally parsimonious branching patterns. This low resolution could furthermore be attributed to close phylogenetic relationship. I propose that a combination of these factors is the cause for a low resolution in Clades D and E, as well as in Clades B and G. It should be noted that low resolution by itself does not provide a strong argument for synonymization of any of the genera in these clades; autapomorphies for the type species of a genus most likely become synapomorphies for almost all species within that genus when more species are added to the analysis.

Character State Transformations on Cladogram

The topology of the cladogram (Fig. 30) supports a single hypothesis for character-state evolution in 13 characters. More than one (and equally parsimonious) transformation series are possible for the remaining five (3, 5, 11, 12, and 18). I chose for the scheme which would place character-state changes as high on the tree as possible; this reasoning prevents placement of less informative synapomorphies to be placed in basal positions. For example, if state (a) occurred in the outgroup, (b) in Clade A (Fig. 30), and (c) in Clade C, I would choose a scheme whereby both (b) and (c) evolved from (a), although it would be equally parsimonious to assume a linear transformation series [(a) → (b) → (c) or (a) → (c) → (b)].

The hypotheses about character state evolution and possible causal schemes are discussed below. The numbers and letters assigned to, respectively, the characters and character states correspond to the numbers and letters in Table 3 and to those in the list of characters in MATERIALS AND METHODS.

Protoconch:—Number of whorls and sculpture (1). From a multispiral, sculptured condition (a) (e.g. Fig. 24C) evolved three other conditions: a paucispiral, smooth condition (b) (e.g. Fig. 15C); a multispiral, smooth condition (c) (e.g. Fig. 9C); and a paucispiral, sculptured condition (d) (e.g. Fig. 23D).

—Transition into teleoconch (2). The apomorphic condition is the absence of an outward-flaring lip and sinusigeral notch (b) (e.g. Fig. 15C). In most of the studied taxa, these features are present (a) (e.g. Fig. 13D). The absence of the outward-flaring lip and sinusigeral notch correlates with the mode of development; species with direct development lack these features, whereas it is present in taxa with a planktonic larval stage. The tree topology suggests that the direct mode of development evolved from a free-swimming mode of development.

Shell Ultrastructure:—Calcitic outer layer (3). Absence of calcite is the plesiomorphic condition (a); presence of calcite is the derived condition. The presence of calcite is arbitrarily quantified into the states "thick" (> 25% of total shell thickness) (b) (e.g. Fig. 15G), and "thin" (< 20% of total shell thickness) (c) (e.g. Fig. 20E). A thick layer probably evolved from a thin layer.

It is difficult to determine whether calcite is present in *Drupa, Vasula* and *Plicopurpura.* Crystallographic (e.g. X-ray diffraction) techniques should be used to determine whether calcite is present in those taxa scored with "?" for this character in Table 3. The lacking data and low resolution of the cladogram does not allow for speculation on evolutionary trends for this character, other than that the lack of calcite is the plesiomorphic condition found in the outgroup, some members of the Rapaninae, and in other neogastropods (Buccinidae, Volutidae, etc.) (Harasewych & Kool, in preparation).

—45° innermost aragonitic layer (4). Absence of this inner layer of aragonite, the crystal planes of which are oriented in a 45°

angle to the growing edge, is the plesiomorphic condition (a); presence of this layer is the derived state (b) (e.g. Fig. 20E). This layer not only adds thickness to the shell, but presumably also gives more strength to it, which may serve as defense to predation.

Operculum:—Morphology of operculum (5). The opercular shape in the outgroup is oval, with a terminal nucleus in the lower right, and with concentric growth lines (a) (Fig. 1A). This condition gave rise to both a D-shaped operculum with upper end rounded and with lateral nucleus in the lower right (b) (e.g. Fig. 1D), and a D-shaped operculum with a lateral nucleus in the center right (e) (e.g. Fig. 1C). From this last condition (e) arose three other opercular morphologies: an inverted tear-shaped operculum with a rounded upper edge, a tapered lower end, and with a lateral nucleus in the lower right (d) (e.g. Fig. 1B); a D-shaped operculum, tapered at the lower end, with an S-shaped left edge (adjacent to columella), and with a lateral nucleus in the lower right (c) (e.g. Fig. 1F); and an ovate-elongate operculum, tapered at the lower end, and with a lateral nucleus in the upper right (f) (Fig. 1E).

The shape of the operculum is, of course, largely dependent on aperture shape; however, it is interesting that the operculum of *Haustrum,* a non-rapanine, is very different in morphology from that of *Purpura* or *Plicopurpura,* whereas these three species have extremely similar apertural shapes. It should be noted that the operculum of *Rapana rapiformis* is scored differently from the other rapanines, but that the operculum of other *Rapana* species is D-shaped and with a nucleus in the center right, as in most other rapanines.

Taki (1950) provided an evolutionary scenario for opercular morphologies in which a D-shaped operculum with an "extranuclear" nucleus (as found in *Purpura*) evolved from an ovate operculum with an "extraeccentric" nucleus (as found in *Muricanthus*).

—Rodlike structures in hypobranchial gland (6). Presence of rodlike structures in the hypobranchial gland, oriented perpendicular to the mantle (b) is the apomorphic condition (Fig. 2A, B). The function of these structures is not known.

—Ventral pedal gland and accessory boring organ (7). In female specimens of the outgroup and in many of the rapanines, the accessory boring organ and ventral pedal gland share a common duct to the outside (a) (Fig. 4B). From this condition arose two conditions: the development of a ventral pedal gland with an opening separate from that of the accessory boring organ (b) (Fig. 4A); and loss of the accessory boring organ (c).

In the majority of taxa studied herein, a single accessory boring organ duct is responsible for the excretion of decalcifying agents and for the intake and tanning of egg capsules. The derived condition of having separate ducts enables the female to specialize both structures further and may allow feeding during periods between laying eggs. This increase in flexibility is of more importance to snails with seasonal patterns in feeding and spawning, than to those that can feed and spawn at any time. The most derived condition is loss of the accessory boring organ, which probably is the result of specialized feeding habits. (*Vexilla* is parasitic on urchins [Kay, 1979; Kool, 1987].)

Mantle Cavity Organs:—Osphradial length relative to ctenidial length (8). The plesiomorphic condition is an osphradial length of less than one-half the ctenidial length (a). This condition gave rise to an osphradial length of at least one-half that of the ctenidium (b) (Fig. 3D).

Numbers of osphradial lamellae vary from about 7–14 per mm; those of the ctenidium from 9–22 per mm. It seems probable that a relatively larger osphradium facilitates the search for food. However, because the osphradium is measured against ctenidium size, it may be that the small size of the ctenidium only causes the osphradium to appear larger than the osphradium in other species. Furthermore, the density of osphradial lamellae may be age and/or size dependent. This character thus does not lend itself for adaptationist schemes.

Female Reproductive System:—Bursa copulatrix (9). A sacklike bursa, usually located anterior to the capsule gland, and with its lumen separate from that of the capsule gland is the plesiomorphic condition (a) (Fig. 4C). From this condition evolved a bursa that is merely an anteriorly located specialized extension of the capsule gland (b) (Fig. 4D).

—Posterior seminal receptacles on dorsal periphery of the albumen gland (10). Absence of these structures is the plesiomorphic condition (a) (Fig. 4F, G); from this condition evolved a development of specialized structures for sperm storage that open into the albumen gland (c) (Fig. 4H). A situation where

two or three seminal receptacles branch off the ovi-sperm duct appears to have evolved from the latter condition (b) (Fig. 4E).

Kool (1988a, b) described in detail why the posterior seminal receptacles, which open directly into the albumen gland, allow a more efficient mode of fertilization, and suggested that this evolutionary novelty may have triggered a radiation in rapanines. Presence of a specialized receptacle branching off the ovisperm duct could be interpreted as an intermediate condition, but the tree topology suggests it is the most highly derived condition.

—Morphology of albumen gland (11). The ancestral condition of albumen gland morphology was most likely a dorsally swollen oviduct, which then developed into a lobular structure (a) (Fig. 4F). Two morphologies evolved from this ancestral state. The ventral side of the oviduct may have invaginated, resulting in an arch-shaped tube, appearing like a tube coiled onto itself (b) (Fig. 4G), and an omega-shaped tube (d) (Fig. 4H). From the last condition (d) arose a more asymmetrical, staff-shaped albumen gland (c) (Fig. 4E).

If, indeed, this is the sequence of evolutionary events in the development in this character, it may be hypothesized that albumen glands became more efficient in the process of coating of albumen due to an increased surface area and a longer route for the eggs to travel (Kool, 1988a, b). Higher efficiency may explain the reduction of the anterior lobe of this gland in a highly derived taxon, such as *Morula*.

Male Reproductive System:—Morphology of penis (12). The outgroup has an elongated, occasionally lightly curved, gradually tapering penis (a) (Fig. 5A). From this shape, several different morphologies evolved: a relatively short, wide, straight or lightly curved penis with a small pseudo-papilla (b) (Fig. 5B); an elongate, wide penis, strongly recurved, club-shaped, with a slightly swollen distal end (d) (Fig. 5F); a consistently strongly recurved penis tapering distally into a flagelliform appendage of varying length (e) (Fig. 5D). From (e) evolved a slightly recurved penis, long and gradually tapering distally (f) (Fig. 5C); the tree topology furthermore suggests that a penis with a large side lobe (c) (Fig. 5E, l, sl) evolved from (e). The side lobe may have some purpose in the copulation process.

—Morphology of penial vas deferens (13). The outgroup has a well-developed duct, semi-closed by interlocking lateral ridges (a) (Fig. 5A). From (a) evolved three states: an open duct, located on the posterior edge of the penis (b); a semi-closed condition, similar to (a), but with minute duct and without lateral ridges, and lying more adjacent to the penial posterior edge (c) (Fig. 5B); and a convoluted, coiling, meandering tube within a larger cavity (duct-within-a-duct system) (d) (Fig. 5D).

Histological studies may show that the dorsal and ventral flaps of tissue in conditions (a) (with lateral ridges) and (c) (without lateral ridges) are held together by cilia. Dissections of well-preserved specimens of *Haustrum* will determine whether the "open" condition is not an artifact of poor preservation.

—Morphology of prostate duct (pallial vas deferens) (14). A prostate duct that is in open connection with the mantle cavity (in the posterior portion) is the plesiomorphic character state (a) (Fig. 5H). A duct closed throughout the prostate developed from this condition (b) (Fig. 5G).

A prostate with a duct in open connection with the mantle cavity may be to some advantage by allowing for an emergency release for sperm in case the snail is forced to withdraw into the shell. However, it is doubtful that the elasticity of the pallial gonoduct could not absorb some extra pressure while the animal is withdrawing. Furthermore, loss of sperm would be prevented in a closed prostate duct.

Alimentary System:—Length of accessory salivary glands (15). A very poorly developed, almost vestigial, minute right accessory salivary gland is present in the outgroup (a). From this condition arose a pair of very long accessory salivary glands (up to over one-half of shell height) (b), from which arose two other conditions: presence of a very well-developed, long (nearly one-half of shell height) right accessory salivary gland (e), and a pair of glands of short to medium length (less than one-fourth of shell height) (c) (Fig. 3F, ra, la). From the latter condition evolved loss of both the left and the right glands (d).

—Length of posterior blind duct of gland of Leiblein (16). The plesiomorphic condition is a long duct ($\geq$ one-half length of gland itself) (Fig. 3F, dgL) which reaches into the dorsal branch of the afferent renal vein (a). From this condition evolved a very short duct ($<$ 1/2 of length of gland itself) which empties into the posterior portion of the cephalic cavity (b) (Fretter & Graham, 1962: fig. 153).

Radula (Rachidian):—Orientation of marginal cusp (17). A marginal cusp in the same plane with the lateral cusp is the plesiomorphic condition (a). From (a) arose a marginal cusp which is in a different plane with the lateral cusps (b) (e.g. Fig. 15E, F).

—Morphology of cusps on rachidian tooth (18). From a rachidian without a marginal area and cusps, with a small, free-standing inner lateral denticle, and long lateral cusps (a) (Fig. 24E) evolved four morphologies; the first, without marginal area and cusps, with large, free-standing inner lateral denticle and long lateral cusps (b) (Fig. 11D); the second, without marginal area, with small marginal cusps, one or more inner lateral denticles and long lateral cusps (c) (e.g. Fig. 15F); the third, without marginal area, with small marginal cusps, a small inner lateral denticle and short, nearly triangular lateral cusps (d) (Fig. 8H); the fourth, without marginal area, with small marginal cusps, with one or more inner lateral denticles and long lateral cusps (g) (e.g. Fig. 7F). From (g) arose four other rachidian morphologies: a wide marginal area, without marginal cusps, with free-standing inner lateral denticle and short lateral cusps (e) (e.g. Fig. 8D); one without marginal area and cusps, with several faint inner lateral denticles and long lateral cusps (f) (Fig. 25C, E); one with wide marginal area with many denticles and a small marginal cusp, a small inner lateral denticle and long lateral cusps (h) (e.g. Fig. 18D); and one with a short marginal area, with small marginal cusps, with or without small inner lateral denticle and with long lateral cusps (j) (e.g. Fig. 22E). From (j) evolved a rachidian without marginal area and cusps, without inner lateral denticles, and with short lateral cusps (i) (Fig. 11I). Three additional morphologies (scored with "?") that arose from (g) are: similar to (i) but with a free-standing lateral denticle in some specimens, and with short lateral cusps (Fig. 13G); also similar to (i), but with slit in central cusp (Fig. 17E); and the last situation, also similar to (i) but with the base of the central cusp nearly as wide as the rachidian itself (Fig. 23C).

The following are synapomorphies for the different clades and taxonomic groups of the consensus tree (Fig. 30).

Clades A, C ("the ingroup"):
(1) layer of calcite of medium thickness (character 3).
(2) accessory salivary glands very long (nearly one-half of shell height) (character 15).

Calcite is absent in several taxa of Clade E, whereas a thick layer of calcite is present in taxa in Clades B and D (see remarks under *Clade G*). Among taxa of both clades, the accessory salivary glands vary from medium in size to absent.

Clade A (Ocenebrinae):
(1) protoconch paucispiral and smooth (Character 1).
(2) operculum D-shaped, with upper end rounded and with lateral nucleus in lower right (character 5).
(3) albumen gland arch-shaped, elongate (character 11).
(4) penis straight or mildly curved with pseudo-papilla (character 12).
(5) short blind duct of gland of Leiblein (character 16).

Clade B (within Ocenebrinae):
(1) transition from protoconch to teleoconch smooth, outward-flaring lip absent (character 2).
(2) layer of calcite thick (character 3).
(3) accessory boring organ separate from pedal gland (character 7).
(4) marginal cusp in different plane than lateral cusp (character 17).
(5) rachidian with small marginal cusps, one or more small inner lateral denticles, and with lateral cusps nearly equal in length to central cusp (character 18).

A thick calcitic layer (2) and separate ducts for the accessory boring organ and ventral pedal gland (3) are also found in Clade C (*Cymia*) and are probably the result of parallel evolution. Absence of an outward-flaring lip (1) may become a synapomorphy for Clade A, once it is shown that the transition from protoconch to teleoconch in *Haustrum haustorium* is smooth.

Clade C (Rapaninae):
(1) operculum D-shaped, with lateral nucleus in center right (character 5).
(2) bursa copulatrix continuous with capsule gland (character 9).
(3) penial vas deferens as duct-within-a-duct (character 13).
(4) prostate gland closed to mantle cavity (character 14).

Clade D:

(1) posterior seminal receptacles on dorsal periphery of albumen gland (character 10).
(2) omega-shaped albumen gland (character 11).
(3) penis strongly recurved, with flagellate pseudo-papilla (character 12).
(4) marginal area absent, marginal cusps small; one or more inner lateral denticles; lateral cusps nearly equal in length to central cusp (character 18).

Clade E:

(1) layer of calcite absent (reversal; see remarks under Clade G) (character 3).
(2) osphradial length at least one-half ctenidial length (character 8).
(3) accessory salivary glands short to medium (character 15).

Clade F:

(1) operculum D-shaped, with tapered lower end, S-shaped left edge, and with lateral nucleus in lower right (character 5).
(2) rodlike structures in the hypobranchial gland (character 6).
(3) 1–3 large seminal receptacles lying over the dorsal periphery of albumen gland, and branching off ovi-sperm duct (character 10).
(4) penis with large side lobe (character 12).
(5) rachidian with very wide, smooth marginal area, without marginal cusps, with small inner lateral denticle free from lateral cusp, and with central cusp much longer than lateral cusps (character 18).

Clade G:

(1) layer of calcite thin (character 3).
(2) innermost aragonitic shell layer with crystal planes oriented in 45° angle to growing edge (character 4).
(3) short marginal area with small marginal cusps; inner lateral denticle small or absent; lateral cusps nearly equal in length to central cusp which is wide at base (character 18).

A thin calcitic layer appears to have evolved in a parallel manner in one taxon in Clade A (*Haustrum*) and in two taxa within Clade C (*Cymia, Rapana*). This layer is absent in many taxa of Clade E (reversal as synapomorphy for this Clade) and is present again in the taxa of Clade G. This character-state distribution suggests that this character needs more detailed study and that the pattern of parallelism, convergence and reversal in character 3 may only be the result of inadequate understanding of this character.

Congruence between Proposed Phylogeny and Fossil Record

There are several reasons for not basing a branching sequence on the fossil record of rapanines *a priori.* First, rapanines do not fossilize well in their rocky intertidal environment and have a poor, incomplete fossil record. Thus, an extant taxon with a short fossil history may be part of a primitive lineage with fossil members which have either not yet been discovered or have not been identified as close allies of the extant species.

The second reason for not using the fossil record *a priori* is the problem of taxon identification, especially above the species level, which at most may be based on superficial shell characters. It is difficult to identify phylogenetic relationships among Recent taxa on the basis of external shell morphology alone and even more so to determine phylogeny from fossil shells. For example, because of convergence in shell shape, what may be identified as a fossil species of *Morula* may not be related to Recent *Morula s.s.* species.

Thirdly, fossil records taken from the literature are often unreliable because limits have not been set for most rapanine genera. This causes the scope of genera to vary widely among authors. For example, some of the fossil records of so-called "*Thais s.s.*" may not be based on fossils of the type species of *Thais,* which has a very limited geographical distribution. Rather, they may be based on fossils of the nominal species "*haemastoma,*" which many authors have placed under *Thais,* but is herein shown to belong in the genus *Stramonita.* If *Stramonita* had a longer fossil record than *Thais s.s.,* the geological record of *Thais* would be erroneously set back to the time *Stramonita* appeared.

Finally, it is nearly impossible to determine the geological origin of a genus prior to knowing which species should be included in that genus; the record of a genus may be based on a geologically younger species (e.g. the type), while other (older) members of that genus are incorrectly allocated to another genus.

It is clear—to the dismay of many paleontologists—that the meager fossil record (in this case of the Rapaninae), cannot *a priori* be interpreted with any degree of certainty. Nev-

ertheless, the fossil record is potentially useful. A phylogenetic tree resulting from suites of primarily anatomical, radular, shell ultrastructural, and protoconch characters can be compared to ultrastructural data supplied from the fossil record (for example *Ecphora*). Furthermore, congruence between the phylogenetic hypothesis (tree topology) and the fossil record can then support a cladogram and at least suggest relationships. A detailed study of the shell ultrastructure of fossil Rapaninae and closely related taxa may provide further insight into evolutionary relationships among both extant and fossil taxa.

Congruence of Proposed Phylogeny with Recent Zoogeographical Patterns

A comprehensive study, ideally of monographic nature, based on character suites (such as presented in this study), is necessary prior to determining the zoogeographical range of a genus. Only after questions of relationship among species have been solved, distribution patterns for genera may appear and can be interpreted. For example, the distribution of the genus *Nucella* is far more extensive if some "*Thais*" species from the South African Province are shown to belong to *Nucella s.s.* I predict that many range extensions of genera treated herein will be revised when new limits are set for each genus.

Preliminary geographical patterns for the genera are discussed below, following the branching sequence of the consensus cladogram (Fig. 30).

Clades A, B (Fig. 30): The genus *Nucella* occurs from the eastern Atlantic (northern Europe) to the western Atlantic (northeastern U.S.) Ocean and in the North Pacific (California to the Aleutians to Japan). Preliminary anatomical data (Kool, unpublished data) suggest that the South African muricids, "*Thais*" *dubia* (Krauss, 1848), "*T.*" *squamosa* (Lamarck, 1816), and "*T.*" *wahlbergi* (Krauss, 1848), are ocenebrines; further research may reveal that these species should be placed in *Nucella,* as suggested by Kilburn & Rippey (1982), thus extending the range of the genus *Nucella* considerably. *Forreria* is limited to the North American West Coast. If future studies reveal that this genus is synonymous with *Chorus* Gray, 1847, the range would be extended to northwest South America. The genus *Haustrum* is limited in distribution to New Zealand (some records from Australia). The Recent terminal taxa of Clade A (Fig. 30) live in cool to cold water environments. This similarity in habitat may be considered an additional synapomorphy of Clade A.

Clade C: This clade has representatives from the Atlantic, eastern Pacific, and Indo-Pacific oceans. Only minor patterns can be detected in this clade when superimposing geographic distribution onto the topology of the tree. Most of the genera in the Rapaninae (*Rapana, Vexilla, Nassa, Pinaxia, Drupa, Cronia, Purpura,* and *Mancinella*) have representatives only in the Indian and Pacific oceans. *Rapana* inhabits the Black Sea in addition, but was introduced there by man. *Nassa* comprises at most two species, *N. serta* and *N. "francolina,"* the former occurring in the Indian Ocean, the latter in the central and western Pacific Ocean and on the Cocos-Keeling Islands (Maes, 1967). However, these two taxa may be conspecific (see "Remarks" under treatment of *Nassa*). A similar distribution pattern is found in the genus *Drupa: Drupa lobata* (Blainville, 1832), from the Indian Ocean, and *D. grossularia,* from the Pacific Ocean and Cocos-Keeling Islands (Maes, 1967), may also be conspecific. Other species of *Drupa,* such as *D. morum* and *D. ricinus,* occur throughout the Indo-Pacific. Although most species of *Morula* live in the Indo-Pacific, some representatives inhabit the (sub) tropical Atlantic (Kool, unpublished data) and eastern Pacific Oceans.

Cymia tecta, the only living representative of the genus *Cymia* (Clade C, at base, Fig. 30), is limited to the Panamic Province, as are *Vasula melones, Neorapana muricata,* and *Tribulus planospira* (Clade G). Several species of *Stramonita* and *Thais* are known from the tropical eastern Pacific as well, but the type of *Stramonita* occurs in the (sub)tropical eastern and western Atlantic, and so does the type of *Thais.* I suspect that future studies of "*Stramonita*-like" and "*Thais*-like" taxa from the Indo-Pacific may reveal that *Stramonita* and *Thais,* like *Morula,* have an almost global distribution.

The monotypic genera *Concholepas* and *Dicathais* have limited distributions. *Concholepas* is found exclusively in western South America (Chile), while *Dicathais* is endemic to temperate Australia and New Zealand. Fossils of what are believed to be representatives of *Concholepas* have been reported from Australia (Vokes, 1972: 31) and South Africa (Kensley, 1985).

Plicopurpura has one representative in the Panamic Province, and one in the western Atlantic (see "Remarks" under treatment of this genus, and Kool, 1988b). Occurrence of what appears to be a *Plicopurpura* species in Réunion and Mauritius (Drivas & Jay, 1987) is under investigation.

Protoconchs: Reproductive Mode and Phylogenetic Implications

Protoconch morphology has been shown to be indicative, at least to a degree, of relationship and modes of development of gastropods (Shuto, 1974; Jablonski, 1982). A paucispiral, smooth protoconch, with smooth transition from protoconch to teleoconch, is usually indicative and typical of species with a crawl-away larva. A multispiral protoconch with varying degrees of sculpture, outward-flaring lip, and sinusigeral notch for accommodation of the velar lobes, is usually indicative of a planktonic larval phase.

The species used as outgroup in the cladistic analysis, the muricine, *Muricanthus fulvescens,* has the greatest number of protoconch whorls (4.5–4.75), and a pattern of microscopic pustules on most of its whorls, with an outward-flaring lip and sinusigeral notch (Fig. 24C, F). The protoconch of *Nucella* is smooth, paucispiral (about 1.25 whorls), and has a smooth transition into the teleoconch (Fig. 15C, D). In contrast to *Nucella,* all rapanine genera examined have multispiral protoconchs, varying from two to at least 4.25 whorls (completely intact specimens of protoconchs may reveal numbers as high as 4.75), with outward-flaring lip and sinusigeral notch, and with sculptural patterns varying from subsutural plicae to pustulate whorls.

Within Clade D no distinct trend in reduction or increase in number of whorls is visible; some of the highest numbers of whorls occur in Clade F (*Morula, Cronia*). Most rapanine species have three to four protoconch whorls. *Concholepas, Thais, Plicopurpura,* and *Vexilla,* have a relatively low number of whorls, varying from two to about three.

A certain degree of convergence in protoconch morphology is apparent. Although the rapanine protoconch usually has one to three-and-a-half more whorls than the protoconch of the ocenebrines herein examined, *Vexilla* is an exception in having only two whorls. A very high number of whorls is found both in the outgroup and in the rapanines, *Morula* and *Nassa.*

Despite some degree of convergence in protoconch whorl number, the cladogram provides great predictive power for missing data on protoconch morphology. For example, I predict that well-preserved protoconch specimens of the species of Clade G (Fig. 30) will reveal a sculptural pattern as found in most members of Clade E (3–4.5 whorls, with subsutural plicae). The cladogram furthermore predicted that *Haustrum haustorium* has a paucispiral, smooth protoconch, which I found confirmed in Suter (1913) prior to the final computer analysis. Scanning electron micrographs will reveal if the protoconch of *Haustrum haustorium* lacks an outward-flaring lip and sinusigeral notch, as suggested by the cladogram. The protoconch of *Cymia* is more difficult to predict because of its position between the ocenebrine clade (Clade A, Fig. 30) and the remaining members of the rapanine clade (Clade D).

Evidence obtained from protoconch morphology indicates that all members of the Rapaninae studied herein (Clade C, Fig. 30) probably have planktonic larvae. It has always been believed that rapanine ("thaidine") gastropods displayed two very different modes of development: lecithotrophic (direct) and planktotrophic (indirect). For example, *Nucella,* traditionally included in Thaididae/nae of authors, has direct development with "crawl-away" hatchlings (Ankel, 1937; Spight, 1979) and lays egg capsules containing nurse eggs (Spight, 1979). However, as shown previously (Kool, 1993), *Nucella* is to be excluded from Rapaninae and to be included in Ocenebrinae. It is now clear that a planktonic larval stage is typical for Rapaninae and that the direct mode of development is a synapomorphy for Clade B (Fig. 30) and, perhaps, for Clade A if *Haustrum* is revealed to be lecithotrophic.

It should be noted that although one basic protoconch type is present in the Rapaninae (multispiral and [usually] sculptured), and another in the Ocenebrinae (paucispiral and smooth), protoconch morphology varies greatly within the Muricinae. Therefore, depending on which muricine species is used as outgroup, the character state "multispiral" is either the apomorphic or the plesiomorphic condition. Perhaps the muricine outgroup should be coded "either multispiral, sculptured or paucispiral, smooth" in future analyses.

Phylogenetic Relationships Between Rapaninae and Other Muricid Taxa

In this study two taxa were examined in less detail (*Acanthina* and *Trochia*). Some of the data on these lesser-understood taxa indicate or, at least, suggest their relationships with the taxa studied in detail. An "incomplete" and sometimes scattered data base based on anatomical, radular, protoconch, opercular, and shell ultrastructural characters, yielded several conclusions about phylogenetic relationships between taxa studied in detail and those within the Muricidae.

For example, a few anatomical, protoconch, and shell ultrastructural data suggest that *Acanthina* is very closely related to *Nucella* and should also be excluded from Rapaninae. *Nucella* and *Acanthina* both appeared in the Miocene, and *Acanthina* also occurs in cold to temperate waters (California—North Mexico, Chile), and overlaps in geographic range with the range of *Nucella emarginata* (Deshayes, 1839).

The monotypic genus *Trochia* from South Africa, with a paucispiral protoconch of about 1.5 whorls (Fig. 28C, D), and similar to *Nucella* in shell ultrastructure (Fig. 15C, D), should also be excluded from Rapaninae. Results from future anatomical studies may reveal justification for synonymization of *Trochia* with *Nucella.* Kilburn & Rippey (1982) referred the nominal species, *cingulata,* to *Nucella* instead of *Trochia.* Egg capsule morphology, however, differs greatly among *Trochia cingulata* and members of *Nucella* (Kilburn & Rippey, 1982; D'Asaro, 1991).

Forreria (Fig. 26A–F) may be closely related to the genus *Chorus,* an eastern Pacific genus from the Chilean waters. Future studies may show that *Chorus* and *Forreria* are merely synonyms. Both genera have a labial tooth (a structure also found in *Acanthina*), and have a very similar, distinct shell shape.

The fossil genus *Ecphora* (Fig. 29A–E), has been allocated to different muricid families [Rapanidae (Wenz, 1941); Thaididae (Petuch, 1988, in Ecphorinae Petuch); Muricidae (Ward & Gilinsky, 1988)]. The protoconch of *Ecphora* cf. *quadricostata* (Say, 1824) (Fig. 29C, D) is multispiral and counts about three smooth whorls, similar to *Cronia* and *Dicathais,* but lacks an outward-flaring lip and sinusigeral notch as does, for example, *Nucella.* Based on these criteria it could belong to either the Ocenebrinae or the Rapaninae. The shell ultrastructure consists of an aragonitic layer with crystal planes oriented perpendicular to growing edge (15–30%), an aragonitic layer with crystal planes oriented parallel to growing edge (25–35%), and a calcitic layer (45–55%) (Fig. 29E). This type of shell ultrastructure is found in *Nucella* and related taxa, such as *Trochia* and *Forreria,* but also in *Concholepas* and *Dicathais.* The shell of *Ecphora* (Fig. 29A, B) bears resemblance to both the ocenebrine *Trochia* (Fig. 28A, B) and the rapanines *Dicathais* (Fig. 9A, B) and *Rapana* (Fig. 25A). However, based on the absence of an outward-flaring lip and sinusigeral notch, I place *Ecphora* provisionally in the Ocenebrinae.

The protoconch and radula of *Urosalpinx cinerea* (Say, 1822) (Fig. 27E–G) are very similar to those of *Nucella* (Fig. 15C–F). Further studies of *Urosalpinx* species are likely to confirm a close tie with *Nucella.* Although *Urosalpinx* lacks a calcitic outer layer (Petitjean, 1965), it may belong in a clade with *Nucella, Acanthina, Trochia,* and *Forreria.*

Radular Evolution in the Rapaninae

Patterns of rapanine radular morphology are not usually congruent with present taxonomic classifications of rapanines and closely allied muricids (Bandel, 1984; Fujioka, 1985; Kool, 1987), because these classifications are based solely on shell morphology and are thus unreliable (see INTRODUCTION). Now that monophyly has been established for the Rapaninae, patterns in radular morphology can be discussed against a phylogenetic background. Comparisons between findings presented here and reports from the literature are discussed below in an order reflective of the branching sequence in the cladogram (Fig. 30).

Clade A: Troschel (1866–1893) included *Haustrum haustorium* in the genus *Polytropa* (= *Nucella*), based on the width of the rachidian tooth. Cooke (1919) pointed out that the rachidian tooth in *Haustrum* (Fig. 11D) is very different from the rachidian found in *Nucella* (Fig. 15F) and *Forreria* (Fig. 26E), and suggested that either *Haustrum* was the "progenitor" of the *Thais* and *Nucella* groups (making a clear distinction between the "*Nucella*" group and the "*Thais*" group [pp. 103, 109]), or was derived from one of them. Later in the same paper, he stated that *Haustrum* is primitive. Troschel (1866–1893) suspected a close tie between *Nucella* and *Acanthina* but

proclaimed separate generic status for both taxa. The position of *Nucella, Acanthina* and *Haustrum* on the cladogram (Fig. 30) is largely congruent with both Troschel's and Cooke's conclusions.

According to Cooke (1919) and Wu (1968) there are some similarities between the bases of the rachidian teeth of *Morula* and *Nucella,* suggesting a relatively close tie between these two genera. Bandel (1984) noted close similarity between the radula of *Ocenebra erinacea* and a *Morula* radula depicted by Cernohorsky (1969). These conclusions are not supported by the branching pattern in the cladogram. Kool (1993) has shown the high degree of similarity in radular morphology between *Ocenebra* and *Nucella.*

Clade C: Cymia (Fig. 8H) is considered a "link between *Morula* and *Thais*" by Cooke (1919) who based this conclusion on radular resemblances among these three genera. *Cymia* has a radular morphology somewhat atypical of rapanines and, derived from the cladogram, is the most primitive member of the rapanines examined herein.

Tanaka (1958) deemed the rachidian tooth of *Rapana* (Fig. 25C) to be very similar to that of *Purpura* (Fig. 18D). I do not agree; the rachidian of *Rapana* has three large cusps and no marginal area, or marginal cusp, whereas *Purpura* has a wide marginal area with well-developed denticles and a pronounced marginal cusp.

Clade D: Troschel (1866–1893) placed *Nassa* (Fig. 13G) close to *Plicopurpura* (as "*Patellipurpura*") (Fig. 17E), based on rachidian tooth morphology. Cooke (1919) disagreed, placing *Nassa* close to *Vexilla* (Fig. 23C). Furthermore, Cooke (1919) placed the genera *Rapana, Concholepas, Pinaxia,* and *Drupa* close to *Thais.* I agree with Cooke on the close evolutionary relationship between *Nassa* and *Vexilla,* and the close ties among the other four taxa, although *Rapana* and *Concholepas* are located at the base of Clade D.

Cooke (1919) considered the morphology of the rachidian tooth in the genus *Plicopurpura* (Fig. 17E) distinct enough to justify separation of this genus (as "*Patellipurpura* Dall") from *Thais* (Fig. 20F) (and, presumably, from *Purpura*). My conclusions are in agreement with those of Cooke (Kool, 1988b). Cooke also stated that the rachidian tooth morphology must be primitive, based on the distribution of this genus (occurring on both sides of the Panamic Isthmus). I do not agree with this statement; the rachidian tooth morphology of *Plicopurpura* is unique and should be considered as derived.

Clade F: Authors generally agree that the rachidian teeth of *Cronia* (Fig. 8D) and *Morula* (Fig. 12G) are extremely similar (Cooke, 1919), and that *Morula* and *Drupa* (Fig. 10C) are more distantly related than their shell morphologies suggest (Cooke, 1919; Emerson & Cernohorsky, 1973). The tree (Fig. 30) and data presented by Kool (1987) show that *Drupa* and *Morula* are not sister taxa.

Clade G: Arakawa (1962) allotted full generic status to *Mancinella,* based on the morphology of the rachidian tooth (Fig. 11I). I agree and recognize *Mancinella* as a full genus. Cooke (1918) proposed the subgenus *Neorapana* under *Acanthina* for *Acanthina muricata.* He considered *Neorapana* to be a close, New World relative of *Rapana* based on radular and shell morphology. (Note: his drawing of a *Neorapana muricata* rachidian tooth does not resemble that of *Neorapana muricata.*)

Fujioka (1985a) suggested from ontogenetic data that a complex pentacuspid ("comb-" or "sawlike") rachidian tooth may be a primitive condition in Thaidinae of authors, whereas a simple monocuspid rachidian tooth may represent a derived condition. He presented a pattern of transformations in radular morphology for several genera and species (including *Nucella* and other non-rapanines). The major drawback of using terms such as "comblike" or "sawlike" or as "pentacuspid" or "tricuspid" is that a division in these categories is artificial and may not reflect homology. Furthermore, they are too general and allow for different interpretations. For example, I would interpret the "sawlike" condition in *Drupa* as more comblike and homologous with the comblike condition in *Purpura;* additionally, I consider the "sawlike" condition in *Drupa* as being very different from the sawlike condition in *Nucella,* or in *Concholepas.*

The cladogram (Fig. 30) is, however, congruent in some aspects with the pattern discussed by Fujioka (1985a). "Sawlike" radula are found in several taxa at the bases of Clades D and E (Fig. 30) (*Rapana, Stramonita, Concholepas,* and *Dicathais*), as well as in the taxa *Nucella* and *Forreria* (Clade B; non-rapanines). Some of the other taxa on Clades E and G have relatively narrow, tricuspid rachidians (*Nassa, Mancinella*), several of which have only small lateral cusps (*Neora-*

pana, Vexilla, Plicopurpura). *Haustrum,* a non-rapanine, clearly has a wide, pentacuspid, but not comblike, rachidian tooth. A more or less comblike condition occurs only in more derived rapanines, such as *Drupa, Purpura,* and *Pinaxia,* and appears to be the derived condition. *Morula* and *Cronia* both have a wide rachidian due to the wide marginal area, but only the central cusp is well developed in these taxa.

Several other authors have attempted to group muricids on the basis of rachidian cusp number (tricuspid and pentacuspid [Arakawa, 1962; Wu, 1965b, 1967, 1973]). However, as is clear from this paper, divisions in Muricidae based on this character, result in para- and polyphyletic groups. Only after monophyly has been established can this character be used to provide a basis for further resolution within clades.

Evolution in Egg Capsule Morphology

Patterns in egg capsule morphology are not obvious. The egg capsules of *Haustrum haustorium,* a non-rapanine, resemble those of the rapanine *Purpura persica,* and the egg capsules of *Nucella* spp. are also similar to those of certain rapanines.

Habe (1960) recognized two different types of egg capsules in muricids: (1) vase-shaped or pillar-shaped, with a short stalk (e.g. Fig. 6A), and (2) lenticular, with a broad base. He included several species from the Muricinae, Thaidinae (of authors), and two species of the Rapaninae (of authors) in the first category, other muricids (trophonines etc.) in the second. This division is too simplistic, and numerous exceptions can be found (for example, *Purpura bufo* and *Thais deltoidea* have egg capsules with broad bases and lack a stalk).

Bandel (1976) provided a phylogenetic hypothesis for evolution of egg capsule morphology, after recognizing different "Formengruppe." He placed members of *Nucella, Thais, Stramonita* (as "*Thais*"), and *Rapana* together into one of these categories, exclusive of *Thais deltoidea,* which he placed into a category with members of *Coralliophila.* This indicates a case of convergence in egg capsule morphology.

When the egg capsule morphologies of more rapanine type species, some of which were recently described and illustrated by D'Asaro (1991), become known, a search for overall patterns in egg capsule morphology may reveal certain evolutionary trends.

Systematic Conclusions and New Taxonomic Arrangement

The cladogram (Fig. 30) indicates that Thaididae/nae of authors is paraphyletic and consists of two taxonomic groups: Clade A, comprising *Haustrum, Nucella, Forreria, Acanthina,* and *Trochia;* and Clade C, comprising *Cymia, Rapana, Stramonita, Concholepas, Dicathais, Vasula, Thais, Tribulus, Neorapana, Purpura, Mancinella, Drupa, Plicopurpura, Pinaxia, Vexilla, Nassa, Morula,* and *Cronia.* However, a clear cut-off point for either group is not obvious; some parallelism is evident in several character states found in members of Clade A and in taxa at the base of Clade C (long accessory salivary glands, separate ventral pedal gland [females] and boring organ, very thick outer calcitic layer, lack of posterior seminal receptacles [females]). Furthermore, the tree topology reveals a parallelism in the morphology of the prostate duct [males] (not in open connection to mantle cavity) between *Haustrum* and the members of Clade C. These taxon groups are not sufficiently distinct from one another, nor are they sufficiently distinct from Muricinae to warrant family status for either Clade A or C. I therefore agree with Ponder (1973) that the family Muricidae contains several subfamilies, and that Muricoidea includes, amongst other groups, the Buccinidae and Muricidae.

The taxonomic revision of the Thaididae/nae of authors (Clades A and C, Fig. 30) has important nomenclatural consequences. First, the taxa on Clade A are placed in the Ocenebrinae (Kool, 1993) rather than Thaidinae. Secondly, the higher category name of the taxa in Clade C (the remains of Thaididae/nae of authors) needs to be reevaluated. Because *Rapana* is monophyletic with the other taxa in Clade C (Fig. 30) the name for this natural group becomes Rapaninae Gray, 1853, which has priority over Thaidinae Jousseaume, 1888, rendering Thaidinae a junior subjective synonym of Rapaninae.

The high degree of similarity in radular morphology among *Tribulus, Neorapana,* and *Vasula* of unresolved Clade G (Fig. 30), and the fact that two of these taxa are monotypic, suggests that these taxa should be allotted subgeneric status under *Thais.* Perhaps further studies will justify synonymization of these genera with *Thais. Mancinella* and

Purpura, however, are sufficiently different from the other four taxa and from one another to be conserved as separate genera. In the more resolved output trees, the latter two taxa are separate from the other four, which often form a polytomy in many of the trees.

The polytomous Clade B (Fig. 30) suggests a close relationship among *Acanthina, Trochia,* and *Nucella,* but the low resolution is most likely the result of the lack of morphological data for the former two taxa. Data on the egg capsule morphology of *Trochia* (Kilburn & Rippey, 1982) support separate generic status for this monotypic taxon, but anatomical and/or molecular studies of the South African *Nucella*-like species are necessary before any conclusions can be drawn.

The newly proposed classification for the taxa examined in this study is as follows:

MURICOIDEA Rafinesque, 1815

Muricidae Rafinesque, 1815

Rapaninae Gray, 1853
[+ Thaidinae Jousseaume, 1888]
Concholepas Lamarck, 1801
Cronia H. & A. Adams, 1853
Cymia Mörch, 1860
Dicathais Iredale, 1936
Drupa Röding, 1798
Mancinella Link, 1807
Morula Schumacher, 1817
Nassa Röding, 1798
Pinaxia H. & A. Adams, 1853
Plicopurpura Cossmann, 1903
Purpura Bruguière, 1789
Rapana Schumacher, 1817
Stramonita Schumacher, 1817
Thais Röding, 1798
Neorapana Cooke, 1918
Tribulus Sowerby, 1839
Vasula Mörch, 1860
Vexilla Swainson, 1840

Ocenebrinae Cossmann, 1903
[+ Ecphorinae, Petuch, 1988
+ Nucellinae Kozloff, 1987]

Acanthina Fischer von Waldheim, 1807
Ecphora Conrad, 1843
Forreria Jousseaume, 1880
Haustrum Perry, 1811
Nucella Röding, 1798
Trochia Swainson, 1840

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APPENDIX 1

Species Examined Thaididae/nae of authors:

Concholepas concholepas (Bruguière, 1789)
Cronia amygdala (Kiener, 1835)
Cymia tecta (Wood, 1828)
Dicathais orbita (Gmelin, 1791)
Drupa morum Röding, 1798
Haustrum haustorium (Gmelin, 1791)
Mancinella alouina (Röding, 1798)
Morula uva (Röding, 1798)
Nassa serta (Bruguière, 1789)
Neorapana muricata (Broderip, 1832) *1
Nucella lapillus (Linnaeus, 1758)
Pinaxia versicolor (Gray, 1839)
Plicopurpura patula (Linnaeus, 1758) *2
Purpura persica (Linnaeus, 1758)
Stramonita haemastoma (Linnaeus, 1767)
Thais nodosa (Linnaeus, 1758)
Tribulus planospira (Lamarck, 1822)
Vasula melones (Duclos, 1832)
Vexilla vexilla (Gmelin, 1791)
Acanthina monodon (Pallas, 1774) *3
Trochia cingulata (Linnaeus, 1771) *3
Ecphora cf. *quadricostata* (Say, 1824) *3

Rapaninae, of authors:

Forreria belcheri (Hinds, 1844)
Rapana rapiformis (Born, 1778) *4

Muricinae:

Muricanthus fulvescens (Sowerby, 1841) *5

*1 Specimens of the type species of *Neorapana* were typical "*Neorapana tuberculata*" (Sowerby, 1835) morphs; it appears that *N. tuberculata* and *N. muricata* are synonyms. *Neorapana muricata* (Broderip, 1832) is the senior synonym of *Neorapana tuberculata* (Sowerby, 1835) (see "Remarks" under *Neorapana*).

*2 The type species of *Plicopurpura* (*Plicopurpura columellaris* Lamarck, 1816) was not examined, but was substituted by its very similar congener *Plicopurpura patula* (Linnaeus, 1758) because well-preserved anatomical material of this species was available (Kool, 1988b).

*3 These taxa were examined to test if synapomorphies present in some taxa could be recognized in these, facilitating taxonomic allocation. Therefore they were only examined for synapomorphic (diagnostic) characters.

*4 *Rapana rapiformis* (Born, 1778) is a typical rapanine, but it is not the type of *Rapana;* it was included in this study because well-preserved specimens were available.

*5 *Muricanthus fulvescens* (Sowerby, 1841) was chosen to represent the Muricinae as an outgroup in the cladistic analysis, because many living and well-preserved specimens were available.

APPENDIX 2

List of abbreviations used in text.

AMS:	Australian Museum, Sydney.
ANSP:	Academy of Natural Sciences, Philadelphia.
LACM:	Los Angeles County Museum.
MGH:	Myroslaw George Harasewych.
SEM:	Scanning electron micrograph.
SPK:	Silvard Paul Kool.
USNM:	United States National Museum.
ZMA:	Zoologisch Museum, Amsterdam.

APPENDIX 3

Voucher numbers	
Concholepas concholepas	
USNM 706703	Anatomy: Playa Caleta, Chile
AMNH 132968	Protoconch: Catrihue, Tierra del Fuego, Chile
NMNH 857055	Radula: Valparaiso, Chile
USNM 518777	Ultrastructure: Antofagasta, Chile
USNM 706703	Shell: Playa Caleta, Chile
Cronia amygdala	
USNM 836880	Anatomy: Magnetic Island, Queensland, Australia
USNM 836880	Radula: Magnetic Island, Queensland, Australia
USNM 836880	Ultrastructure: Magnetic Island, Queensland, Australia
USNM 795252	Shell: Collaroy, New South Wales, Australia
Cymia tecta	
ANSP 355766	Anatomy: Vera Cruz, Panama
MCZ 302757	Anatomy: Punta Guanico, Panama
ANSP 355766	Radula: Vera Cruz, Panama
USNM 589636	Ultrastructure: Venado Beach, Ft. Knobbe, Canal Zone, Panama
USNM 216294	Shell: Panama City, Panama
Dicathais orbita	
USNM 836862	Anatomy: Botany Bay, New South Wales, Australia
USNM 681578	Protoconch: Omapere, Hokianga Harbour, New Zealand
USNM 836862	Radula: Botany Bay, New South Wales, Australia
USNM 836862	Ultrastructure: Botany Bay, New South Wales, Australia
USNM 618246	Shell: Ulladulla Harbour, New South Wales, Australia
Drupa morum	
USNM 857059	Anatomy: Pago Bay, Guam, U.S.A.
USNM 720340	Protoconch (*D. grossularia*): Garumaoa Island, Tuamotu Islands
USNM 857059	Radula: Pago Bay, Guam, U.S.A.
USNM 857059	Ultrastructure: Pago Bay, Guam, U.S.A.
USNM 672111	Shell: Tongatapu, Tonga Islands
Haustrum haustorium	
AMS no number	Anatomy: Titirangi Bay, New Zealand
AMS no number	Radula: Titirangi Bay, New Zealand
USNM 531495	Ultrastructure: Rangitoto Island, New Zealand
USNM 531495	Shell: Rangitoto Island, New Zealand
USNM 76300	Shell: New Zealand
Mancinella alouina	
AMS no number	Anatomy: Lizard Island, Queensland, Australia
AMS no number	Radula: Lizard Island, Queensland, Australia
AMS no number	Ultrastructure: Lizard Island, Queensland, Australia
USNM 669734	Shell: Pescadores Islands, China Sea
Morula uva	
USNM 857058	Anatomy: Pago Bay, Guam, U.S.A.
USNM 587364	Protoconch: Kwajalein Atoll, Marshall Islands
USNM 857058	Radula: Pago Bay, Guam, U.S.A.
USNM 685003	Ultrastructure: Motu Akaiami, Aitutaki, Cook Islands
USNM 684893	Shell: Aitutaki, Cook Islands

(*continued*)

Nassa serta	
USNM no number	Anatomy: Pago Bay, Guam, U.S.A.
USNM 719808	Protoconch (*N. "francolina"*): Nossi Be, Madagascar
ANSP 269309	Larval shell: Gatope Island, New Caledonia
USNM no number	Radula: Pago Bay, Guam, U.S.A.
USNM 631480	Ultrastructure: Gigmoto, Catanduanes Islands, Philippine Islands
USNM 89600	Shell: Samoa Islands
USNM 618429	Shell: Low Wooded Island, N. Queensland, Australia
Neorapana muricata	
USNM 836661	Anatomy: Puerto Peñasco, Sonora, Mexico
USNM 60718	Protoconch: Acapulco, Mexico
USNM 836661	Radula: Puerto Peñasco, Sonora, Mexico
USNM 836661	Ultrastructure: Puerto Peñasco, Sonora, Mexico
USNM 749212	Shell: San Carlos, Sonora, Mexico
Nucella lapillus	
USNM 857053	Anatomy: Kittery, Maine, U.S.A.
USNM 416825	Protoconch: Manchester, Massachusetts, U.S.A.
USNM 857053	Radula: Kittery, Maine, U.S.A.
USNM 857053	Ultrastructure: Kittery, Maine, U.S.A.
USNM 191106	Shell: Shetland Islands, Scotland
USNM 191094	Shell: Balta Sound, Shetland Islands, Scotland
Pinaxia versicolor	
USNM 262193	Anatomy: Ambatoloaka, Madagascar
USNM 709294	Protoconch: Kuri Island, Hawaii, U.S.A.
ANSP 262193	Radula: Ambatoloaka, Madagascar
ANSP 262193	Ultrastructure: Ambatoloaka, Madagascar
USNM 673781	Shell: Mogadishu, Somalia
Plicopurpura patula	
USNM 857056	Anatomy: South Miami Beach, Florida, U.S.A.
USNM 734594	Protoconch: San Blas Islands, Panama
USNM 857056	Radula: South Miami Beach, Florida, U.S.A.
USNM 736748	Ultrastructure: Cozumel Island, Mexico
USNM 662235	Shell: Mujeres Island, Mexico
Purpura persica	
ZMA no number	Anatomy: Krakatoa, Indonesia
MNHL no number	Protoconch: Tjoba, Tidore, Indonesia
ZMA no number	Radula: Krakatoa, Indonesia
ZMA no number	Ultrastructure: Krakatoa, Indonesia
USNM 700108	Shell: Taiohae Bay, Nukuhiva, Marquesas Islands
Stramonita haemastoma	
USNM 857063	Anatomy: Sebastian, Florida, U.S.A.
USNM 597536	Protoconch: Cocoa Beach, Florida, U.S.A.
USNM 857063	Radula: Sebastian, Florida, U.S.A.
USNM 857063	Ultrastructure: Sebastian, Florida, U.S.A.
USNM 597536	Shell: Cocoa Beach, Florida, U.S.A.
Thais nodosa	
USNM no number	Anatomy: Ascension Island
AMNH 5172	Protoconch: Cape Verde Islands
USNM no number	Radula: Monrovia, Liberia
USNM no number	Ultrastructure: Ascension Island
USNM 767917	Shell: Monrovia, Liberia
Tribulus planospira	
LACM no number	Anatomy: Galápagos Islands, Ecuador
USNM 708234	Protoconch: Malpelo Island, Colombia
LACM no number	Radula: Galápagos Islands, Ecuador
USNM 558161	Ultrastructure: Ensenada de los Muertos, Mexico
USNM 678916	Shell: Academy Bay, Isla Santa Cruz, Galápagos Islands
Vasula melones	
USNM 664731	Anatomy: Palo Seco, Panama
USNM 796187	Radula: Marchena, Punta Estego, Galápagos Islands
USNM 664731	Ultrastructure: Palo Seco, Panama
USNM 732982	Shell: Stony Point, Ft. Amador, Panama

Vexilla vexillum	
USNM 836956	Anatomy: Pupukea Beach, Oahu, Hawaii, U.S.A.
USNM 718391	Protoconch: Tulear, Madagascar
USNM 836956	Radula: Pupukea Beach, Oahu, Hawaii, U.S.A.
USNM 836956	Ultrastructure: Pupukea Beach, Oahu, Hawaii, U.S.A.
USNM 622852	Shell: Mauke, Cook Islands
Forreria belcheri	
USNM no number	Anatomy: Off San Francisco, California, U.S.A.
USNM no number	Radula: Off San Francisco, California, U.S.A.
USNM 169034	Ultrastructure: San Pedrao, California, U.S.A.
Collection MGH	Shell: Catalina Island, California, U.S.A.
Rapana rapiformis	
BMNH no number	Anatomy: Ause Major, Mahe, Seychelles
USNM 655026	Protoconch: South Pagi Island, Indonesia
BMNH no number	Radula: Ause Major, Mahe, Seychelles
BMNH no number	Ultrastructure: Ause Major, Mahe, Seychelles
BMNH no number	Shell: Ause Major, Mahe, Seychelles
Muricanthus fulvescens	
USNM 857064	Anatomy: off Cape Canaveral, Florida, U.S.A.
USNM 621380	Protoconch: 30°18′N, 88°34′W, Gulf of Mexico
USNM 857064	Radula: off Cape Canaveral, Florida, U.S.A.
USNM 857064	Ultrastructure: off Cape Canaveral, Florida, U.S.A.
Collection SPK	Shell: off Cape Canaveral, Florida, U.S.A.
Acanthina monodon	
USNM 2778	Protoconch: Valparaiso, Chile
USNM 131004	Shell: Valparaiso, Chile
Trochia cingulata	
AMNH 128952	Protoconch: Sea Point, Cape Town, South Africa
AMNH 128952	Ultrastructure: Sea Point, Cape Town, South Africa
USNM 2752	Shell: Cape Good Hope, South Africa
Urosalpinx cinerea	
USNM no number	Protoconch: Ft. Pierce, Florida, U.S.A.
USNM no number	Radula: Ft. Pierce, Florida, U.S.A.
Ecphora cf. quadricostata	
USNM no number	Protoconch: St. Mary's Co., Maryland, U.S.A.
USNM no number	Ultrastructure: St. Mary's Co., Maryland, U.S.A.
MCZ 263350	Shell: Chancellor Pt., St. Mary's Co., Maryland, U.S.A.

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PHYLOGENETIC RELATIONSHIPS AND GENERIC REVIEW OF THE BITTIINAE (PROSOBRANCHIA: CERITHIOIDEA)

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ABSTRACT

The anatomy of seven members of the *Bittium* group is described, clarifying the status of the genus-level taxa comprising it. *Bittium reticulatum,* the type species of *Bittium* Gray, is described in depth, thereby establishing criteria for comparisons with other taxa of Bittiinae. The type species of *Stylidium* Dall and *Lirobittium* Bartsch, and representatives of *Bittiolum* Cossmann and *Cacozeliana* Strand are examined and compared with *Bittium, s.s.* Results of anatomical studies and a phylogenetic analysis using the Hennig86 and CLADOS programs, with *Cerithium* as an outgroup, establish monophyly for Bittiinae Cossmann and reveal six different genus-level taxa. A new genus, *Ittibittium,* from the Indo-Pacific, is proposed. Synonymies of each genus-level taxon and representative species examined are presented. Brief accounts of the ecology and zoogeography of each taxon are given. Two taxa formerly attributed to the *Bittium*-group are herein excluded from it and referred to *Cerithium* Bruguière. These are *Cerithium zebrum* Kiener, 1841, and *Cerithium boeticum* Pease, 1861. The subfamily Bittiinae Cossmann, 1906, is thought to comprise nine genera (four of which were not included in phylogenetic analyses) : *Bittium* Gray, 1847; *Bittiolum* Cossmann, 1906; *Ittibittium* gen. n., *Stylidium* Dall, 1907; *Lirobittium* Bartsch, 1911; *Cacozeliana* Strand, 1928; *Argyropeza* Melvill & Standen, 1901; *Varicopeza* Gründel, 1976; *Zebittium* Finlay, 1927. The genus *Cassiella* Gofas, 1987, of uncertain placement, is included as a possible member of the group.

Key words: Bittiinae, *Bittium,* Cerithioidea, anatomy, taxonomy, phylogenetic analysis.

INTRODUCTION

Shells of most small-sized cerithiids are notably difficult to classify, even to familial and generic levels. There has been much confusion and disagreement among malacologists as to the limits and subdivisions of genus-level taxa, because most genera have been defined or based upon convergent shell features alone. Reflective of this unstable taxonomy, unreliable curatorial systems exist in most museums, where many lots of small-sized cerithiid taxa are randomly intermixed with each other and with immature specimens of larger-shelled genera, such as *Cerithium.* These mixed lots frequently are assigned to the convenient "trash basket" category *Bittium.*

The genus *Bittium* Gray, 1847, *sensu lato,* comprises many poorly understood species placed in the family Cerithiidae Bruguière, 1789. The concept of *Bittium* has been generally broad, encompassing many other diverse genera, and opinions on the relationships of the genus with other small-shelled cerithiid groups have also been varied. For these reasons and due to the lack of good anatomical characters, most of the small-sized cerithioideans were left out of my analysis of cerithioidean phylogeny (Houbrick, 1988).

The most recent revision of the *Bittium* group was published by Gründel (1976), who based his taxonomy and phylogeny of the group on sculptural characters of the protoconch (embryonic spiral formation), ontogenetic sculptural development of the teleoconch, and overall shell form. Gründel (1976) included many fossil and extinct taxa in his revision, but did not consider radular, opercular, and anatomical characters of Recent taxa. Although he noted the similarities of *Bittium* and *Cerithium* Bruguière, 1789, he indicated that *Cerithium* differs considerably from *Bittium* in shell form, sculpture, aperture, and especially in ontogenetic sculptural development. On the basis of the ontogeny of early spiral shell sculpture, Gründel (1976: 38) believed that genera in the *Bittium* group (*Bittium, Lirobittium, Bittiolum, Semibittium*) were descendents of the Jurassic genus *Procerithium* Cossmann, 1902, of the family Procerithiidae Cossmann, 1906. Indeed, he remarked that *Bittium* and *Procerithium* shared greater

TABLE 1. *Bittium*-group genera and species used for anatomical studies (asterisk indicates type species).

Genus	Species	Geographic Region
Bittium	**reticulatum* (DaCosta, 1778)	São Miguel, Azores
Bittium	*impendens* (Hedley, 1899)	Honolulu, Hawaii
Bittiolum	*varium* (Pfeiffer, 1840)	Ft. Pierce, Florida
Bittiolum	*alternatum* (Say, 1822)	Provincetown, Massachusetts
Ittibittium	*parcum* (Gould, 1861)	Honolulu, Hawaii
Lirobittium	*subplanatum* Bartsch, 1911	Palos Verdes, California
Lirobittium	*attenuatum* (Carpenter, 1864)	Catalina Id., California
Stylidium	**eschrichtii* (Middendorf, 1849)	Carmel, California
Cacozeliana	**granaria* (Kiener, 1842)	Albany, Western Australia

similarities in ontogenetic sculptural development and overall shell morphology than did *Bittium* and *Cerithium.* Gründel (1976: 40) noted that the genera *Argyropeza* Melvill & Standen, 1901, and *Varicopeza* Gründel, 1976, usually placed near *Bittium,* were strikingly similar in their ontogenetic sculptural development and morphologies to species of the Jurassic genus *Cryptaulax* Tate, 1869 (Procerithiidae), and stated that he considered *Argyropeza* and *Varicopeza* to be Recent members of Procerithiidae. Under Procerithiidae, he assigned the *Argyropeza-Cryptaulax* group to the subfamily Cryptaulaxinae Gründel, 1976, which he believed showed many of the "ancient characteristics" of the family, and the *Bittium-Procerithium* group to the subfamily Procerithiinae Cossmann, 1902. Gründel (1976) considered both subfamilies to have developed independently of one another and to have been separate since the Dogger (Middle Jurassic).

Houbrick (1977) discussed the status of *Bittium* Gray, 1847, and included a historical review, extensive synonymy, and a conchological redescription of the genus. This paper noted that most of the supraspecific taxa associated with the *Bittium* group are parochial in conception and scope, based on specific rather than generic characters, and convey little or misleading phylogenetic information about the group. In the interest of pragmatism and taxonomic parsimony, it was suggested that many of the generic and subgeneric names be abandoned or synonymized with *Bittium, sensu lato,* until the entire group was properly evaluated on the basis of more than shell characters.

Since Gründel's (1976) work and my paper on *Bittium* (Houbrick, 1977), studies on a number of *Bittium*-like genera and other small-shelled cerithioidean taxa have been published: *Dahlakia* (Houbrick, 1978), *Argyropeza* (Houbrick, 1980a), *Varicopeza* (Houbrick, 1980b, 1987a), *Glyptozaria* (Houbrick, 1981a), *Alaba* and *Litiopa* (Kosuge, 1964; Houbrick, 1987b; Luque et al., 1988), *Colina* (Houbrick, 1990a), *Plesiotrochus* (Houbrick, 1990b), and *Diala* (Ponder, 1991). Many of these papers include anatomical data that have helped partially to untangle the confusing mixture of cerithiid genera of similar small-shelled morphology.

The relationships of small-shelled species of the family Obtortionidae Thiele, 1925, which are very similar to those of members of the Bittiinae, remain uncertain because anatomical characters are unknown. It is unclear if Obtortionidae constitutes a separate family or should be included under Bittiinae.

MATERIALS AND METHODS

The goals of this study are threefold: first, to examine the anatomy of *Bittium reticulatum* (DaCosta, 1778), the type species of the genus, thus setting the limits of the genus with a description of distinctive anatomical characters; second, to study the anatomy of a number of other "*Bittium*" species, thereby establishing the validity or artificiality of other component groups or closely related higher taxa; and third, to make a phylogenetic analysis of the group based on a morphological data set that includes more than shell characters.

This revision is based primarily on collections of preserved material in the USNM and on living material studied in the field. Fossils representing extinct genera and species were not considered, although a brief survey of extinct forms and their possible relationships to living members of the *Bittium*-group is in-

cluded. The great number of species and higher category groups traditionally included under *Bittium, sensu lato,* and the difficulties of obtaining good anatomical material precluded an exhaustive, comprehensive anatomical study of all members the group. Instead, I decided to look at representative taxa of genera assigned to the *Bittium*-group comprising species having diverse shells from widely different geographic regions. A total of seven *Bittium*-group species representing five higher taxa (genera) from different localities were examined by dissecting live-collected material and by studying living populations *in situ,* where possible. These species are listed below in Table 1 and include the type species of *Bittium* Gray, 1847, *Stylidium* Dall, 1907, and *Cacozeliana* Strand, 1928, and representative species of *Bittiolum* Cossmann, 1906, *Lirobittium* Bartsch, 1911, and a new genus, described herein. Two other species, each having a distinctive shell morphology, and considered as putative genera formerly attributed to "*Bittium*," *s.l.,* were also studied in the field: "*Bittium*" *zebrum* (Kiener, 1841) from Pago Bay, Guam, and Enewetak Atoll, Marshall Islands; and "*Bittium*" *boeticum* (Pease, 1861), from Honolulu, Hawaii. When the soft parts of these two species were examined, they were found to lack an epipodial skirt, and the ciliated ridge tract and spermatophore bursa in the lateral lamina of the pallial oviduct, characters distinctive of members of the *Bittium*-group. Therefore, both species were excluded from the *Bittium*-group and assigned to *Cerithium* Bruguière. Due to the current alpha-level taxonomic disarray of the *Bittium*-group, I have attempted to present a comprehensive, annotated synonymy and have illustrated the shells of the species studied in this review. I hope that this will give other workers an unequivocal idea about the species and genera they represent.

All specimens were dissected under water in wax-filled petri dishes using a Wild M-5 dissecting microscope. Methylene blue was used to enhance anatomical features during dissection. Sections were made at 5 μm and stained with Hematoxolin and Eosin. Photomicrography was done using a Zeiss Photomicroscope III.

The emphasis of this study is on the anatomy of *Bittium reticulatum,* the type species of *Bittium, s.s.,* which is the criterion against which other *Bittium*-group genera are described and compared in this paper. Descriptions of *Bittiolum, Cacozeliana, Stylidium, Lirobittium,* and a new genus described herein, are less detailed and emphasize the anatomical differences from *Bittium reticulatum.*

The anatomy of the genera *Argyropeza* and *Varicopeza* is only superficially understood. Anatomical knowledge about *Zebittium* Finlay, 1927, and *Cassiella* remains unknown, because I was unable to obtain preserved material of species representing them; consequently, only the shells are considered in this review.

Phylogenetic Analysis

The guiding principles of this study are those of phylogenetic systematics (Hennig, 1966; Wiley, 1981). The Hennig86 computer package, version 1.5, ie and bb options (copyright James S. Farris, 1988) and CLADOS, version 1.2 program (copyright Kevin C. Nixon, 1988, 1991, 1992) were used to analyse data and construct trees.

Phylogenetic analysis of six genus-group taxa of the Bittiinae (*Bittium, Ittibittium, Bittiolum, Lirobittium, Stylidium,* and *Cacozeliana*) was undertaken using 21 morphological characters comprising 51 character states derived from the shell, operculum, radula, and soft anatomy of the taxa listed in Table 1. Initially, there were 30 characters, but these were reduced to 21. Seven of the 21 characters were multi-state characters. Autapomorphies defining terminal branches, which were not part of multistate series, were not included in the analysis, but were retained for the diagnosis of each genus-group taxon. Multistate characters were unordered.

Genus-Group Taxa Analysed

Six genus-group taxa were included: *Cacozeliana, Lirobittium, Stylidium, Bittium, Ittibittium,* and *Bittiolum* (Table 1). The phylogenetic analysis excluded poorly known genera that have been assigned without justification to Bittiinae, such as *Zebittium* and *Cassiella.* Although the shell morphologies, opercular and radular characters of *Argyropeza* and *Varicopeza* have been well studied (Houbrick, 1980a, 1980b), these genera also were left out of the analysis because of lack of anatomical data.

Outgroup Selection

The genus *Cerithium* Bruguière, family Cerithiidae Férussac, 1819, was selected as the

TABLE 2. Comparison of dentition of radular teeth among genera (C = central or main cusp; numbers signify no. of denticles).

Taxon	Rachidian	Lateral	Inner Marginal	Outer Marginal
Bittium	2–3+C+2–3	1+C+3–6	3–4+C+4	3–4+C+0
Bittiolum	3+C+3	2+C+3–4	3–4+C+2–3	6+C+0
Ittibittium	2+C+2	1+C+3–4	2+C+3	5+C+0
Lirobittium	6+C+6	6+C+15–17	15–19+C+5–6	15–19+C+0
Stylidium	2+C+2	1+C+3–4	4–5+C+3	4+C+0
Cacozeliana	2+C+2	1+C+3–4	5–6+C+3–4	4+C+0
Argyropeza	2–3+C+2–3	1+C+5–6	5–6+C+4–5	5–6+C+0
Varicopeza	3–4+C+3–4	1+C+5–6	3–4+C+3	3+C+0

outgroup to root the trees generated by the analyses. The *Bittium*-group traditionally has been considered as a subfamily (Bittiinae) of Cerithiidae by various authors (see below, for history). *Cerithium,* subfamily Cerithiinae, is the most appropriate group to use for outgroup comparison, because it is the closest sister group that is well known anatomically. The anatomy of *Cerithium* species has been described by Houbrick (1971, 1978, 1992) and is very similar to that of Bittiinae members, However, *Cerithium* species have more generalized and less complex external features. Several external anatomical features of members of the *Bittium*-group, such as a metapodial mucus gland, and the epipodial skirt and associated papillae, are lacking in *Cerithium.* The anatomy of such small-sized snails as *Bittium* may be highly derived and/or modified due to their reduction in size. *Cerithium* species are generally much larger animals than "*Bittium*" species, but a number of species are very small and often are confused with "*Bittium*" species.

Among small-shelled cerithioideans, *Litiopa* and *Alaba,* family Litiopidae, were considered as possible outgroup candidates. These small snails have external features, such as an epipodial skirt and epipodial tentacles, similar to those seen among members of the Bittiinae, and are well known anatomically; however, they differ from bittiid species in internal anatomy (Kosuge, 1964; Houbrick, 1987b; Luque et al., 1988). Phylogenetically, Litiopidae is far removed from the family Cerithiidae (Houbrick, 1988: 114), and is therefore rejected as a suitable outgroup.

Another group of small-shelled species, the Dialidae, was also considered as a possible outgroup. However, only one species is known anatomically (Ponder, 1991), and Healy (1986) has shown that the paraspermatozoa of *Diala* are unique and highly derived among cerithioideans. Ponder's (1991) phylogenetic analysis showed that dialids were closely related to litiopids and far removed from Cerithiidae (Ponder, 1991: 514). *Diala* was therefore rejected as an outgroup.

Characters

The characters listed below comprise three categories: shell characters (1–5), anatomical characters (6–19), reproductive characters (20–21). Radular characters were eliminated from the final analysis because of their autapomorphic condition. Nevertheless, radular characters are important diagnostic characters of genera and are summarized in Table 2.

Because the polarities of multistate characters were largely speculative, all character states were left unordered; i.e., the integer assignment was arbitrary. The coding of these characters and their states are presented in Table 3. An annotated list of the morphological characters and character states used in the phylogenetic analysis is presented below:

Shell Characters: 1. Shell sculpture—0 = spiral; 1 = cancellate. Most members of the subfamily are characterized by a markedly cancellate shell sculpture, in contrast to *Cerithium* species where spiral elements dominate sculptural patterns (Houbrick, 1992). Exceptions are species of the genera *Stylidium* and *Ittibittium,* where spiral sculpture dominates and axial ribs are either lacking or poorly developed.

2. Anal canal—0 = well developed; 1 = weakly developed or missing. A well-developed anal canal is present in *Cerithium* members (the outgroup), but occurs only in two genera of the *Bittium*-group, *Cacozeliana* and *Varicopeza,* and is exceptionally well developed in the latter genus (Houbrick, 1980b).

TABLE 3. Data matrix derived from morphological characters of species representing six genus-group taxa of Bittiinae. *Cerithium* is the outgroup.

	Character																			
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bittium	1	1	0	1	0	1	1	0	0	0	2	0	1	2	1	1	1	1	1	0	0
Ittibittium	0	1	0	1	0	0	1	0	0	1	2	1	0	1	1	0	0	0	1	1	1
Stylidium	0	1	1	1	2	0	0	1	1	0	1	0	2	1	1	1	1	1	1	0	1
Cacozeliana	1	0	1	0	2	2	2	0	0	0	1	0	0	0	0	1	1	1	0	0	0
Bittiolum	1	1	0	1	1	0	1	0	0	1	3	0	1	1	1	0	1	1	1	0	0
Lirobittium	1	1	1	1	0	1	0	1	1	0	1	1	2	1	1	0	1	1	1	2	1

3. Varices—0 = present; 1 = absent. Varices, thickened, former growth lines, are a common feature of most cerithiids and occur among members of Bittiinae with the exception of *Lirobittium* and *Stylidium.*

4. Anterior canal—0 = well developed; 1 = weakly developed. The anterior siphonal canal is a strong feature on most cerithiids, but in smaller-shelled taxa frequently is poorly developed (most Bittiinae) or absent (*Cassiella, Cerithidium*).

5. Protoconch sculpture—0 = two spiral lirae; 1 = one spiral lira; 2 = entirely smooth. Most outgroup species have strong spiral sculptural elements on their protoconchs (Houbrick, 1992). Bittiinae genera range from species with spiral sculpture to those having only one weak spiral lira or no sculpture, but this is probably reflective of the type of development.

Anatomical Characters: 6. Opercular morphology—0 = ovate shape; 1 = round, circular shape; 2 = round shape with fringed spiral edges. *Cerithium* species have operecula with an ovate shape (Houbrick, 1992), and it is thought herein that the more circular shape observed among several *Bittium*-group taxa are modifications due to size reduction, although this is not always the case (exceptions in *Ittibittium* and *Bittiolum,* both small shelled genera). The spirally fringed condition seen in *Cacozeliana* departs from the norm and is probably derived.

7. Snout shape—0 = wide; 1 = narrow, elongate; 2 = short, narrow. This character is a variable feature among cerithiids. *Cerithium* species usually have large, wide, muscular snouts (Houbrick, 1992), whereas they tend to be narrow and elongate in members of the Bittiinae, especially among taxa of the *Bittium* clade (*Bittium, s.s., Ittibittium, Bittiolum*).

8. Cephalic tentacle length—0 = elongate; 1 = short. Among cerithiids and the Bittiinae, cephalic tentacles are usually elongate and much longer than the snout, but in the eastern Pacific genera *Lirobittium* and *Stylidium,* the tentacles are much shorter than the length of the snout.

9. Eye size—0 = normal; 1 = small; 2 = large. Most cerithiids have eyes of normal size, but in such deep-water species as *Argyropeza* and *Varicopeza,* the eyes are very large, possibly an adaptation to water depth and poor light. In contrast, the eyes of *Styliodium* and *Lirobittium* species are exceptionally small.

10. Metapodial mucus gland—0 = absent; 1 = present. Although this structure is absent in the outgroup, it does occur among a few other cerithioidean groups (Litiopidae [*Alaba, Litiopa*], Cerithiidae [*Colina*]; Houbrick, 1987b, 1990a, respectively). This gland may be an adaptation to an algal and/or high energy habitats. Species having a metapodial gland are known to use the mucus thread secreted by the gland to anchor themselves while they climb about the algal fronds (Houbrick, 1987b, 1990a).

11. Epipodial skirt—0 = rudimentary; 1 = well developed, smooth; 2 = well developed, papillate along edges; 3 = well developed, scalloped. *Cerithium* species have a weak operculigerous lobe on the rear of the foot, which is here interpreted as a rudimentary posterior epipodial skirt. In Bittiinae species, the skirt extends forward along the sides of the foot to form a fully developed epipodial skirt. An epipodial skirt occurs also among small-shelled members of the Litiopidae (Kosuge, 1964; Houbrick, 1987b; Luque et al., 1988) and the Dialidae (Ponder, 1991). Although this character is homoplastic among cerithioideans, an epipodial skirt is characteristic of Bittiinae.

TABLE 4. Comparison of developmental features among Bittiinae genera and species.

Taxon	Max. Shell Length	Protoconch Sculpture	Developmental Type	Egg Size
Bittium reticulatum	15 mm	2 spirals	planktonic	0.1 mm
Ittibittium parcum	6 mm	2 spirals	direct	0.2 mm
Bittiolum varium	7 mm	1 spiral	planktonic	0.1 mm
Lirobittium subplanatum	10 mm	2 spirals	direct	0.5 mm
Stylidium eschrichtii	17.5 mm	smooth	direct	0.2 mm
Cacozeliana granaria	24 mm	smooth	planktonic	0.1 mm
Argyropeza divina	7.6 mm	2 spirals	planktonic	?
Varicopeza varicopeza	10 mm	1 spiral	planktonic	?

12. Ovipositor—0 = present; 1 = absent. This gland, although common among cerithioideans, is absent in some taxa, such as those having internal brooding (Houbrick, 1987c). The absence of an ovipositor in females may be falsely scored, as it is thought that its presence can be easily ascertained only during breeding season; moreover, this gland is also difficult to detect in some preserved specimens. Among Bittiinae, the ovipositor is absent only in *Ittibittium* and *Lirobittium.*

13. Osphradial morphology—0 = bipectinate; 1 = monopectinate; 2 = vermiform. This character varies greatly among Bittiinae genera. Although the osphradium in *Cerithium* species is bipectinate, it is vermiform among most other cerithioidean families, such as the estuarine Potamididae and freshwater families Thiaridae and Pachychilidae (Houbrick, 1988, 1991).

14. Osphradial length—0 = equal to ctenidial length; 1 = a little less than ctenidial length; 2 = one-half the ctenidial length. This is a highly variable character, but often diagnostic of some taxa. No overlap among character states was detected in the species studied.

15. Zygoneurous nervous system—0 = absent; 1 = present. Bouvier (1887) documented a zygoneurous condition among some cerithiids, and this was summarized by Houbrick (1988). Zygoneury is absent in *Cerithium,* and in all Bittiinae except for *Bittiolum.*

16. Common opening to sperm pouch and seminal receptacle openings—0 = close together; 1 = far apart. In *Stylidium* and *Lirobittium,* the openings have a wide separation, whereas in *Bittium* they are not as far apart. In other bittiids and in most other cerithiids, the openings are close together.

17. Spermatophore bursa location—0 = located in medial lamina; 1 = located in lateral lamina. The spermatophore bursa is found in the lateral lamina in most members of the *Bittium*-group, but in *Ittibittium* and in all other known cerithiids, it occurs in the medial lamina (Houbrick, 1988).

18. Ciliated ridge tract—0 = absent; 1 = present. This structure, one of the synapomorphies defining Bittiinae, is lacking in *Ittibittium* members and in most other cerithiids.

19. Seminal receptacle with grape-like morphology—0 = present; 1 = absent. This grape-like configuration may not represent a distinct morphology, but may be due to the highly filled condition of the receptacle. This condition occurs only in *Cacozeliana.*

Reproductive Characters: 20. Spawn morphology—0 = formed into gelatinous string wound into mass; 1 = short gelatinous tube; 2 = balloon-like cluster. A gelatinous string mass is the common spawn morphology seen among cerithioidean taxa and within Bittiinae. The balloon-like cluster of eggs in members of *Lirobittium* is unique, whereas a short gelatinous tube morphology is seen only in *Ittibittium:* both taxa have few, large eggs and undergo direct development (Table 4).

21. Type of development—0 = planktonic; 1 = lecithotrophic (demersal/direct). Most members of the outgroup have a planktonic

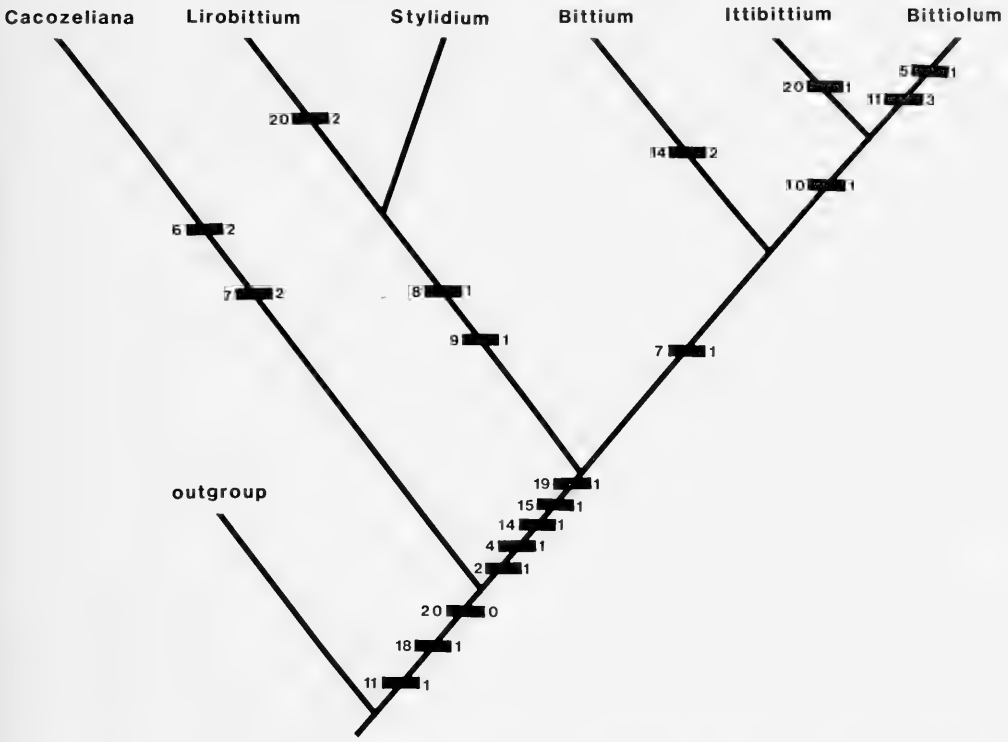

FIG. 1. Cladogram showing relationships among six genera of Bittiinae, using *Cerithium* as the outgroup (L = 41; CI = 70; RI = 53; trees two. Numbers to left of black bars indicate characters: those to right of bars represent character states. Only characters with a CI of 100 are shown).

larval phase in their development. It is thought that planktotrophy can evolve to lecithotrophy but not vice-versa (Strathmann, 1978). Direct developers have larger, fewer eggs per spawn mass (Table 4).

RESULTS

Phylogenetic analysis resulted in two equally parsimonious trees, each with a length of 41 steps, a consistency index of 70, and a retention index of 53 (Fig. 1). The number of steps and the consistency indices of each character used in the construction of the cladogram are shown in Table 5. The supporting branches of both cladograms had identical tree topologies except for the clade supporting *Bittium, Ittibittium,* and *Bittiolum.* In the first tree, illustrated herein (Fig. 1), *Ittibittium* and *Bittiolum* are sister groups of *Bittium,* while in the second tree, *Bittium* and *Bittiolum* are sister groups of *Ittibittium.* Both analyses strongly support the recognition of six genus-level taxa. The monophyly of Bittiinae is established by three synapomorphies (11[1], 18[1], 20[0]) and one homoplastic character (17[1]). The layout of the pallial oviduct, discussed in greater detail below, is the source of two good synapomorphous characters: a ciliated ridge tract and a spermatophore bursa in the medial lamina. An epipodial skirt, while distinctive of the *Bittium*-group, is plesiomorphic, because it occurs also in other cerithioidean groups.

Cacozeliana stands apart at the base of the cladogram from the other taxa and is closest to *Cerithium,* the outgroup. *Cacozeliana* is defined by two autapomorphous characters (6[2], 7[2]) and by two homoplastic characters (5[2], 16[1]). *Cacozeliana* is well separated from all other genera of Bittiinae higher on the tree by five synapomorphies (2[1], 4[1], 14[1], 15[1], 19[1]) and with one homoplastic character (13[1]).

The *Lirobittium-Stylidium* clade, which is

TABLE 5. List of steps and consistency indices of characters used in construction of cladogram.

Character	1	2	3	4	5	6	7	8	9	10	11
Steps	3	1	2	1	3	3	2	1	1	1	3
C.I.	33	100	50	100	66	66	100	100	100	100	100
Character	12	13	14	15	16	17	18	19	20	21	
Steps	2	3	2	1	3	2	2	1	2	2	
C.I.	50	66	100	100	33	50	50	100	100	50	

geographically confined to the west coast of North America, is supported by two synapomorphies (8[1], 9[1]), and two homoplastic characters (13[2], 21[1]) In this clade, *Stylidium* is poorly defined by three homoplastic characters (1[0], 5[2], 16[1]), whereas *Lirobittium* is better founded on one autapomorphy (20[2]) and three homoplastic characters (6[1], 12[1], 16[0]).

The *Bittium* clade is supported by one synapomorphy (7[1]) and two homoplastic characters (3[0], 13[1]). *Bittium, s.s.,* is defined by one autapomorphy (14[2]) and three homoplastic characters (2[0], 12[1], 18[1]). *Ittibittium* and *Bittiolum,* the sister taxa to *Bittium,* are separated from it by one synapomorphy 10[1]). *Bittiolum* is supported by two autapomorphies (5[1], 11[3]) and two homoplastic characters (11[3], 16[0]). A single autapomorphy (20[1]) and six homoplastic characters (1[0], 12[1], 13[0], 16[0], 17[0], 18[0], 21[1]) define *Ittibittium.* The characters listed above are those derived only from the data matrix (Table 3) used in the construction of the cladogram (Fig. 1). Other autapomorphies defining terminal branches but not part of multistate series were not included in the data matrix. These characters are given under the diagnosis of each genus in the systematic portion of this paper.

DISCUSSION

The phylogenetic analysis of morphological characters of the species in Table 1 resulted in recognition of six different morphological groups (Fig. 1), which are herein interpreted as genus-group taxa under the subfamily Bittiinae Cossmann, 1906. Generic names already exist for five of these groups: *Bittium* Gray, 1847; *Bittiolum* Cossmann, 1906; *Cacozeliana* Strand, 1928; *Stylidium* Dall, 1907; and *Lirobittium* Bartsch, 1911. A new genus, from the Indo-Pacific, is described herein. All of the above genera, with the exception of *Stylidium,* are defined by autapomorphous characters. If the cladogram shown in Figure 1 is interpreted strictly, *Ittibittium* and *Bittiolum* may be regarded as subgenera of *Bittium;* however, because this is a preliminary revision of the *Bittium*-group, based on only a few representatives of each genus, and not including other poorly known taxa, it is best not to assign differential rank to genus-group taxa at this stage. Therefore, I have decided to treat all terminal nomina as full genera.

As noted in an earlier paper (Houbrick, 1977), other genus-level taxa have been proposed under the *Bittium*-group or are thought to be linked closely to it. Many of these taxa are synonyms of *Bittium*-group genera described herein or have been proposed for fossils. The subfamily Bittiinae, as understood in this paper, is thought herein to comprise nine, possibly ten, Recent genus-group taxa: *Bittium* Gray, 1847; *Bittiolum* Cossmann, 1906; *Ittibittium* gen. n.; *Stylidium* Dall, 1907; *Lirobittium* Bartsch, 1911; *Cacozeliana* Strand, 1928; *Argyropeza* Melvill & Standen, 1901; and *Varicopeza* Gründel, 1976. The genera *Zebittium* Finlay, 1927, and *Cassiella* Gofas, 1987, are provisionally referred to Bittiinae until more information is available.

Argyropeza and *Varicopeza* have been treated previously by Houbrick (1980a, 1980b, 1987a), but their anatomy remains poorly known and they are not described in great detail here. An epipodial skirt has been recorded in *Varicopeza crystallina* (Houbrick, 1987a: 80), but due to poorly preserved anatomical material, this structure could not be ascertained in *Argyropeza* species; however, the radula of *Argyropeza* species (Houbrick, 1980a) is similar to those of members of the *Bittium*-group.

Anatomical knowledge about potential *Bittium*-group species as yet unstudied, such as *Cassiella* from the eastern Atlantic, *Zebittium* from New Zealand, and the many species of small-shelled, *Bittium*-like cerithioideans from the Indo-Pacific, may reveal even more new genus-level taxa to be included under Bittiinae.

SYSTEMATIC TREATMENT OF BITTIINAE

The species studied have been placed into groups (genera) according to the above phylogenetic analysis. The type- or representative species of each genus is described, and notes on reproductive biology and ecology are included, when possible. Shell-length measurements for each species represent the largest specimen observed. Representatives of other genera for which anatomical material was lacking are described from shell morphology and radular morphology, if available.

BITTIINAE COSSMANN, 1906

Bittiinae Cossmann, 1906: 61.
Procerithiinae Cossmann, 1906, *sensu* Gründel, 1976 (in part).

Diagnosis

Shell small, turreted, narrowly elongate to pupate, with moderate spiral and axial sculpture frequently cancellate and/or beaded. Aperture with short but distinct anterior canal. Spiral sculpture usually 4–5 spiral cords per whorl. Animal with epipodial skirt, opercular lobe, and pallial oviducts comprising large sperm bursa and seminal receptacle in posterior part of medial lamina, and spermatophore bursa and ciliated ridge tract in posterior lateral lamina. Ciliated gutter leading from oviduct down right side of foot in females. Glandular ovipositor at base of right side of foot in most species. Nervous system dialyneurous. Spawn consisting of gelatinous, winding strings.

Taxonomic Remarks

The *Bittium*-group (Bittiinae Cossmann, 1906) has been placed under Cerithiidae by nearly all authors (Cossmann, 1906; Thiele, 1929; Wenz, 1938; Golikov & Starabogatov, 1975; Ponder & Warén, 1988), except Gründel (1976), who assigned the group to the Jurassic family Procerithiidae Cossmann, 1906 (erroneously cited by Cossmann as 1905). He allocated 12 genus-group taxa to the subfamily Procerithiinae (= Bittiinae). Of these, *Bittium, Bittiolum, Semibittium* and *Procerithium* were treated as full genera; *Cerithidium* Monterosato, 1884, *Rasbittium* Gründel, 1976, *Lirobittium* Bartsch, 1911, *Cacozeliana* Strand, 1928, and *Stylidium* Dall, 1907, were considered to be subgenera of *Bittium.* The extinct taxa *Cosmocerithium* Cossmann, 1906, *Infracerithium* Gründel, 1974, and *Rhabdocolpus* Cossmann, 1906, were treated as subgenera of *Procerithium.* Gründel (1976) also included *Argyropeza* Melvill & Standen, 1901, *Varicopeza* Gründel, 1976, and the extinct genus *Cryptaulax* Gründel, 1976, with subgenera *Pseudocerithium* Cossmann, 1884, and *Xystrella* Cossmann, 1906, in the *Bittium* group under the subfamily Cryptaulaxinae Gründel, 1976. Excluding the Jurassic taxa, the Recent genera *Argyropeza* and *Varicopeza* should probably be included in the Bittiinae, because the few morphological and anatomical characters known about these taxa strongly suggest affinity to this subfamily. The other extinct genus-group taxa and *Procerithium* should be excluded from Bittiinae, because the evidence supporting a relationship of these taxa with the *Bittium*-group is based solely on the ontogenesis of spiral sculpture as seen on the early shell spire, a character which is, at best, tenuous: more characters are needed to lend credence for such a relationship. While Gründel's (1976) hypothesis poses interesting questions, it is founded mostly on shell sculpture, which is taxonomically informative but potentially phylogenetically misleading. Considering the Jurassic age of the *Procerithium* group and the great likelihood of homoplasy in shell morphology, the belief that the *Bittium*- and *Procerithium*- groups are of the same lineage is largely speculative, cannot be falsified, and should not be accepted as evidence for a phylogeny (Houbrick, 1988).

The name *Elassum* Woodring, Bramlette & Kew, 1946, has been traditionally associated with the *Bittium*-group in the literature, and was proposed by Woodring et al. (1946: 68) for Pleistocene and Recent material from southern California previously named *Bittium californicum* Dall & Bartsch, 1901, and originally assigned to the subgenus *Elachista* Dall & Bartsch, 1901. *Bittium californicum* is the type species of *Elachista* by monotypy. However, as *Elachista* is preoccupied, a new name, *Alabina* Dall, 1902, was proposed to replace it. Woodring et al. (1946) did not believe the taxon *californicum* Dall & Bartsch, 1901, was an *Alabina* and thus proposed *Elassum* to accomodate it, noting that the species was more *Bittium*-like than *Alabina*-like. Because *Elachista, Elassum,* and *Alabina* have the same type species, *Elassum* becomes a junior synonym of *Alabina.* The shell of the type species somewhat resembles

those of members of the *Bittium*-group, and I concur with Woodring et al. (1946) that it possibly should be included as a component genus of the *Bittium*-group; however, as there is no preserved material of living animals of this taxon to confirm this supposition, *Alabina* [= *Elassium*] is not further treated herein.

Houbrick (1977: 103) initially placed 13 nomina into the synonymy of *Bittium, sensu lato.* Subsequent studies on the *Bittium*-group and evidence derived from anatomical characters presented herein now allow exclusion of six genera originally included in that synonymy and a more focused diagnosis of *Bittium, s.s.* An annotated list of taxa previously included in the *Bittium*-group, but now excluded, is presented below (Jurassic genera not included):

1. *Bittinella* Dall, 1924 (type species: *Bittium hiloense* Pilsbry & Vanatta, 1908). The type species of this genus is a rissoid of the genus *Isseliella* Weinkauff, 1881, subfamily Rissoininae (Ponder, 1985: 95; Kay, 1979: 80). *Bittium parcum* Gould, 1861, has been erroneously assigned to *Bittinella* (see below).

2. *Bittiscalia* Finlay & Marwick, 1937 (type species: *Bittium simplex* Marshall, 1917). It is unclear to which group this extinct species should be assigned. Although Finlay & Marwick (1937: 44) placed it under Cerithiidae, they noted its similarity to *Zeacumantus* Finlay, a batillariid (Houbrick, pers. obser.). Their drawing of the type species (Finlay & Marwick, 1937: pl. 5, fig. 20) shows a shell with an anterior canal that is a wide shallow notch, similar to poorly developed anterior canals seen in some *Bittium* and *Alabina* species. Because this is a fossil, we may never know with certainty the correct family assignment. Although the authors placed it under Cerithiidae, they were obviously equivocal about this assignment. It is best to leave *Bittiscalia* under the broader category of Cerithiidae and to exclude it from the more narrow assignment of Bittinae.

3. *Brachybittium* Weisbord, 1962 (type species: *Bittium* (*Brachybittium*) *caraboboense* Weisbord, 1962). The type species, a fossil, appears to be an immature or fragmentary *Cerithium* species, judging from its illustration (Weisbord, 1962: pl. 15, figs. 5–6).

4. *Cerithidium* Monterosato, 1884 (type species: *Cerithium submamillatum* Rayneval & Ponzi, in Rayneval et al., 1854). *Cerithidium* was introduced by Monterosato (1884) who noted that it was characterized by a rounded aperture and lack of an anterior canal. Monterosato listed a single species under the genus, *Cerithium submamillatum* Rayneval & Ponzi, 1854, which he considered a synonym of *Turritella pusilla* Jeffreys, 1860. As Gofas (1987: 110) remarked, the former name was originally given to a Pleistocene fossil which is not conspecific with the Recent species. Gofas (1987) remarked that the designation of *Cerithium submamillatum* as the type species of *Cerithidium* by Cossmann (1906) should prevail over that of *Turritella pusilla* by Wenz (1940). I agree with Gofas (1987: 109–110) that both species are congeneric and have sculpture similar to *Bittium reticulatum;* however, in a *Cerithidium* species examined by Ponder (Ponder, in litt.), the female pallial oviduct was closed, which is very different from the open systems known in all other members of Bittiinae. A closed pallial oviduct has not yet been demonstrated in the type species of *Cerithidium,* but on the basis of the closed system noted by Ponder, *Cerithidium* is excluded provisionally from Bittiinae.

5. *Dahlakia* Biggs, 1971 (type species: *Dahlakia leilae* Biggs, 1971). The type species is a junior synonym of *Cerithium proteum* Jousseaume, 1930 (Houbrick, 1978), and I believe both names are probable synonyms of *Cerithium scabridum* Philippi, 1848.

6. *Eubittium* Cotton, 1937 (type species: *Bittium lawleyanum* Crosse, 1863) [not *Eubittium* Cossmann, 1902]. The syntypes of the type species of this genus (MNHN, Paris) are *Batillariella estuarina* (Tate, 1893), which is a batillariid (family Batillariidae), and not closely related to Cerithiidae. In any case, the name *Eubittium* Cotton is a secondary homonym.

7. *Paracerithium* Cotton, 1932 (type species: *Bittium lawleyanum* Crosse, 1863) [not *Paracerithium* Cossmann, 1902]. This taxon is a secondary homonym and has the same type species as the previous taxon, which is a batillariid.

8. *Sundabittium* Shuto, 1978 (type species: *Cerithium fritschi* Boettger, 1883). It is highly unlikely that this fossil genus is related to the *Bittium* group. Shuto himself (1978: 152) was equivocal in assigning it to *Bittium.* The figures of *C. fritschi* depicted by Martin (1914: pl. 5, figs. 132–134) suggest an *Abyssochrysos* species, but this assignment needs confirmation by examination of the type material.

Discussion

The subfamily Bittiinae is characterized by small-shelled species generally having cancellate sculpture and short canals. Monophyly

for Bittiinae is tentatively established by the synapomorphous layout of the pallial oviduct (see description under *Bittium reticulatum*; Fig. 6C); i.e., the presence of three sperm chambers: a large bursa (1), and smaller seminal receptacle (2) in the posterior half of the medial lamina, and a spermatophore bursa (3) in the posterior lateral lamina. The position of the spermatophore bursa in the lateral lamina appears to be a unique synapomorphy defining Bittiinae, but this needs to be confirmed by observation of spermatophores in the bursa in other members of the subfamily. This character does not occur in *Ittibittium,* a new genus described herein; thus, it had a CI of 50 in the analysis. The ciliated ridge tract (Fig. 6B, C, ctr) on the lateral lamina epithelium leading into the spermatophore bursa is also a synapomorphy defining Bittiinae. This is an uncommon feature among cerithioideans, and is unusually long. Some plesiomorphic characters, such as the well-developed epipodial skirt and epipodial tentacles, occur in other cerithioidean groups, but in combination with the above synapomorphous features, are characteristic of the Bittiinae. *Ittibittium,* new genus, deviates from other members of the subfamily in having the albumen gland protrude beyond the posterior mantle cavity into the visceral coil. In other respects, it generally agrees with the remaining genera of the Bittiinae.

The Recent genera treated herein are each characterized by external anatomical characters (Fig. 2), which allow easy classification of living animals. Two genera of the subfamily (*Bittiolum* and *Ittibittium, gen. n.,* have a large metapodial mucus gland marked by an elongate slit in the middle of the sole (Fig. 2), leading deep into the center of the foot. While the epipodial skirt and opercular lobe are characteristic of Bittiinae, these characters and the metapodial mucus gland also occur in species of *Alaba* H. Adams & A. Adams, 1854, and *Litiopa* Rang, 1829 (Litiopidae Fischer, 1885), in members of *Colina* H. Adams & A. Adams, 1854 (Cerithiidae Férussac, 1819), and in species of *Plesiotrochus* Fischer, 1878 (Plesiotrochidae Houbrick, 1990b) (Kosuge, 1964; Houbrick, 1987b; Luque et al., 1988; Houbrick, 1990a, 1990b, respectively). I have previously pointed out the anatomical features shared by *Colina* with members of the Bittiinae (Houbrick, 1990a: 50–51). Species of *Plesiotrochus* Fischer, 1878, also have a papillate epipodial skirt and an elongate metapodial slit leading into a large metapodial mucus gland, but differ considerably from members of the *Bittium*-group in other anatomical characters (Houbrick, 1990b: 247–248), and are an unusual family.

The relationship of the *Bittium*-group to other small-shelled cerithioidean genera such as *Scaliola* A. Adams, 1860, and *Finella* A. Adams, 1860, remains unclear because the anatomy of these taxa is still unknown. Ponder (1991) recently described the anatomy of a species of *Diala* A. Adams, 1861, which resulted in his recognition of a separate family, Dialidae Ludbrook, 1941. According to Ponder (1991: 504–506), *Diala* species have a weak epipodial fold (epipodial skirt), a pair of lateral opercular lobes, and a posterior opercular flap, which appear to be homologous with the epipodial skirt and opercular lobe described in the Bittiinae members above. However, unlike the situation in Bittiinae, *Diala* species lack the metapodial mucus gland and the glandular ovipositor on the right side of the foot in females. Additionally in *Diala* species, the lateral lamina of the pallial oviduct does not have a sperm pouch and the paraspermatozoa are unique among Cerithioidea (Healy, 1986).

The rachidian radular tooth of most members of the *Bittium*-group is characterized by being wider than tall and usually has a basal plate with concave sides. This differs from the hour-glass shape of the rachidian tooth found in small-sized species of *Diala, Litiopa, Alaba,* and *Varicopeza* (Ponder, 1991: fig. 3F, G; Houbrick, 1987a: figs. 14, 19; 1987b: figs. 9, 10), taxa frequently confused with *Bittium*-group members. For dental cusp patterns among Bittiinae taxa, see Table 2.

Although members of Bittiinae are primarily grazers of epiphytic microalgae, many species appear to feed on particulate matter gathered by cilia and mucus on the anterior ctenidial filaments when the animal is stationary.

The ultrastructure of the sensory epithelium of the osphradia of members of the *Bittium*-group is typical of Cerithioidea, and Haszprunar (1985: 479) has shown that the osphradial cells bear paddle cilia. The osphradial classification of Bittiinae species falls under Haszprunar's (1985) group "Si2." Haszprunar (1985) repeated the Fretter & Graham (1962: 367) statement that the osphradium is a "simple brown ridge," but this is not concordant with my observations of the pectinate condition in many taxa of the group.

The phylogeny and relationship of members of the *Bittium*-group will remain unclear until the anatomy of other cerithioidean taxa is

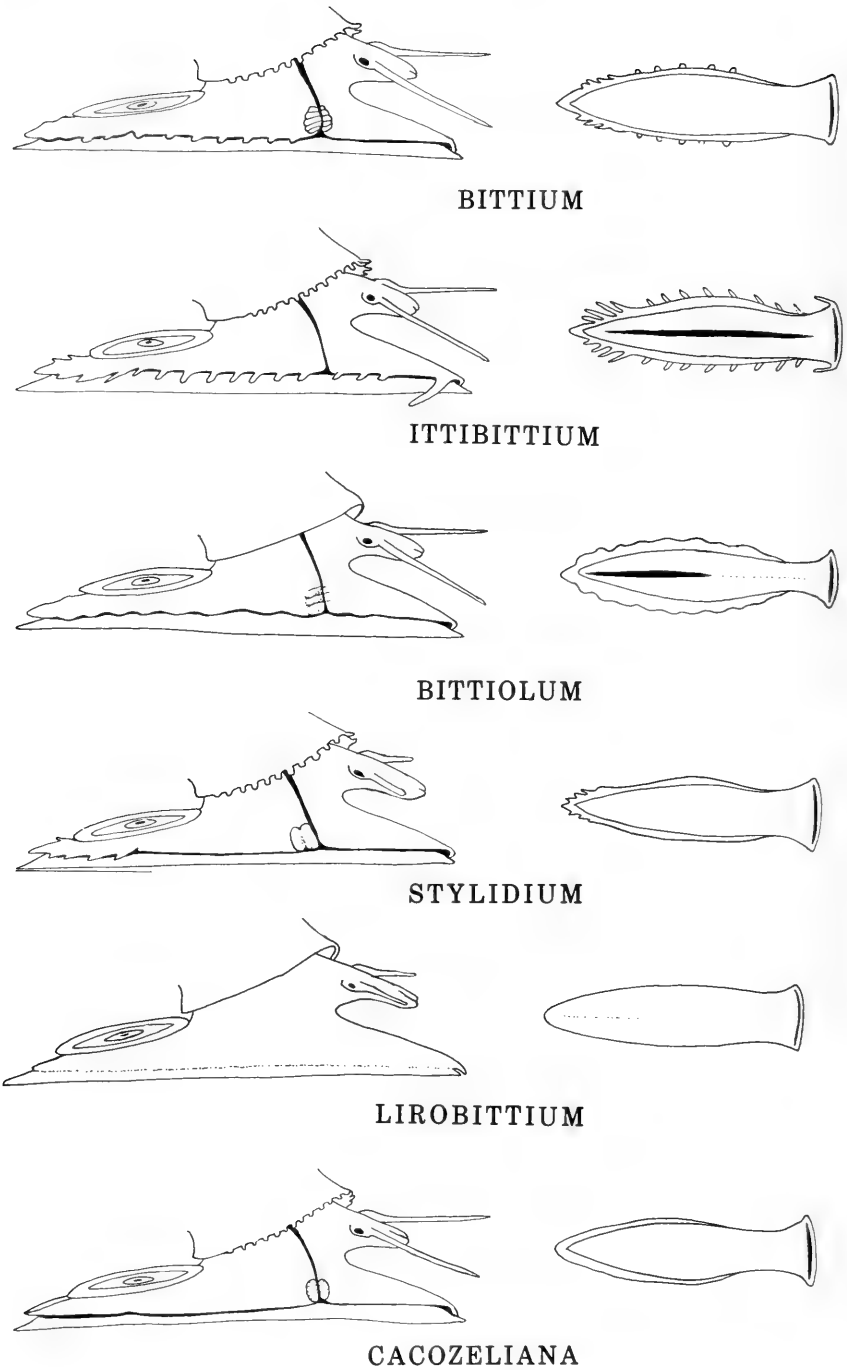

FIG. 2. External anatomical characters of five genera of the *Bittium*-group. Figures to left represent right lateral views of headfoot, showing mantle edge, ciliated gutter, ovipositor and epipodial skirt configuration; figures to left show sole of foot, anterior mucus gland, metapodial mucus gland (when present) and configuration of epipodial skirt.

better understood and a phylogenetic analysis can be accomplished.

BITTIUM GRAY, 1847

Bittium Gray, 1847a (Oct.): 270 (Type species by subsequent designation, Gray, 1847b: *Strombiformis reticulatus* DaCosta, 1778). Thiele, 1929: 211; Wenz, 1940: 755; Nordsieck, 1968: 68; Houbrick, 1977: 103.

Cerithiolum Tiberi, 1869: 263 (Type species by original designation, *Strombiformis reticulatus* DaCosta, 1778).

Manobittium Monterosato, 1917: 20 (Type species by monotypy, *Cerithium latreillei* Payraudeau, 1826, = *S. reticulatus*). Thiele, 1929: 212.

Inobittium Monterosato, 1917: 20 (Type species by monotypy, *Cerithium lacteum* Philippi, 1836, = *S. reticulatus*). Thiele, 1929: 212; Wenz, 1940: 757.

Rasbittium Gründel, 1976: 53 (Type species by original designation, *Cerithium latreillei* Payraudeau, 1826, = *S. reticulatus*).

Diagnosis

Shell small, elongate, with short anterior canal and sculptured with 4–5 spiral cords with many aligned small beads formed where axial riblets are crossed by spirals. Operculum circular, paucispiral with subcentral nucleus. Epipodial skirt with many small, short papillae. Opercular lobe with small pointed papillae. Well-developed ovipositor comprising parallel glandular ridges and bisected by egg-laying gutter on right side of foot near edge of epipodial skirt. Osphradium ridge-like, weakly monopectinate, one-half the ctenidial length. Openings to sperm bursa well separated from opening to seminal receptacle.

Remarks

Bittium Gray, 1847a, was first proposed in manuscript by Leach in 1818 for a classification of British Mollusca, and it was subsequently made available by Gray (1847a). Leach's list referred *Bittium* and several other diverse genera to Purpuridae and under the 65th entry listed *Murex reticulatum, M. tuberculare, M. adversum, M. elegantissimum,* and *M. spenceri,* consecutively, under *Bittium.* Besides *Bittium reticulatum,* the other species listed by Leach represent two genera, *Triphora* Blainville, 1828, and *Cerithiopsis* Forbes & Hanley, 1851. Neither a description of *Bittium* nor a type species were given. Three months later, Gray (1847b) cited only *Bittium reticulatum* (Da Costa, 1778) under *Bittium,* and this citation is a subsequent designation. (Gray's system is explained in his introduction, pp. 129–130, and the species so listed are to be taken as type designations). The earliest diagnosis of *Bittium* is that of H. Adams & A. Adams (1854) who besides describing shell characters, noted the operculum, epipodial skirt, and opercular lobe.

My original paper on *Bittium* (Houbrick, 1977) reviewed the nomenclatural history of the genus, and should be consulted for detailed information about the confusion and taxonomic problems between *Bittium* and other taxa of small-shelled cerithioideans. Subsequent to that review, there have been many changes and the synonymy of *Bittium* originally published (Houbrick (1977: 103) has been modified herein: some taxa have been excluded, and genera not originally included have been added. A commentary on the present synonymy follows: *Cerithiolum* is an objective junior synonym of *Bittium:* both genera share the same type species, *Bittium reticulatum.* Gründel (1976) regarded *Cerithidium* and *Rasbittium* Gründel, 1976, as subgenera under *Bittium, s.s.,* but as shown before, *Cerithidium* is excluded from Bittiinae. *Rasbittium* is a primary objective synonym of *Manobittium* as seen in the synonymy above. *Manobittium* and *Rasbittium* are considered subjective junior synonyms of *Bittium* because both share the same type species, *Cerithium latreillei,* which is considered by me and a number of authors to be conspecific or subspecific with *Bittium reticulatum* (see Verduin, 1976). The eastern Atlantic species, *Cerithium lacteum,* which is the type species of *Inobittium,* also is considered herein to be conspecific with *Bittium reticulatum.* Wenz (1940: 757) regarded *Inobittium* as a synonym of *Lirobittium,* but I see no close resemblance between the shells of the two. Should *Cerithium lacteum* be a distinct species, as thought by Verduin (1976), the differences are certainly not of generic weight; consequently, *Inobittium* is regarded as a subjective junior synonym.

Discussion

The genus *Bittium* is characterized by a cancellate, beaded shell sculpture formed by 4–5 dominant spiral cords and numerous axial rib-

lets (Fig. 3A-E), a circular operculum with subcentric nucleus (Fig. 3F), and by the small papillae along the edge of the epipodial skirt and opercular lobe (Fig. 2). The ovipositor in females is a highly developed, raised glandular lump at the base of the foot near the sole edge, forming a series of parallel, glandular ridges bisected by the deep ciliated egg-laying groove (Fig. 4B, ovp). The ridge-like monopectinate osphradium is unusual in having the pectins on its right side. It is half the length of the ctenidium. The openings to the sperm bursa and seminal receptacle in the lateral lamina of the pallial oviduct (Fig. 6B, C, osr, osp) are well separated from each other in contrast to most other members of the *Bittium*-group.

The shells of small-sized *Cerithium* species frequently are erroneously misclassified as *Bittium* species. Gründel (1976) presented several conchological features that he believed separated the two genera. He stated that *Cerithium* differs from *Bittium* in having a more complex aperture, but this is only true for larger *Cerithium* species: some small species, such as *Cerithium atromarginatum, Cerithium egenum,* and *Cerithium zebrum,* have apertures like those of *Bittium* (Houbrick, 1978). Gründel (1976) further indicated that ontogenetic sculptural development in *Cerithium* begins with a single primary spiral cord that becomes stronger and more prominent, forming a keel that is not integrated with the weaker axial riblets; moreover, there are many fine spiral threads of varying strength. In *Bittium,* whorl sculpture begins with two spirals that quickly become four primary spiral cords forming a network with sharply defined axial riblets. The so called "definitive" shell characters proposed by Gründel (1976) are unreliable, because the more species that are examined, the more exceptions and ambiguities one encounters.

Marcus & Marcus (1963) cited the presence of a metapodial mucus gland in *Bittium reticulatum,* crediting this information to Fretter (1948). However, no such gland was observed in living or preserved, sectioned specimens from the Azores; furthermore, Ponder (in litt.) did not note this structure on specimens of *Bittium reticulatum* from the western coast of Sweden. Fretter's (1948: 628) paper merely cites the presence of this gland in such small gastropods as *Bittium, Cerithiopsis,* and *Triphora,* but as she mentioned only generic names, it is unclear what "*Bittium*" species she actually observed.

All living, observed members of the Bittiinae appear to be feeders of epiphytic microalgae, such as diatoms, which occur commonly on sea grasses. Most species occur in large populations and are highly gregarious.

Species of the genus *Bittium* appear to be primarily concentrated in the eastern Atlantic: the *Bittium reticulatum* complex and species closely related to it are commonly found throughout the Mediterranean, north African, and western European regions, and appear to be adapted to temperate and cold waters. *Bittium impendens* from the Indo-Pacific, which differs from the Atlantic *Bittium* species only in lacking a monopectinate osphradium, is herein included under the genus *Bittium.* If this species truly belongs in *Bittium s.s.,* and if other anatomically unknown Indo-Pacific species are examined, the geographic distribution of the genus *Bittium* may be far wider than is now thought.

Bittium reticulatum (Da Costa, 1778) (Figs. 3–6)

Strombiformis reticulatus Da Costa, 1778: 117, pl. 8, fig. 13.
Murex reticulatus (Da Costa). Montagu, 1803: 272.
Cerithium latreillei Payraudeau, 1826: 143.
Cerithium lacteum Philippi, 1836: 195.
Cerithium reticulatum, Risso, 1826: 157; G. B. Sowerby, 1855: pl. 15, fig. 8; Jeffreys, 1867: 258; 1869: pl. 80, fig. 4; 1885: 57.
Bittium reticulatum, Watson, 1886: 540; Bucquoy et al., 1884: 212–215, pl. 25, figs. 3–9; Tryon, 1887: 150–151, pl. 29, figs. 78–83; Dautzenberg, 1889: 40–41.

Description

Shell (Fig. 3A–H): Shell elongate, reaching 15 mm in length, comprising 9–10 moderately inflated whorls. Protoconch (Fig. 3G) comprising two weakly sculptured whorls. Early whorls beginning with two spiral cords and broad subsutural ramp (Fig. 3H). Adult whorls sculptured with 4–5 spiral cords beaded where many small axial riblets cross over them, creating cancellate sculpture. Suture deeply impressed. Body whorl a little under one-third shell length, having weak basal constriction and small anterior canal weakly reflexed to left. Body whorl sculptured with five major spiral cords and 5–6 weaker cords on its base. Aperture ovate, a little over one-third shell length, with concave columella having

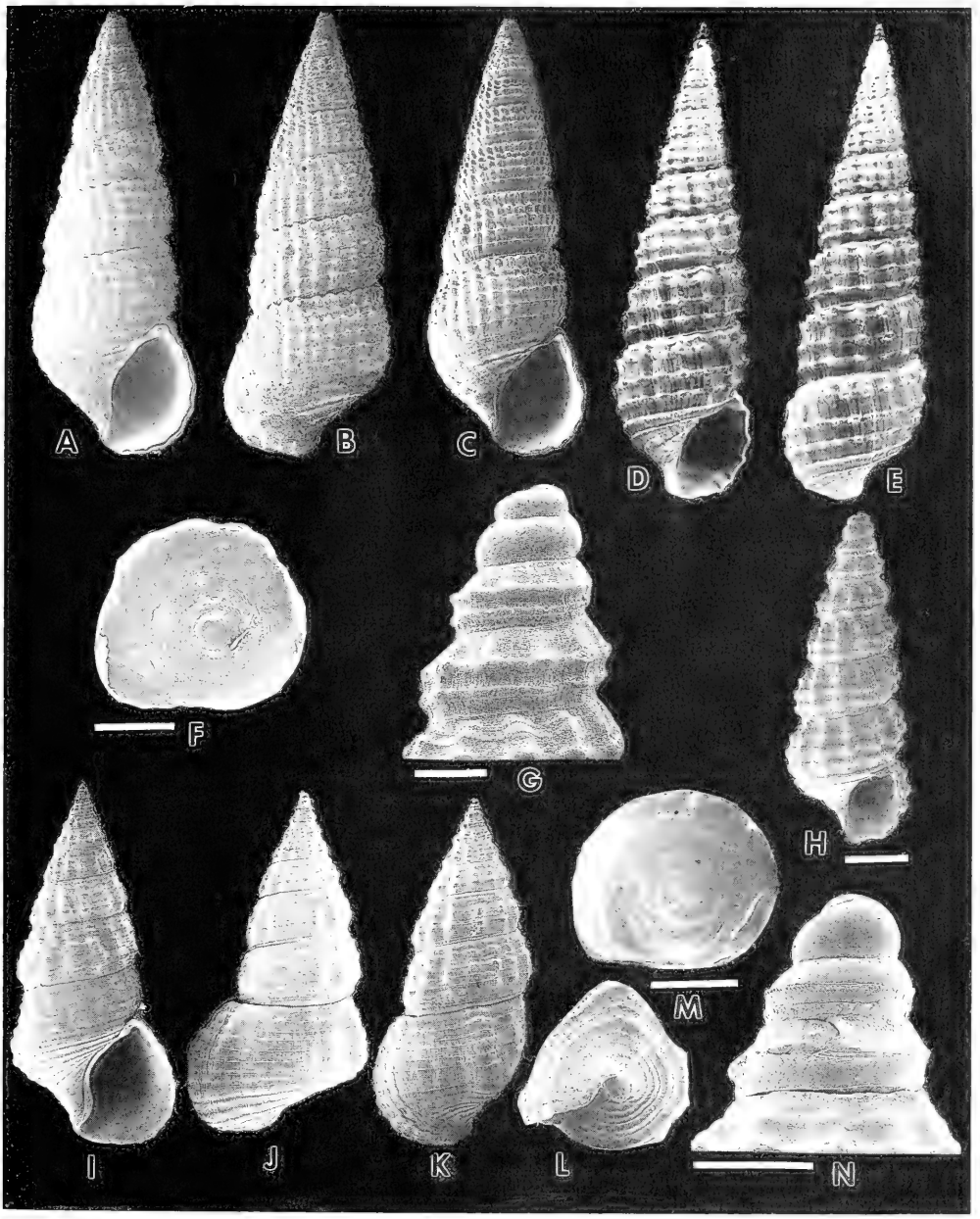

FIG. 3. Representatives of genus *Bittium:* A–H, *B. reticulatum;* I–N, *B. impendens.* A–C, SEM micrographs of *B. reticulatum* from São Miguel, Azores (USNM 878030), 6 mm length; D, E, *B. reticulatum* from Tunisia (USNM 754051), 11 mm length; F, SEM micrograph of operculum of *B. reticulatum,* bar = 0.5 mm; H, SEM micrograph of immature shell of *B. reticulatum,* bar = 0.5 mm; I–L, SEM micrographs of shell of *B. impendens* from Honolulu, Hawaii (USNM 857098), 5 mm length; M, SEM micrograph of operculum of *B. impendens,* bar = 0.5 mm; N, SEM micrograph of protoconch of *B. impendens,* bar = 150 μm.

slight columellar callus; anterior canal short, shallow; anal canal very small; outer lip rounded, weakly crenulate. Periostracum thin, light tan.

Animal (Figs. 4–6): Head-foot of animal pigmented light yellowish-brown overlain by large dark brown blotches and small white spots. Visceral mass with 8 visceral whorls, comprising mostly digestive gland and overlying gonads. Ovary white; testis dirty yellow. Stomach about one whorl in length. Kidney large, light tan, about two-thirds whorl in length. Columellar muscle white, broad, short, about one-half length of pallial cavity. Head (Fig. 4A) with elongate, narrow snout (Fig. 4B, sn), flattened dorso-ventrally, expanded at bilobed tip, with bright yellow, oval-shaped oral pad at antero-ventral end (Fig. 4A, C, 1). Cephalic tentacles (Fig. 4A, t) elongate, narrow, with broad peduncular bases each with large dark eye. Foot narrow, elongate, crescent shaped anteriorly. Deep transverse slit (Fig. 4C, amg) between epipodial lips marks entrance to large ovate anterior mucus gland extending via central duct deep into anterior foot. Epipodium separated from lower foot and densely ciliated sole by deep, laterally placed groove (Fig. 4B, epg) forming broad epipodial skirt (Fig. 4B, C, eps) extending posteriorly on each side of foot from corners of anterior epipodial lips of anterior mucus gland around entire foot base, joining behind and below opercular lobe. Lateral epipodial skirt scalloped along edges of each side of median and posterior parts of epipodium, having small papillae (Fig. 4B, C, ep); epipodial skirt forming long opercular lobe (Fig. 4B, C, opl). Sole of foot (Fig. 4C, s) indistinctly divided into two parallel axial parts, forming anterior longitudinal fold. No metapodial mucus gland. Operculum (Fig. 3F) corneous, tan, circular, paucispiral with subcentral nucleus and with thin, transparant border. Ciliated gutter (Fig. 4B, C, cg) emerging from right side of mantle cavity (Fig. 4C, ex) and running down right side of foot; ciliated gutter leads to large glandular ovipositor (Fig. 4B, C, ovp) and egg-laying pit at base of epipodium in females. Ovipositor oval-shaped, comprised of glandular, transparant white tissue formed into many parallel pleats divided transversely by deep central slit. Mantle bilobed at edge, having smooth outer lobe and inner lobe with many small papillae, becoming smooth ventrally. Mantle papillae (Fig. 4B, C, mp) slender, darkly pigmented, each with white spot. Mantle edge thickened at inhalant (Fig. 4C, inh) and exhalant siphons.

Pallial Cavity: Pallial cavity deep, comprising about two whorls. Osphradium olive colored, ridge-like, pectinate on right side only, bordered on each side by narrow ciliated strip. Osphradium wide, about one-half ctenidial length, beginning close behind inhalant siphon and extending length of ctenidium. Ctenidium bluish-gray, comprising numerous finger-like, triangular filaments with narrow bases. Hypobranchial gland narrow, glandular comprising several kinds of large gland cells that stain dark blue. Rectal tube distended, filled with elongate, ovoid-shaped fecal pellets. Pallial gonoducts open, beginning behind mantle edge and extending posteriorly as far as kidney.

Reno-pericardial System: Kidney large, about two-thirds whorl in length, beginning at anterior end of style sac, extending anteriorly well into mantle cavity roof, lying over one-third of posterior pallial gonoduct. Kidney with simple kidney opening, but no renopericardial duct. Pericardium typically monotocardian, lying adjacent to posterior wall of mantle cavity.

Alimentary System: Mouth (Fig. 4A, m) lying antero-ventrally on snout, opening into oral cavity between two semicircular lips (Fig. 4A, C, 1). Buccal mass (Fig. 4D, bm) relatively small, about one-third snout length, loosely attached to snout wall by numerous thin muscle strands. Jaw tan, semicircular, comprised of cuticular cones and lying on either side of entrance to anterior buccal cavity. Radular ribbon (Fig. 5A; Table 2) folded beneath buccal mass and radula sac emerging behind it. Rachidian tooth (Fig. 5C) with dorso-ventrally compressed basal plate with concave sides rounded base and with V-shaped base buttressed on each side with a basal lateral extension; rachidian broader above than below, having cutting edge with slightly concave top, and comprising large, spade-shaped central cusp flanked on each side by 2–3 small, pointed denticles. Lateral tooth (Fig. 5B) with broad basal plate comprising long, ventrally extending, central pillar having small pustule on its face, and with moderately long lateral extension; cutting edge comprising very large spade-shaped cusp with one inner denticle and 3–6 outer denticles. Marginal teeth (Fig. 5A) curved, elongate, with broad, swollen shafts, narrowing and becoming spatulate at tips; inner marginal tooth with tip having long

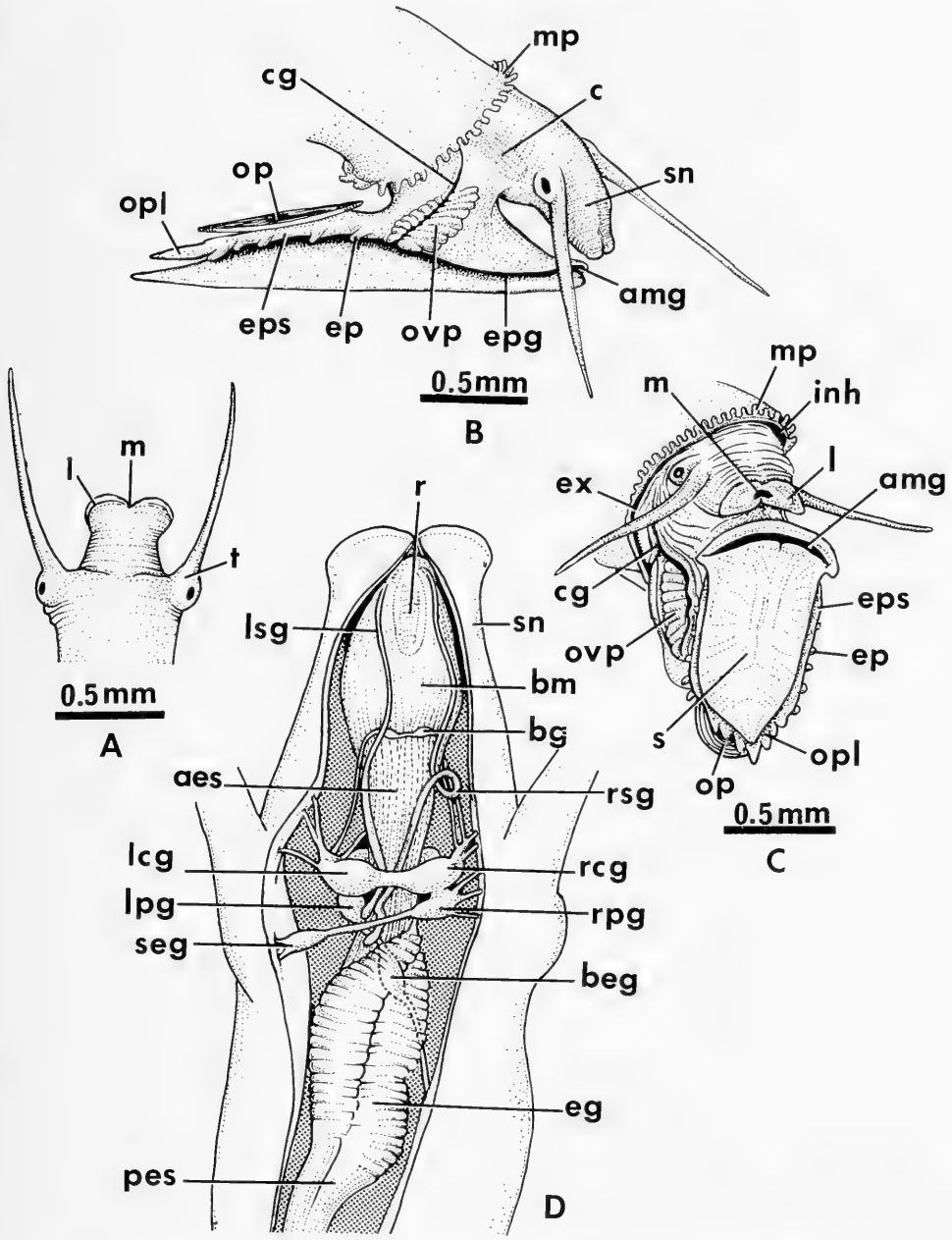

FIG. 4. Anatomical representations of *Bittium reticulatum*. A, head and snout; B, lateral view of headfoot; C, head and sole of foot; D, anterior alimentary system exposed by dorsal longitudinal cut through wall of buccal cavity. aes = anterior esophagus; amg = anterior mucus gland; beg = subesophageal gland; bg = buccal ganglion; bm = buccal mass; c = ciliated strip; cg = ciliated gutter; eg = esophageal gland; ep = epipodial papilla; epg = epipodial groove; eps = epipodial skirt; ex = exhalant siphon; inh = inhalant siphon; l = lip; lcg = left cerebral ganglion; lpg = left pleural ganglion; lsg = left salivary gland; m = mouth; mp = mantle papilla; op = operculum; opl = opercular lobe; ovp = ovipositor; pes = posterior esophagus; rcg = right cerebral ganglion; rpg = right pleural ganglion; rsg = right salivary gland; s = sole; seg = supraesophageal ganglion; sn = snout; t = tentacle.

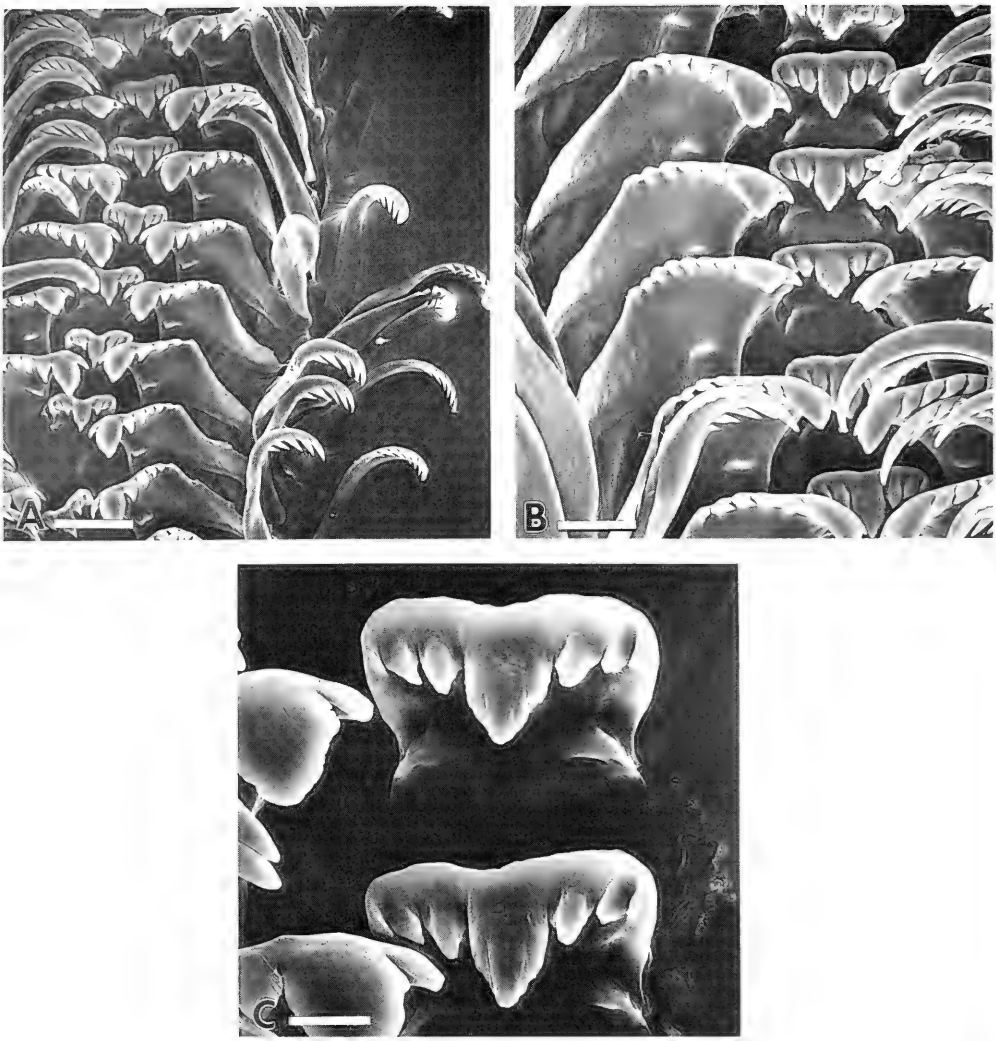

FIG. 5. Scanning electron micrographs of radula of *Bittium reticulatum* from São Miguel, Azores (USNM 878030). A, half row with marginal teeth folded back, bar = 19 μm; B, rachidian and lateral teeth, bar = 15 μm; C, detail of rachidian teeth, bar = 4 μm.

central cusp, 3–4 inner denticles, 4 outer denticles; outer marginal tooth same, but lacking outer denticles. Salivary glands (Fig. 4D, rsg, lsg) comprising pair of narrow, uncoiled, shiny tubes, beginning behind nerve ring, extending through it anteriorly, opening into far anterior portion of buccal cavity. Buccal cavity opening and enlarging immediately behind nerve ring, having pair of prominent dorsal folds and smaller pair of smaller ventral folds. Interior mid-esophageal walls highly folded, forming large, olive-brown esophageal gland (Fig. 4D, eg). Internal epithelium of esophageal gland (Fig. 7A, B, eg) forming numerous transverse folds or lamellae, staining dark blue with Methylene blue. Posterior esophagus (Fig. 4D, pes) narrow and straight, running on top of columellar muscle, entering into left side of stomach. Stomach large, comprising about one whorl of visceral mass, including style sac. Esophageal opening into median ventral part of stomach floor. Large

sorting field with many fine folds adjacent to right side of esophageal opening. Minor typhlosole bordering right side of esophageal opening. Large central elevated pad in center of stomach adjacent to single duct to digestive gland lying short distance below esophageal opening. Digestive gland comprising single brown lobe consisting of digestive cells and secretory cells with dark brown granules. Gastric shield on right side of stomach having cuticular lining with protruding, toothed edge. Depressed epithelial pocket on floor of stomach adjacent to posterior part of gastric shield. Style sac short, about one-third the stomach length, nearly spherical, and containing crystalline style. Style sac adjacent to but separate from intestine opening, except for limited connection where both enter stomach. Anterior part of stomach with many parallel ciliated folds and closed off from style sac by major typhlosole. Internal intestinal walls with many fine folds where exiting stomach. Intestine curves around style sac, turns to right, and runs straight forward. Rectum with thin muscular wall, terminating in anal-bearing papilla.

Nervous System: Nervous system epiathroid, dialyneurous. Nerve ring comprised of large ganglia. Pleural ganglia (Fig. 4D, rpg, lpg) close to cerebral ganglia (Fig. 4D, rcg, lcg). Cerebral connective equalling length of cerebral ganglion. Buccal ganglia (Fig. 4D, bg) small, lying at posterior edge of buccal mass. Subesophageal ganglion (Fig. 4D, beg) very close to left pleural ganglion (Fig. 4D, lpg). Supraesophageal connective moderately long, about twice length of right pleural ganglion; dialyneury between left pallial nerve and nerve emerging from supraesophageal ganglion (Fig. 4D, seg). Visceral ganglion located in floor of posterior mantle cavity.

Reproductive System: Testis creamy yellow, overlying dark brown digestive gland, extending anteriorly about five whorls, ending one-half whorl before stomach. Testicular ducts on inner side of visceral coil, joining to form spermatic duct, enlarging anteriorly, becoming seminal vesicle and containing two kinds of spermatozoa: euspermatozoan with single long flagellum and paraspermatozoan with [four ?] flagellae. Males aphallate. Male pallial gonoduct (Fig. 6A) open, comprising two thin walled laminae (Fig. 6A, 11, ml) with thicker transverse glandular folds at their attached bases bordering gonaductal groove (Fig. 6A, gd). Posterior half of male gonoduct thick, glandular, comprising prostate gland (Fig. 6A, pg). Anterior half of male gonoduct glandular, not as thick, putative spermatophore-forming organ (Fig. 6A, so).

Ovary opaque white, thin-walled, overlying digestive gland, extending anteriorly, ending about one-half whorl before stomach. Coelomic oviduct (Fig. 6B, C, cod) short tube, highly ciliated within, beginning anterior to stomach with duct wall lying against pericardium (no connection), ending at posterior mantle cavity where circular sphincter muscle separates it from pallial oviduct. Female pallial oviduct (Fig. 6B, C) large, comprising two laminae, enlarged and glandular at their bases, attached basally to each other and to mantle floor, forming ciliated oviductal groove (Fig. 6B, C, ovg). Posterior end of pallial oviduct closed. Medial, free lamina with wide anterior ciliated sperm gutter (Fig. 6B, C, sg) along its edge leading to two, well-separated, pocket-like openings. First opening (Fig. 6B, C, osp) leading into large, deep bursa having smooth inner epithelium and containing large numbers of non-directed spermatozoa (Fig. 7C, D, sp); ciliated gutter continuing posteriorly to open (Fig. 7C, osr) into pouch-like, muscular seminal receptacle (Fig. 6C, B sr; 8C, D, sr) containing oriented euspermatozoa with heads embedded in receptacle walls. Lateral lamina attached to pallial wall, having anterior ciliated tract comprising many parallel elongate, fine ciliated folds (Fig. 6B, C, ctr; 7A, B, ctr) running posterior to open into thin-walled tube leading into posterior pouch-like bursa having highly vacuolated epithelium and functioning as spermatophore bursa (Fig. 6B, C, sb). Ciliated tract and folds opening to seminal receptacle on lateral lamina located opposite sperm gutter and opening to seminal receptacle of medial lamina, both edges interdigitating to form closed system. Posterior half of glandular portion of both laminae opaque white color, comprising albumen gland (Fig. 6B, C, ag; 7C, D, ag); anterior half dirty white, comprising capsule gland (Fig. 6B, C, cg; 7A, B, cg).

Spawn comprising thin gelatinous string (about 25 mm length, uncoiled) tightly coiled clockwise or irregularly folded on itself and attached to substrate. Jelly string containing many small opaque eggs (0.65 μm diameter) each within thin, transparent hyaline capsule (110 μm diameter). Entire spawn mass contains about 800 eggs. Free swimming bilobed planktotrophic veliger larval stage present. Larval shell ranging from 170–330 μm, de-

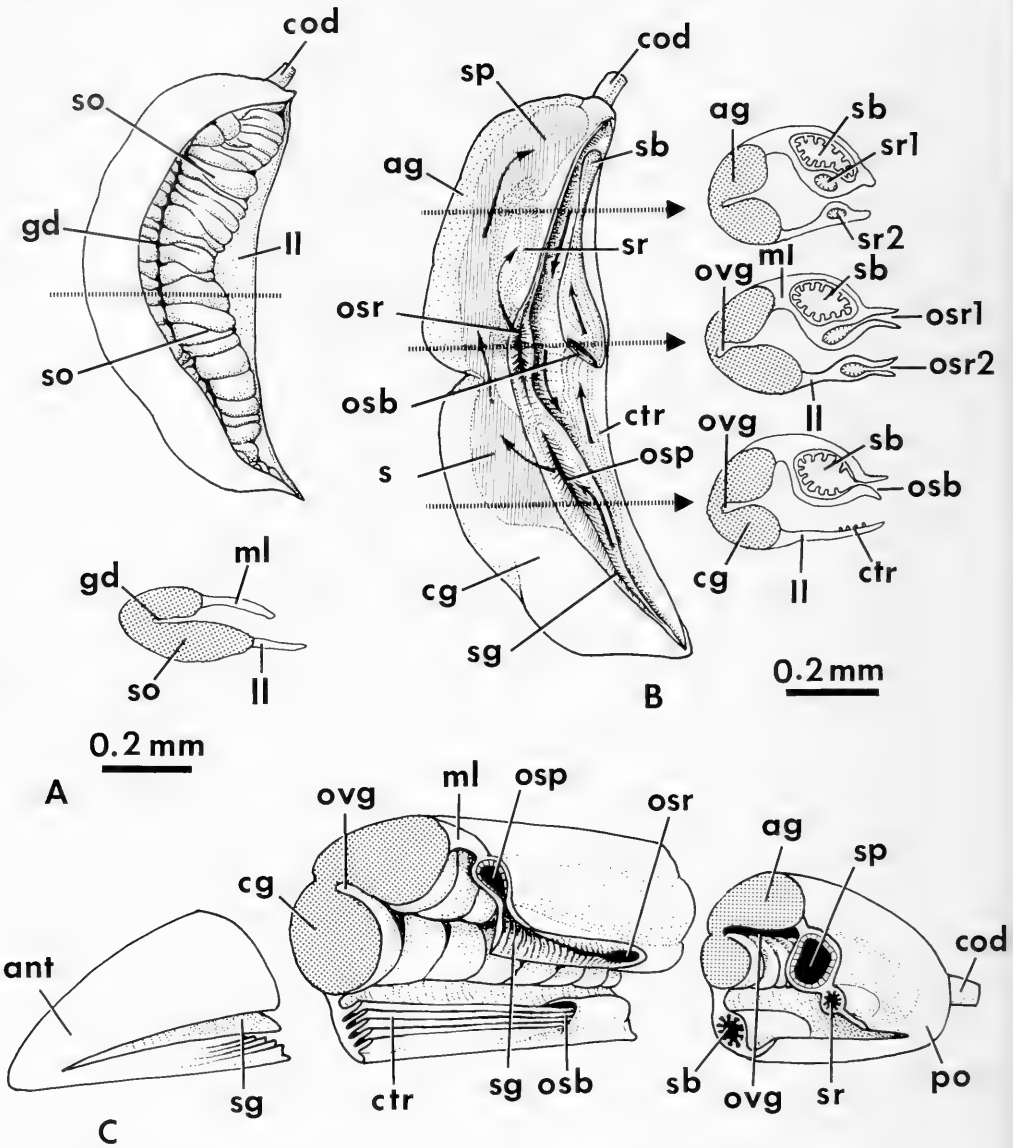

FIG. 6. Representation of pallial gonoducts of *Bittium reticulatum*. A, male pallial gonoduct, showing section through mid-duct beneath, represented by dotted line; B, pallial oviduct showing three cross sections of duct represented by dotted arrows and sections to right; C, reconstruction of pallial oviduct showing configuration of ducts and glands (anterior to right). ag = albumen gland; ant = anterior; cg = capsule gland; cod = coelomic oviduct; ctr = ciliated ridge tract; gd = gonaductal groove; ll = lateral lamina; ml = medial lamina; osb = opening to spermatophore bursa; osp = opening to sperm bursa; osr = opening to seminal receptacle; ovg = oviductal groove; po = closed portion of pallial oviduct; sb = spermatophore bursa; sg = sperm gutter; sp = sperm bursa; sr = seminal receptacle; so = spermatophore-forming organ.

pending upon age. Larval shell with rounded, nearly smooth whorls having thin spiral thread forming weak keel and with deep sinusigeral notch (Thorson, 1946: 192, fig. 109).

Discussion

The status of the many specific and subspecific names comprising the *Bittium reticu-*

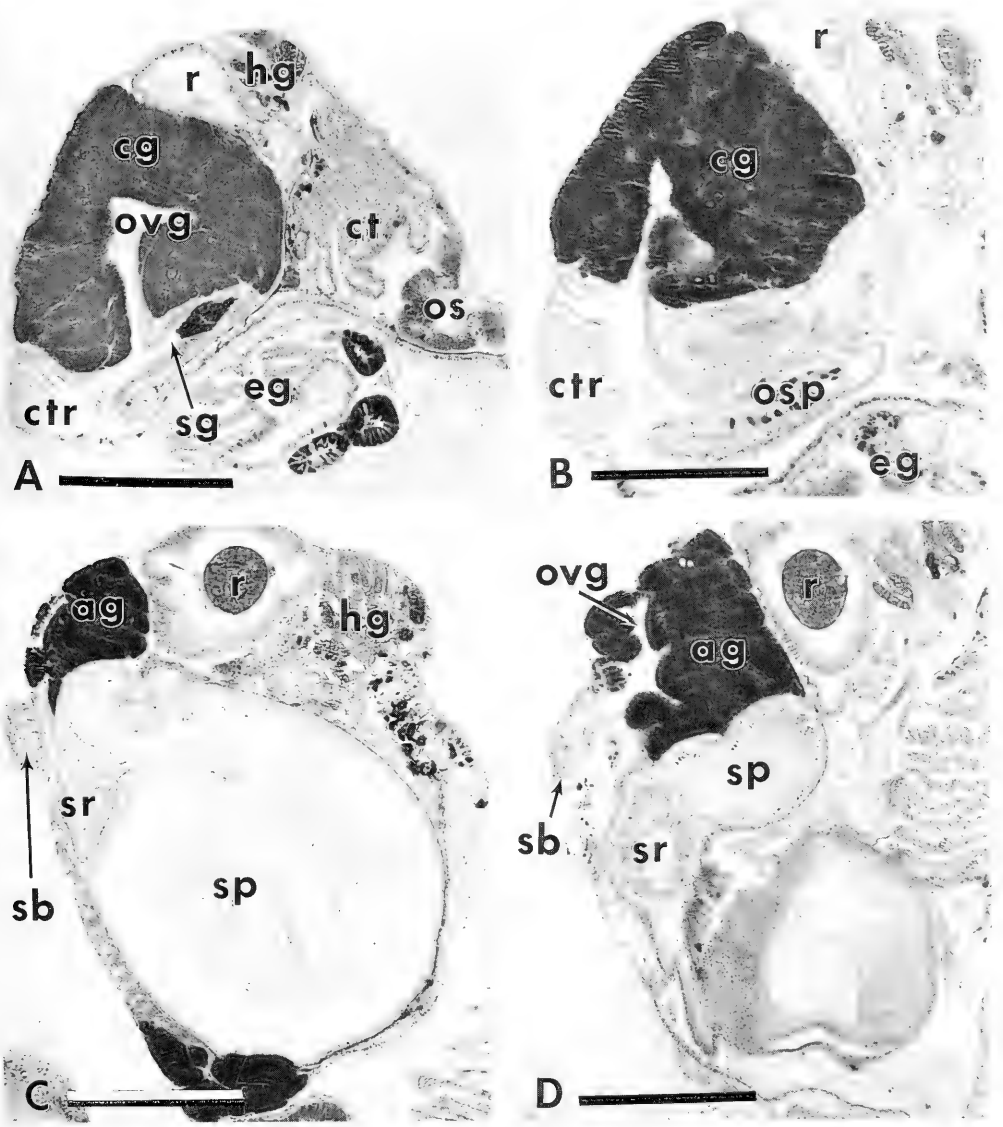

FIG. 7. Successive sections, anterior to posterior, through pallial oviduct of *Bittium reticulatum*. A, anterior of pallial oviduct showing relationship of mantle cavity organs to oviduct, bar = 0.25 mm; B, mid-section showing ciliated ridge tract and opening to sperm bursa, bar = 0.25 mm; C, section through enlarged sperm bursa in posterior pallial oviduct, bar = 0.25 mm; D, section through closed posterior of pallial oviduct, bar = 0.25 mm. ag = albumin gland; cg = capsule gland; ct = ctenidium; ctr = ciliated ridge tract; eg = esophageal gland; hg = hypobranchial gland; os = osphradium; osp = opening to sperm bursa; ovg = oviductal groove; r = rectum; sb = spermatophore bursa; sg = sperm gutter; sp = sperm bursa; sr = seminal receptacle.

latum complex is controversial (Verduin, 1976). It is not my intention to address alpha-level problems in this generic review, but the Azorean population used for the anatomical study herein is considered by some as a sub-species or a closely related species of the *Bittium reticulatum* complex. *Bittium reticulatum* is exceedingly variable in shell sculpture throughout its range (compare Figs. 2A, C, D), but this is not unusual among cerithioide-

ans. The pallial oviduct described by Johansson (1947) and notes and sketches made by Ponder (Ponder, in litt.) on the anatomy of specimens from western Sweden agree substantially with my observations of Azorian specimens. For the purposes of this study, the *Bittium reticulatum* complex is regarded in the broad sense (*sensu lato*), as a single species.

The epipodial skirt, characteristic of members of the *Bittium*-group, forms a highly ciliated lateral groove where it overhangs the foot, and carries detrital particles posteriorly to the back of the foot where they are discarded.

The posterior roof of the pallial cavity is covered by the anterior extension of the renal organ, which overlays the posterior pallial gonoduct. The renal organ opens via a muscular sphincter, the renal opening, into the posterior pallial cavity.

The ridge-like osphradium of *Bittium reticulatum* is unusual in being pectinate on its right side. Although these pectins are small, they are clearly visible and very unlike simple nonpectinate osphradia of closely related taxa.

The rachidian tooth of the radula of *Bittium reticulatum* is similar to those of members of other genera in the group, but unlike that of *Cacozeliana* (see below). Table 2 gives the comparative dentition of the radular teeth.

Bittium reticulatum has three sperm storage spaces, two connected to the ciliated groove of the non-glandular portion of the medial free lamina, and one in the posterior part of the non-glandular attached lateral lamina (Fig. 6B, 11). It is not entirely clear how these three bursae function. Of the two bursae in the medial lamina, the smaller one is clearly the seminal receptacle, because oriented euspermatozoa are found in it, exclusively (Fig. 7C, D, sr). The larger bursa (Fig. 6B, sp) contains considerable numbers of unoriented sperm, and much nondescript material (presumably disintegrating paraspermatozoa and degenerating spermatophores), although some euspermatozoa occur with heads oriented on the inner wall epithelium, especially near the opening to the sperm gutter (Fig. 7D). Although this large bursa in the medial lamina contains spermatophores in most cerithiids, this is not the case in members of the *Bittium*-group, where it appears to function as a sperm storage and ingesting area. It is inferred that the pouch in the posterior of the lateral lamina (Fig. 6C, sb, Fig. 7C, D, sb) functions as a spermatophore bursa in *Bittium reticulatum* and probably in most other members of the *Bittium*-group, because Marcus & Marcus (1963) found spermatophores in this structure in the western Atlantic *Bittiolum varium.* I was unsuccessful in finding spermatophores in either structure in specimens of *Bittiolum varium* from Florida. A new genus from the Indo-Pacific, *Ittibittium,* described herein, deviates from the typical pallial oviduct layout in lacking the spermatophore bursa in the lateral lamina and in having the albumen gland protrude posteriorly beyond the back of the pallial cavity into the visceral coil.

The spawn of *Bittium reticulatum* was first described and figured by Meyer & Möbius (1872), and the spawn and larvae described by Lebour (1937) and Graham (1988). Spawn, larvae, veliger, protoconchs, and juvenile shells of this species were described and well illustrated by Thorson (1946: 192, fig. 109). Other depictions of the larval shell of this species are those of Fretter & Pilkington (1970: 10–11, fig. 6) and Richter & Thorson (1975: pl. 3, figs. 16–17). According to Graham (1988), British *Bittium reticulatum* is a summer breeder and attaches its spawn to shells, stones or weeds. Spawn comprises a cylindrical ribbon about 3 mm in diameter, having a total length of 25 mm, and coiled in tight spirals. A spawn mass contains about 1000 eggs, which develop to veliger larvae.

The geographic range of the *Bittium reticulatum* complex is broad, comprising western Europe, the Azores, North Africa, and the Mediterranean.

Bittium impendens (Hedley, 1899) (Fig. 3, I–N)

Cerithium impendens Hedley, 1899: 434–435, fig. 23 (Holotype: AMS C5944; type locality: Funafuti Atoll, Ellice Islands); Kay, 1979: 118, 120, fig. 45A.

Description

Shell: (Fig. 3I–N). Shell short, stout, with wide base, reaching 7 mm length and comprising 8–9 convex whorls. Protoconch (Fig. 3N) comprising 2.5 whorls; protoconch 1 smooth; protoconch 2 sculptured with thin central, spiral keel and weak presutural spiral thread; lower part of each whorl with microscopic pustules. Whorls slightly pendant abapically, constricted at suture. Adult shell sculptured with 3–4 major spiral cords inter-

spersed with spiral threads. Spiral cords weakly beaded and beads aligned to form axial riblets. Suture well defined. Weak varices randomly distributed. Body whorl very broad, about one-half the shell length, with prominent wide, dorsal varix (Fig. 3J, L); body whorl sculptured with about 14 spiral cords and strongly constricted at base. Aperture a little over twice shell length, broadly ovate, with short, wide, shallow anterior canal and smooth outer lip extending widely at shell base (Fig. 3I).

Animal: Headfoot pinkish white, blotched with brown, covered with white spots and with chestnut stripes. Kidney bright pink. Right side of foot in females with ciliated gutter ending in small ovipositor at edge of lateral groove. Epipodial skirt having very small pustules or protuberances along lateral edges on each side of foot; opercular lobe scalloped and pointed at end. Sole of foot pink, without metapodial mucus gland. Mantle edge fringed dorsally with papillae; underside of inhalant siphon with three large papillae. Marginal teeth of radula having three inner denticles. Osphradium a thin brown ridge, non-pectinate. Openings to sperm pouch and seminal receptacle in medial lamina close to each other, situated within common aperture at end of sperm gutter in edge of anterior third of medial lamina adjacent to opening of spermatophore bursa of lateral lamina. No ciliated tract leading to spermatophore bursa.

Discussion

Examination of the type lot (holotype and 7 paratypes) of *Cerithium impendens* confirms that the Hawaiian specimens studied herein are conspecific with this taxon. This species has not been cited frequently in the literature.

The assignment herein of *Bittium impendens* to the genus *Bittium* is made with some doubt. The shell morphology of this widespread Indo-Pacific species is quite different from that of the type species of *Bittium, Bittium reticulatum* (compare Fig. 3A–E and 3I–L), and unlike the shells of other eastern Atlantic *Bittium* species. In addition, the osphradium is ridge-like rather than monopectinate, and there does not appear to be a ciliated tract associated with the spermatophore bursa on the lateral lamina. Instead, the opening to the spermatophore bursa is adjacent to the two openings of the bursae in the medial lamina. The radula of *Bittium impendens* is very similar to that of *Bittium reticulatum* except that the marginal teeth have fewer outer and inner denticles. Aside from these differences, the animal shares most of the anatomical features of *Bittium reticulatum.* Although an argument could be made that this species represents yet another new genus, I have conservatively placed *Bittium impendens* under *Bittium, s.s,* with a query, because it does have many characters in common with the type species of *Bittium.*

The shell of *Bittium impendens* differs from other *Bittium*-group genera by its fir-tree outline and wide body whorl with prominent dorsal varix (Fig. 3I–L). The protoconch (Fig. 3N) is smooth except for a thin spiral thread and a deep sinusigeral notch, indicative of a planktonic larval phase. Judging from specimens from other regions that appear to be conchologically conspecific, this species has a wide Indo-Pacific distribution, occurring from central Pacific islands throughout the Indo-West-Pacific to east Africa.

ITTIBITTIUM, New Genus

Diagnosis

Shell small, reaching 6 mm length, with inflated whorls and dominant spiral sculpture of 4–5 cords. Protoconch with depressed, concave apex, broad sutural ramp, sculptured with minute axial striae and two strong spiral cords. Operculum ovate, paucispiral with eccentric nucleus. Each side of propodium with elongate papilla. Epipodial skirt laterally fringed with slender papillae. Large opercular lobe having elongate papillae. No ovipositor in females. Sole of foot with long, central longitudinal slit marking entrance into large metapodial mucus gland. Osphradium weakly bipectinate. Albumen gland extending past posterior of pallial cavity into visceral coil. No spermatophore bursa in lateral lamina of pallial oviduct. Spawn comprising short gelatinous tube.

Type Species: Bittium parcum Gould, 1861.

Etymology: A compound of "itti," American vernacular prefex for very small, and *Bittium.*

Remarks

This genus is perhaps one of the most distinctive of the *Bittium* group, in terms of its unusual protoconch and anatomical features.

The protoconch with depressed apex and broad sutural ramp (Fig. 8I) is unique among the *Bittium*-group. The distinctive propodial and epipodial papillae, well-developed epipodial skirt, and long metapodial mucus gland are conspicuous autapomorphiic characters in living specimens (Fig. 2). The lack of a spermatophore bursa in the lateral lamina of the pallial oviduct and the protrusion of the albumen gland through the posterior pallial cavity into the visceral coil are highly unusual autapomorphies, and set *Ittibittium,* gen. n., apart from the rest of the Bittiinae. The placement of the spermatophore bursa in the lateral lamina is one of the synapomorphous character used in this review to define the subfamily Bittiinae; therefore, it is noteworthy that *Ittibittium,* gen. n., has lost this feature. The spawn mass of *Ittibittium,* gen. n., is also unusual in being a simple, short tube.

In some museum collections, *Bittium parcum* and species similar to it are incorrectly assigned to *Bittinella* Dall, 1924, a genus based on *Bittium hiloense* Pilsbry & Vanatta, 1908, which has been shown to be a rissoid of the genus *Isselia* (Ponder, 1985: 95; Kay, 1979: 80).

Ittibittium parcum (Gould, 1861)
(Figs. 8–11)

Bittium parcum Gould, 1861: 387 (Lectotype, R. Johnson, 1964, USNM 2040; type locality Okinawa, Ryukyu Islands); G. B. Sowerby, 1866: pl. 18, fig. 125; Tryon, 1887: 155, pl. 30, fig. 20; R. Johnson, 1964: 122, pl. 12, fig 14; Kay, 1979: 120, figs. 22D, 45D, E.

Cerithium hawaiensis Pilsbry & Vanatta, 1905: 576 (Holotype ANSP; type locality: Hilo, Hawaii).

Description

Shell (Fig. 8): Shell small, pupate-elongate, comprising about 8 inflated, angulate whorls and reaching 5.8 mm length. Protoconch (Fig. 8F-I) comprising two concave whorls, concavely flattened apex, very broad sutural ramp sculptured with minute axial striae (Fig. 8F); protoconch whorls sculptured with two strong, keel-like spiral cords, with central spiral cord becoming dominant one. Early whorls sharply angulate (Fig. 8I); first post-larval whorl with keel-like median spiral cord; second whorl with another spiral cord above keel and third whorl having 3 spiral cords above keel. Adult whorls angulate, sculptured with keel-like median cord, 7–8 minor spiral cords, each cord abapically overlapped by successive one. Eight to nine weak to strong axial ribs occasionally on whorls, especially on upper ones (Fig. 8J). Varices randomly placed. Suture moderately impressed. Body whorl (Fig. 8L) slightly constricted at base, comprising a little less than half shell length, sculptured with 15–19 weak flattened spiral cords, occasional weak axial ribs and with broad varix. Aperture about one-third shell length, ovate with smooth outer lip and short broad anterior canal. Slight columellar callus present. Periostracum thin, nearly transparent.

Animal: Animal pigmentation highly variable, ranging from greenish-yellow to pink and brown and covered with white blotches. Cephalic tentacles wide at bases, elongate, twice snout length. Snout elongate, narrow, bilobed at tip. Operculum (Fig. 8K) thin, corneous, tan, circular-ovate, paucispiral with subcentral nucleus. Anterior part of foot crescent-shaped, cowl-like, having single long papilla on each side (Fig. 2). Narrow transverse slit at edge of propodium leading into large, spherical anterior mucus gland, staining deep purple in toluidine blue. Lateral epipodial skirt with about 10 small, slender papillae along edges (Fig. 2) on each side of foot, extending posteriorly to large opercular lobe having long papillae along its edges; papillae show through edges of opercular border. Sole of elongate, narrow foot having deep, centrally placed, narrow longitudinal slit (Fig. 2) beginning behind anterior mucus gland slit (Fig. 2) and extending posteriorly to back of foot; slit leading by way of ciliated duct into deep, massive, metapodial mucus gland, staining deep purple in toluidine blue. Males with ciliated strip on right side of foot, emerging from right side of mantle cavity and extending down to edge of sole. Ciliated gutter on right side of foot in females deep, running down side of foot and extending through lateral epipodial groove (Fig. 2). No ovipositor present. Mantle edge dorsally fringed with many small papillae.

Pallial Cavity: Osphradium a little less long than ctenidium, broad, about one-third ctenidial width, dark brown, weakly bipectinate with small pectins on each side but unconnected dorsally; osphradium becoming monopectinate at inhalant siphon. Ctenidium narrow, extending length of pallial cavity, comprising

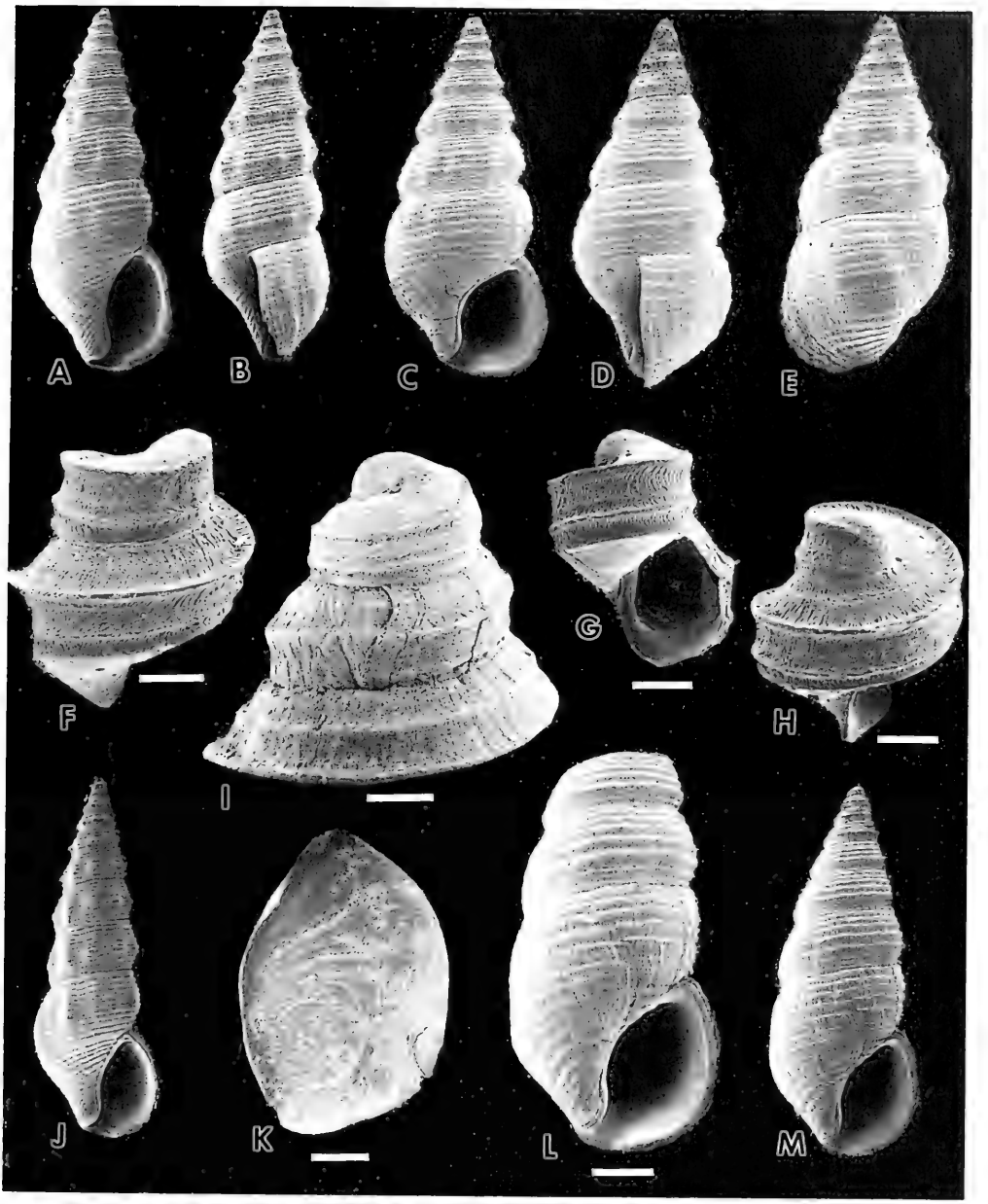

FIG. 8. SEM micrographs of *Ittibittium parcum* from Honolulu, Hawaii (USNM 857100). A, B, apertural and lateral views of shell, 3.6 mm length; C–E, apertural, lateral and dorsal views of shell, 3.6 mm length; F, newly hatched larval shell showing protoconch and details of whorl sculpture, bar = 63 μm; G, H, embryonic shells removed from eg capsule, bar = 23 μm; I, larval and early whorls of shell, bar = 0.4 mm; J, shell with strong axial ribs, 5.3 mm length; K, operculum, bar = 0.2 mm; L, detail of penultimate and body whorl, showing details of sculpture and aperture, bar = 0.6 mm; M, apertural view of shell, 3.6 mm length.

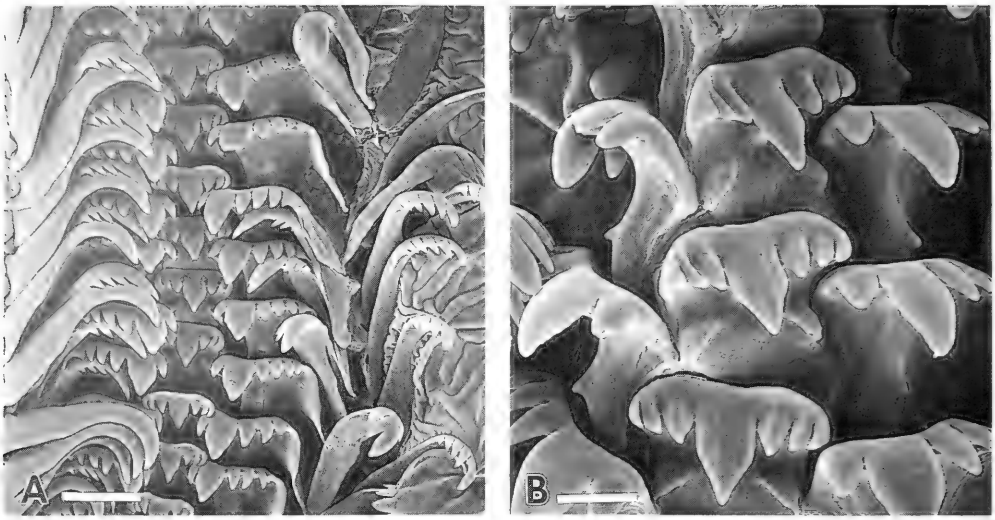

FIG. 9. SEM micrographs of radula of *Ittibittium parcum* from Honolulu, Hawaii (USNM 857100). A, middle of radular ribbon with right marginal teeth folded back, bar = 30 μm; B, detail of rachidian and lateral teeth, bar = 8 μm.

long, finger-like, triangular filaments. Hypobranchial gland partially overlaying rectum, well developed, composed of several large, dark-staining glandular cells.

Reno-pericardial System: Pericardium lying adjacent to posterior pallial wall. Kidney large, extending from anterior of style sac forward, into roof of posterior pallial cavity.

Alimentary System: Snout tip and lips of mouth yellow. Buccal mass large, about two-thirds snout length. Radula (Fig. 9A) short, about one-tenth shell length. Rachidian tooth having weak hour-glass shape and cutting edge with large central cusp flanked by 2 denticles on each side. Lateral tooth (Fig. 9B) having cutting edge with large pointed cusp, one inner denticle, 3–4 outer denticles. Inner marginal tooth with 2 inner denticles, large elongate major cusp and 3 outer denticles; outer marginal tooth with 5 inner denticles. Salivary glands paired, comprising tangled mass behind nerve ring, extending through it anteriorly as slender tubes. Esophagus becoming wide behind nerve ring, developing lateral glandular pouches with many small transverse internal folds, comprising short esophageal gland. Stomach large, about one whorl in length, having single opening to digestive gland, central raised pad, gastric shield, short crystalline style and style sac, about two-thirds the stomach length. Intestine leaving stomach looping dorsally and across anterior style sac, turning sharply, running anteriorly, adjacent to right side of kidney and albumen gland. Rectum slightly wavy, wide, containing large ovoid fecal pellets.

Nervous System: Cerebral ganglia very large, twice size of pleural ganglia. Subesophageal ganglion very close to left pleural ganglion. Supraesophageal ganglion separated from right pleural ganglion by connective two-thirds ganglion length.

Reproductive System: Testis white, overlaying brown digestive gland. Males aphallate with open pallial gonoducts. Pallial oviduct open, with large albumen gland extending through posterior of mantle cavity mantle cavity, protruding into visceral coil. Albumen gland staining cream-green in toluidine blue. Capsule gland very large, swollen, staining dark blue in toluidine blue. Large spermatophore bursa in posterior medial lamina. No ciliated ridge tract or seminal receptacle in lateral lamina. Spawn mass comprising wide gelatinous tube covered with thin membrane forming compact, short tube about 2 mm long, and 1.2 mm wide, containing large opaque, compacted eggs each 0.2 mm in diameter. Eggs arranged in short jelly tube about 3–4

deep. Development direct with young snails hatching from eggs.

Discussion

"Bittium" parcum has not been cited commonly in the literature, and due to great interspecific variability in shell sculpture and color, is frequently misclassified or unidentified in museum collections. Shell shape can vary from slender, elongate (Fig. 8J) to shorter, more inflated (Fig. 8C-E), and shell sculpture is highly variable: the axial ribs seen in some specimens may be entirely lacking in others. The protoconch with its flattened apex, broad sutural ramp and concave whorls is highly distinctive and unusual (Fig. 8F-H). However, *Ittibittium parcum* is readily distinguished from by several external anatomical features: (1) the epipodial skirt and opercular lobe are fringed with well-developed papillae; (2) a pair of long epithelial extensions (papillae) of the front of the foot (propodium); (3) the longitudinal slit marking the entrance to the metapodial mucus gland is very long. *Ittibittium parcum* has an unusual pallial oviduct in that the albumen gland projects posteriorly past the posterior end of the mantle cavity into the visceral coil, and there is no seminal receptacle in the lateral lamina of the pallial oviduct.

Living snails are quick, active crawlers, and even when removed from their shells showed a great deal of movement.

The operculum in this species tends to be more ovate than circular: in most other species of the *Bittium*-group, the operculum is circular. The opercular lobe papillae show through the transparent edges of the operculum.

This species undergoes direct development. The embryos pass through a veliger stage and hatch out as juvenile snails after losing the velar lobes. Direct development, while also occurring in *Stylidium,* is not the common mode of development among members of the *Bittium*-group. The comparatively large eggs of *Ittibittium parcum* are each enclosed within individual hyaline capsules about 0.2 mm diameter, and the egg capsules are stacked within a short, wide gelatinous tube and deposited on the substrate in an irregular mass. Here they undergo development, passing through a modified veliger stage and producing a well-developed embryonic shell (Fig. 8F-H), after which they emerge as small snails.

Ittibittium parcum is common in shallow water throughout the Hawaiian chain, and also occurs in French Polynesia (Naim, 1982) where it is very abundant in some localities. Naim (1982) found that this species represented 89% of the molluscan fauna associated with algae in Tiahura Lagoon in French Polynesia.

A species from Western Australia, very similar to the type species, recently has been described in great detail (Ponder, in press), and appears to be closely related to *Ittibittium parcum.*

BITTIOLUM COSSMANN, 1906

Bittiolum Cossmann, 1906: 139. (Type species by original designation: *Bittium podagrinum* Dall, 1892). Wenz, 1940: 755; Olsson & Harbison, 1953: 289–290.

Diagnosis

Shell small, turreted, stout, sculptured with 4 spiral cords and many axial ribs, and occasional weak varices. Protoconch with one spiral lira. Whorls presuturally constricted, body whorl elongate, narrow at aperture and constricted at base, having less width than penultimate whorl. Operculum ovoid-circular, paucispiral and with subcentral nucleus. Anterior canal weakly defined, short. Mantle edge smooth, epipodial skirt scalloped. Foot elongated anteriorly and having median longitudinal slit in posterior part of sole, leading into large metapodial mucus gland. Ovipositor small. Osphradium bipectinate, wide, one-third ctenidial length. Nervous system with right zygoneury and with short supraesophageal connective.

Remarks

Bittiolum species have small shells (Table 3) and are distinctive in having the body whorl elongated and constricted basally so that the aperture width is less than that of the penultimate whorl. The smooth mantle edge, narrow elongate anterior foot, right zygoneury and short supraesophageal connective are autoapomorphous characters of this genus.

The type species of this genus is a Neogene fossil from Florida that has a shell morphology very similar to that of living *Bittiolum varium* and *Bittiolum alternatum.* As the fossil species occurs in mid- to late-Neogene strata, and in the same geographic area as Recent

Bittiolum varium, it is not unreasonable to infer that the two species belong to the same clade, and the living species is considered to be congeneric with *Bittium podagrinum.* Cossmann (1906: 140) pointed out that *Bittiolum varium* (Pfeiffer) (cited as *Cerithium*) occurred from the Pleistocene of Florida and extended into the Recent. He further noted the superficial resemblance of *Bittiolum varium* to some fossils of *Aneurychilus* Cossmann, 1889, which he placed in the Diastomatidae (as Diastomidae, Cossmann, 1906: 174).

Dall (1889) was the first author to confuse American members of *Bittiolum* with the genus *Diastoma* Deshayes, 1850, when he referred *Bittiolum varium* to that genus. Abbott (1974), probably following this cue, later referred western Atlantic species of *Bittium, s.l.,* to *Diastoma* Deshayes, 1850, but this subsequently has been shown to be incorrect (Houbrick, 1977: 102, 1981b), as the latter genus belongs to the Diastomatidae Cossmann, 1894, a totally different lineage represented by individuals of much larger size and different anatomy that are not closely related to the *Bittium*-group (Houbrick, 1981b).

The anatomy of *"Bittium" alternatum,* from the northeastern coast of North America, is identical to that of its southeastern, Caribbean Province congener, *Bittiolum varium.* Thus, these two species and probably all other American western Atlantic species belong in the genus *Bittiolum,* which is also represented by several eastern Pacific species, such as *Bittiolum fastigiatum* (Carpenter, 1864).

Because the two *Bittiolum* representatives studied, *B. varium* and *B. alternatum,* are so alike, they are treated jointly in the section below.

Bittiolum varium (Pfeiffer, 1840) (Figs. 10–11)

Cerithium varium Pfeiffer, 1840: 256.

Cerithium columellare Orbigny, 1842: pl. 23, figs. 13–15; 1845: 244 (in part; syntypes BMNH).

Cerithium gibberulum C. B. Adams, 1845: 5 (Lectotype MCZ 186078, type locality Jamaica).

Bittium varium (Pfeiffer). Tryon, 1887: 152, pl. 29, fig. 86; Perry, 1940: 134, pl. 28, fig. 202.

Cerithium (Bittium) gibberulum (C. B. Adams). Kobelt, 1898: 245–246, pl. 43, fig. 1.

Diastoma varium (Pfeiffer). Abbott, 1974: 107, fig. 1037.

Description

Shell (Fig. 10): Shell turreted, pendent-shaped, comprising about 10 flat-sided whorls and reaching 7 mm length. Protoconch (Fig. 10I) comprising 2.5 whorls; protoconch 1 smooth, protoconch 2 with central keel-like spiral lira and microscopic pustules on abapical part of whorl. Early whorls (Fig. 10H) with two weak spiral lirae, and sculptured with dominant suprasutural spiral cord and two weaker spiral cords above it, and with weak axial ribs. Adult whorls sculptured with 4 spiral cords and 14 strong axial ribs forming small beads at crossover points and producing cancellate pattern. Body whorl elongate, more than one-third shell length, constricted at aperture and more at siphon; body whorl sculptured with about 10 flattened spiral cords and 14 weak axial ribs. Aperture ovate, constricted, not as wide as width of body whorl, narrowing posteriorly and having short, distinct siphonal canal. Columella concave with slight callus. Outer lip of aperture smooth, rounded, thin and pendant, extending beyond siphonal canal. Periostracum thin, tan.

Animal: Snout, cephalic tentacles, and neck slender, extremely long and extensible. Snout bilobed at tip. Foot narrow, extremely elongate anteriorly, three times snout length, and with crescent-shaped propodium (Fig. 2). Deep crescentic transverse slit formed by two lips in anterior foot and leading via a central duct into large anterior mucus gland (Fig. 11A, amg). Corners of anterior pedal lips extending laterally and posteriorly forming unciliated undulating epipodial skirt (Fig. 11A-B, es) delineating lateral groove between epipodium and sole; epipodial skirt weakly scalloped posteriorly (Fig. 2), forming lanceolate opercular lobe, scalloped around edges. Ciliated gutter (Fig. 11B, cg) in both sexes emerging from floor of right side of pallial cavity, running down right side of foot leading into epipodial groove. Ciliated gutter terminating in small glandular ovipositor (Fig. 11B, ovp) at edge of foot in females. Posterior third of sole with median longitudinal slit leading into massive mesopodial mucus gland (Fig. 11A, mmg), extending deeply into head foot up to nerve ring and cephalic hemocoel. Operculum (Fig. 10F, G) corneous, light tan, circular-ovate, paucispiral with subcentric nucleus. Mantle edge (Fig. 11B, me) bilobed, smooth,

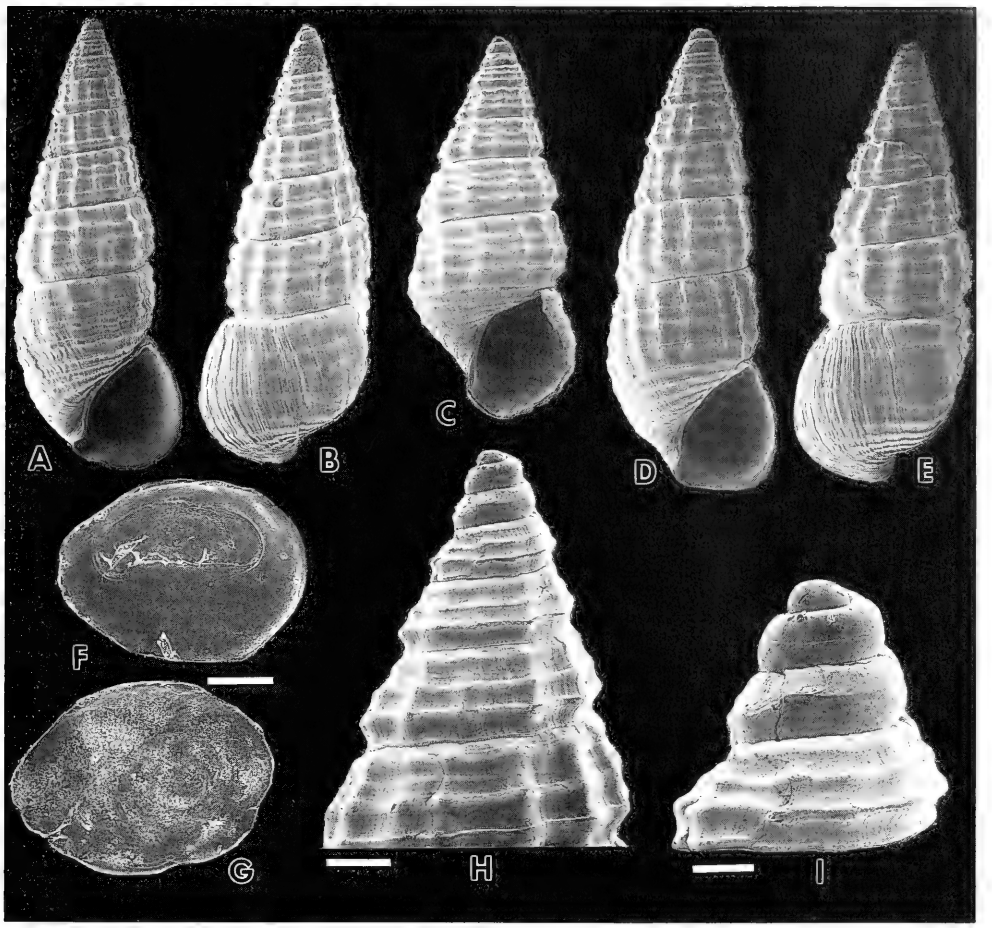

FIG. 10. SEM micrographs of *Bittiolum varium* from Ft. Pierce, Florida (USNM 77639). A, B, D, E, two shells showing sculptural variation and shell shape; length 3.2 mm; C, immature shell, length 2.8 mm; F, G, operculum, bar = 0.2 mm; H, sculpture of early whorls, bar = 0.3 mm; I, protoconch, bar = 88 μm.

without papillae, slightly scalloped, iridescent at edges.

Pallial Cavity: Osphradium wide, one-third ctenidial length, weakly monopectinate, comprising small, dorsally placed pectins, flanked on each side by weak ciliated strip. Ctenidium comprising long, triangular filaments with soft rods and mucus glands.

Alimentary System: Radula (Fig. 11C) short. Rachidian tooth (Fig. 11D) with cutting edge of 3 small denticles on each side of central cusp. Lateral tooth (Fig. 11D) with two outer and 3–4 inner denticles. Inner marginal tooth with 3–4 inner and 2–3 outer denticles. Outer marginal tooth with 6 small inner denticles. Midesophagus with wide ciliated dorsal food groove; posterior esophagus narrow.

Nervous System: Cerebral ganglia slightly larger than pedal ganglia and with short connective (about one-third cerebral ganglion length). Pedal ganglia nearly fused at connective, each with posterior statocyst; two pairs of accessory pedal ganglia present: pair of small propodial ganglia, and larger pair of metapodial ganglia. Subesophageal connective between subesophageal ganglion and left pleural ganglion equal in length to left pleural ganglion; supraesophageal connective about equal in length to subesophageal connective.

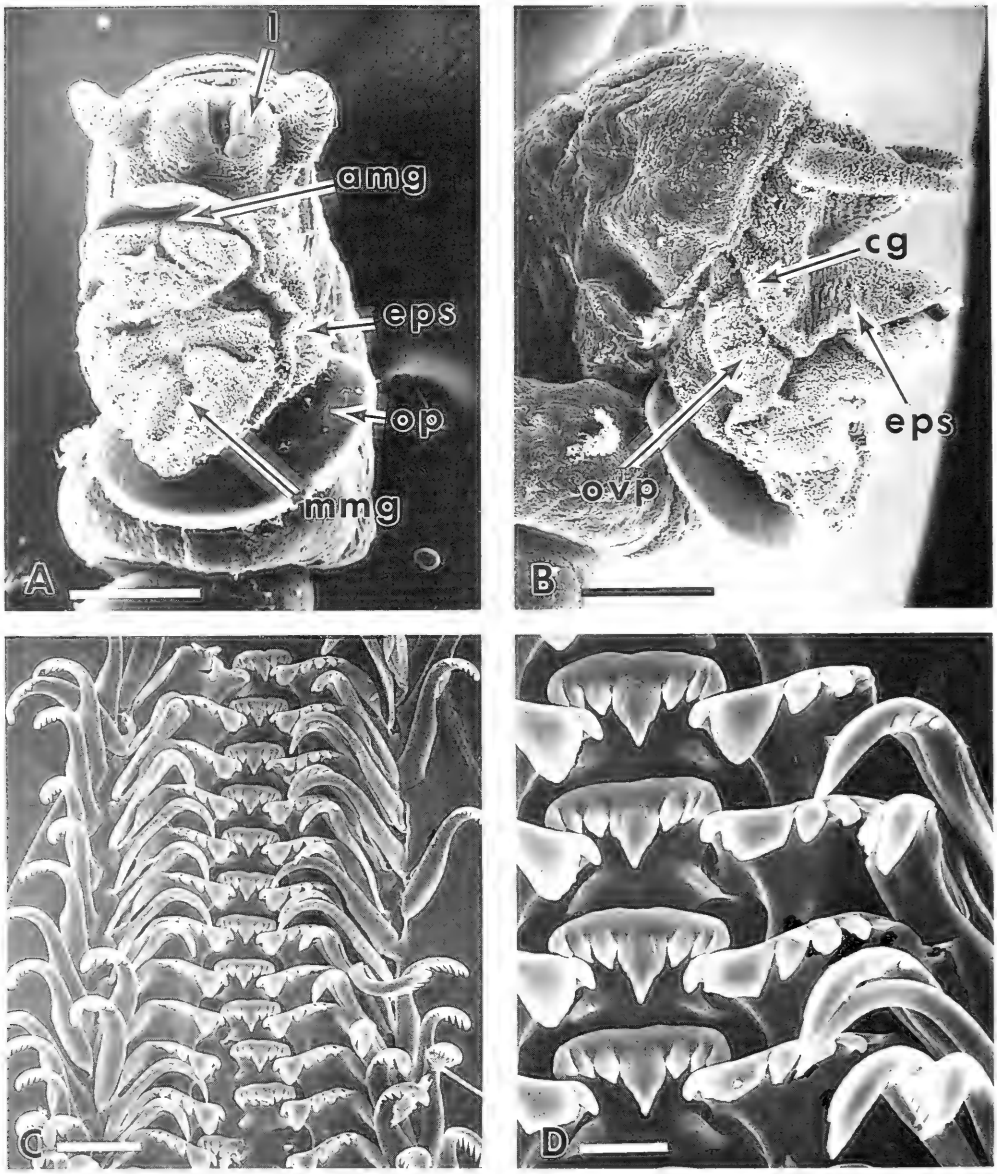

FIG. 11. SEM micrographs of *Bittiolum varium* from Ft. Pierce, Florida (USNM 776639). A, B, critical point dried specimens showing external anatomical features of headfoot, bar = 0.2 mm; C, mid-section of radula, bar = 21 μm; D, detail of rachidian and lateral teeth, bar = 7 μm. amg = anterior mucus gland; cg = ciliated groove; eps = epipodial skirt; l = lip of mouth; mmg = metapodial mucus gland; op = operculum; ovp = ovipositor.

Right zygoneury between subesophageal and right pleural ganglion.

Reproductive System: Ducts of testicular follicles joining to form spermatic duct, moving anterior as seminal vesicle, containing dimorphic sperm. Males producing crescent-shaped spermatophore with flared bifurcate end and pointed, filamentous tip. Spermatophores containing both eu- and parasperma-

tozoa. Ovary cream colored, overlying brown digestive gland, extending forward to stomach. Pallial oviduct open, but closed in far posterior portion. Common aperture to opening of spermatophore bursa in lateral lamina anterior to opening of sperm pouch and opening of seminal receptacle located on edge of medial lamina one-third from posterior of lamina. Opening to spermatophore bursa not adjacent to opening on medial lamina, but located one-third back from anterior of lateral lamina. Spermatophore bursa comprising ciliated and high vacuolated epithelial cells. Spawn mass composed of spirally wound thin jelly string containing many small eggs 100–120 μm in diameter, hatching as veliger larvae, becoming planktotrophic.

Bittiolum alternatum (Say, 1822)

Turritella alternata Say, 1822: 243.
Pasithea nigra Totten, 1834: 369, figs. 7a, b.
Bittium nigrum (Totten), Gould, 1870: 321, fig. 590.
Bittium alternatum (Say), C. W. Johnson, 1915: 127.
Diastoma alternata (Say), Abbott, 1974: 107, fig. 1037.

Description

This species is essentially the same as *Bittiolum varium,* described above, although the shell differs slightly in being more pupoid and less narrowly elongate.

Remarks

Marcus & Marcus (1963) thoroughly described the anatomy of *Bittiolum varium* in Brazil. My work on populations of this species from Florida basically confirms their detailed observations. In addition, the basic anatomy of the Brazilian and Florida specimens is very similar to that of *Bittiolum alternatum* from the American northeastern coast, suggesting that the latter is probably a sister taxon of *Bittiolum varium.*

Bittiolum is the only genus studied in which the mantle edge is smooth, with no trace of papillae, a character noted by Marcus & Marcus (1963). A wavy epipodial skirt and narrowly elongate anterior foot are also distinctive external features (Fig. 2) of both examined *Bittiolum* species. The ovipositor (Fig. 11B, ovp) is barely visible only during the breeding season, but is basically the same as that observed in *Bittium.* The massive metapodial mucus gland located in the posterior part of the sole differs from that seen in *Ittibittium* species, in which the slit is much longer. This gland secretes a string of mucus by which the animal can suspend itself in the algae, but the thread does not have the tensile strength of the mucous threads produced by members of the Litiopidae (Houbrick, 1987b). Except for major differences in external features, the radula and internal anatomy of *Bittiolum varium* is quite similar to that of *Bittium reticulatum.* The radula differs only minor details (Table 2). Although *Bittiolum varium* primarily is a grazer of epiphytic microalgae, Marcus & Marcus (1963: 79) have shown that the snail can use its anterior ctenidial filaments for particle feeding while stationary.

Marcus & Marcus (1963: 88–89) found four spindle-shaped spermatophores, each 1 mm long and 0.06 mm wide, in the bursa of the lateral lamina in *Bittiolum varium,* and noted that the spermatophores dissolve in this bursa. The location of the spermatophore bursa in the lateral lamina is a unique feature among cerithioidean taxa, and this layout is probably the same among other members of the *Bittium*-group, in which the bursa in the lateral lamina has been confirmed. However, spermatophores have not been observed in this bursa in any other species.

Bittiolum varium lays its eggs mostly on seagrasses. In the Indian River, Florida, I observed numerous irregular egg masses comprising strands of eggs embedded in a loose jelly matrix deposited on *Halodule* grass blades and on ramose algae. In the spring, nearly all adults were ripe and egg laying continued through the summer months tapering off in September.

Bittiolum varium has been the subject of a number of ecological investigations. Virnstein & Curran (1986) measured the colonization time of this species in seagrasses in the Indian River, Florida. Hardison & Kitting (1985) found that *Bittiolum varium* fed primarily on diatoms and coralline algae in seagrass meadows of the northwest Gulf of Mexico. Despite the high population densities of this snail (3,000/m^2), little impact on its food could be detected. In Chesapeake Bay, Van Montfrans et al. (1982) found that the grazing activities of *Bittiolum varium,* which selectively eats diatoms from blades of marine grasses,

could have important implications for the abundance and distribution of *Zostera*.

Bittiolum varium has a wide range in the western Atlantic, occurring from Chesapeake Bay south to Florida and the Gulf of Mexico, throughout the Caribbean, and south to Brazil.

STYLIDIUM DALL, 1907

Stylidium Dall, 1907: 178 (Type species by original designation: *Bittium eschrichtii* Middendorf, 1849). Thiele, 1929: 211; Wenz, 1940: 757; Abbott, 1974: 106.

Diagnosis

Shell relatively large, dirty chalky white, smooth, weakly sculptured with four broad spiral cords defined by incised lines. Protoconch unsculptured. Snout twice length of cephalic tentacles. Epipodial skirt poorly developed, smooth along edges, but opercular lobe with small, pointed papillae. No metapodial mucus gland. Osphradium non-pectinate. Common aperture to sperm bursa and seminal receptacle in edge of anterior third of medial lamina of pallial oviduct. Openings to sperm bursa and seminal receptacle well-separated. Long ciliated ridge tract in lateral lamina of pallial oviduct. Development direct.

Remarks

This genus is represented by species living in cold-water habitats from California north to Alaska. The shell is dull and chalky under the periostracum. Shell length can be quite large (Table 3) for a member of the Bittiinae, and the large smooth protoconch, without sinusigeral notch, is indicative of direct development.

At first glance, the shell of *Stylidium* does not appear to fit the *Bittium*-group mold. However, anatomical features, such as the epipodial skirt, large opercular lobe (Fig. 2) and pallial gonoduct configuration unmistakably place it into the Bittiinae. The common aperture to sperm pouch and seminal receptacle is unusual in being located in the far anterior edge of the medial lamina of the palial oviduct, and not adjacent to the opening of the spermatophore bursa of the lateral lamina. The length of the ciliated ridge tract of the lateral lamina is also atypical.

Stylidium eschrichtii (Middendorff, 1849) (Figs. 12–14)

Turritella eschrichtii Middendorf, 1849: 396–397, pl. 11, fig. 1 (Holotype, Zoological Institute, St. Petersburg; type locality, Sitka, Alaska).

Bittium (Stylidium) eschrichtii icelum Bartsch, 1907: 178 (Holotype USNM 15209a; type locality, Neah Bay, Washington); 1911: 388, pl. 57, fig. 3; Ruhoff, 1973: 81.

Bittium eschrichtii (Middendorf). Oldroyd, 1927: 18–19, pl. 79, fig. 4.

Bittium (Stylidium) eschrichtii (Middendorf). Abbott, 1974: 106, fig. 1010.

Description

Shell (Fig. 12): Shell large, turreted, reaching 17.5 mm in length, comprising 9–11 convex whorls. Protoconch (Fig. 12G) has two smooth whorls. Early whorls (Fig. 12E-G) sculptured with three spiral bands. Adult whorls sculptured with 4 weak, widely flattened spiral bands separated from one another by deep incised spiral grooves. Penultimate whorls with 5 wide, spiral, weak bands. Suture well defined, slightly counter-sunk into each abapical whorl. Body whorl a little less than one-third shell length, sculptured with about 8 broad spiral cords and incised lines. Shell base weakly constricted at base; anterior siphon broad and shallow. Aperture ovate having concave columella with weak callus; outer lip of aperture circular, crimped where spiral grooves end. Shell color chalky white-gray, covered by thin tan periostracum.

Animal: Base color dirty white with transverse black stripes on snout, head, and epipodium (Fig. 14A). Ciliated epithelial strip running from mantle cavity floor on each side of headfoot and ending beneath peduncle of each cephalic tentacle. Ciliated gutter on right side of foot in females ending in small pink, glandular ovipositor at foot edge. Snout very long, twice length of cephalic tentacles, wide, bilobed at tip. Eyes very small. Lateral epipodial skirt with minute pointed papillae along edge of posterior third of foot; opercular lobe long, pointed posteriorly, darkly pigmented and with small pointed papillae along edge (Fig. 2). Anterior foot crescent-shaped with long slit along edge leading into centrally placed, ovate mucus gland deep within propodium. No metapodial mucus gland. Operculum (Fig. 12H, I) thick, ovate, paucispiral, with eccentric nucleus. Mantle edge bilobed, with small papillae, and with slightly elongate exhalant siphon. Mantle roof folded longitudinally over exhalant siphon forming dorsal, posteriorly extending ridge.

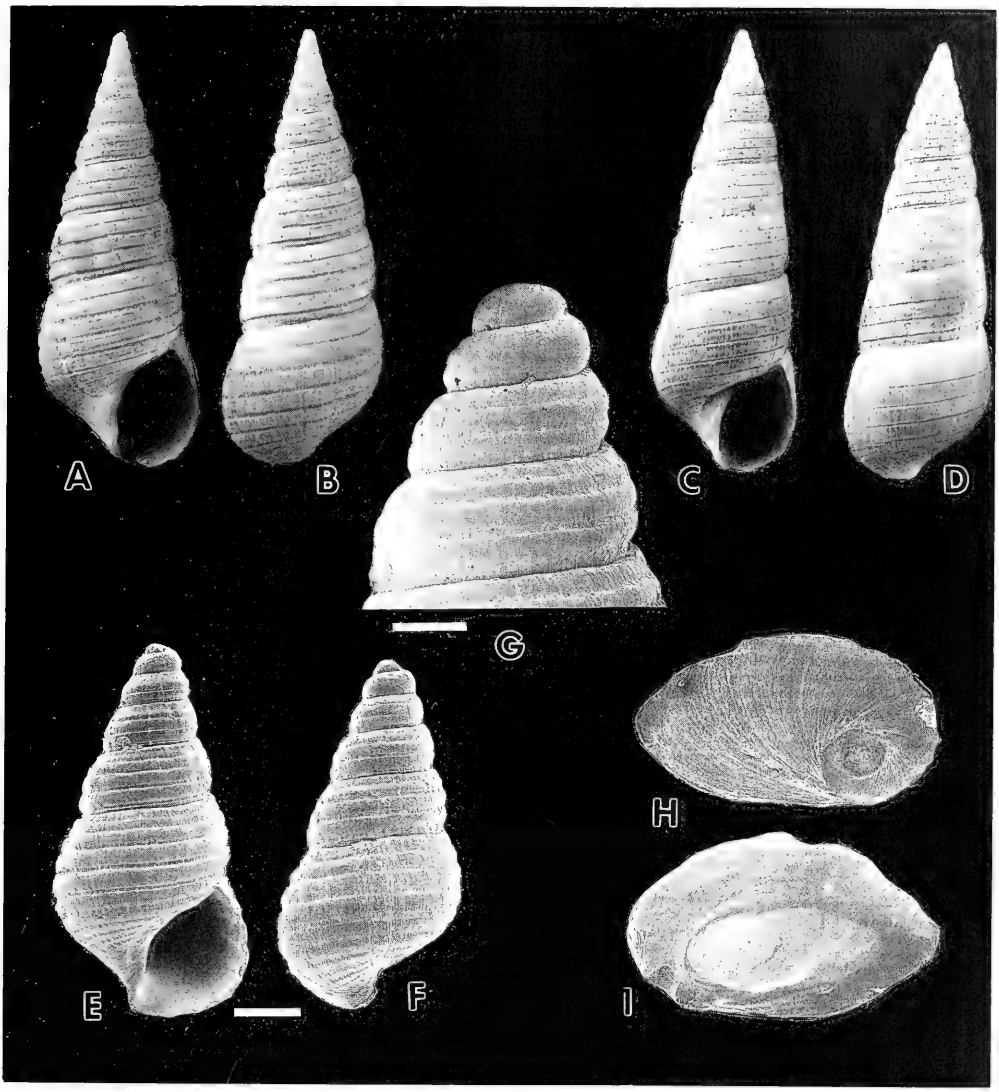

FIG. 12. *Stylidium eschrichtii* from Carmel, California. A–D, two shells showing sculptural variation (USNM 804376), 22.4 and 20.2 mm length, respectively; E, F, SEM micrographs of immature shells showing early sculptural patterns, bar = 0.5 mm; G, SEM micrograph of protoconch and early whorls, bar = 0.3 mm; H, I, SEM micrographs of operculum, showing eccentric nucleus and attachment scar, 2.4 mm length.

Pallial Cavity: Osphradium tan, vermiform, non-pectinate, extending length of pallial cavity, but slightly shorter than ctenidium. Ctenidium pink, comprising long, finger-like filaments twice length of their attached bases.

Alimentary System: Radular ribbon (Fig. 13A) short. Lateral tooth (Fig. 13B) with long lateral basal extension and cutting edge with 3 inner denticles, and 3–5 outer denticles; inner marginal tooth with 4–5 inner and 3 outer denticles. Paired salivary glands vermiform, loosely compacted, lying mostly anterior to nerve ring, but beginning behind it as thick swellings, and passing through as thin tubes. Stomach large, about one whorl in length; internally with large sorting area and roundish central pad; single opening to digestive gland on right side of pad; 6–7 large transverse ribs

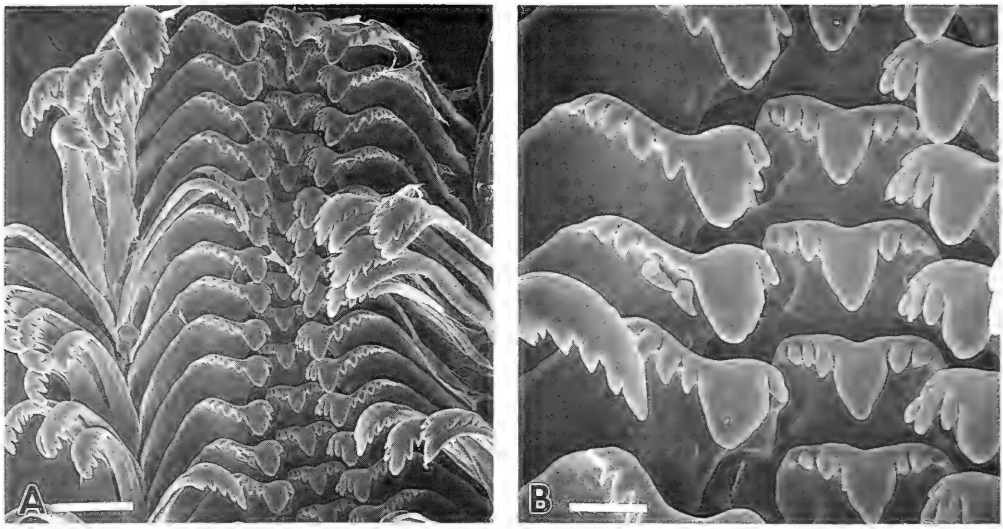

FIG. 13. SEM micrographs of radula of *Stylidium eschrichtii* (USNM 804376); A, section of mid-radular ribbon with marginal teeth folded back, bar = 38 μm; B, detail of rachidian and lateral teeth, bar = 12 μm.

on left side of pad, posterior to cuticular gastric shield; short, wide style sac one-half stomach length, separate from intestinal opening. Intestine opening separated from lumen of style sac by typhlosole ridge.

Nervous System (Fig. 14): Nerve ring large with thick commissure connecting cerebral ganglia. Dialyneury (Fig. 14B, d) between left pallial nerve and nerve arising from supraesophageal ganglion. Supraesophageal connective (Fig. 14A, sec) twice length of right pleural ganglion. Subesophageal ganglion (Fig. 14A, sbe) closely adjacent to left pleural ganglion.

Reproductive System Posterior half of pallial oviduct with thick, white, opaque albumen gland comprising flocculant transverse glandular ridges; mid-section of pallial oviduct with thin, weak glandular transparent walls; very thick, opaque transverse glandular ridges present in anterior third of pallial oviduct, comprising capsule gland. Sperm gutter in anterior edge of medial lamina having elongate common aperture to spermatophore bursa and seminal receptacle. Openings to sperm pouch and seminal receptacle within common aperture well separated. Long tube within edge of medial lamina leading to posteriorly placed pouch-like seminal receptacle. Large sperm pouch with internal transverse epithelial folds, occupying posterior third of medial lamina. Very long ciliated ridge tract beginning in anterior part of lateral lamina, leading into posterior spermatophore bursa. Spawn comprising thin gelatinous string wound into irregular mass. Eggs 0.2 mm in diameter. Development direct.

Remarks

Several subspecific taxa have been described, but it is debatable if all of these nominal taxa are good subspecies or merely clinal/ecophenotypic varieties of *Stylidium eschrichtii*. Abbott (1974) synonymized the subspecies *icelum* Bartsch with *S. eschrichtii*.

Stylidium eschrichtii is characterized by its chalky gray, smooth shell sculptured with broad flattened spiral cords. The protoconch is large, unsculptured, and lacks a sinusigeral notch (Fig. 12G). The ovate operculum (Fig. 12H, I) with eccentric nucleus is a departure from a more circular operculum with subcentral nucleus, as seen in other bittiid species. Shell length seems to vary greatly among populations, but some individuals can be very large, approaching 18 mm length (Table 3). Large shell size appears to be more common in northern populations.

This species lives on intertidal to subtidal rubble in cool waters of the northeastern Pacific. I observed a large intertidal population living among the intertices of gravel and algae

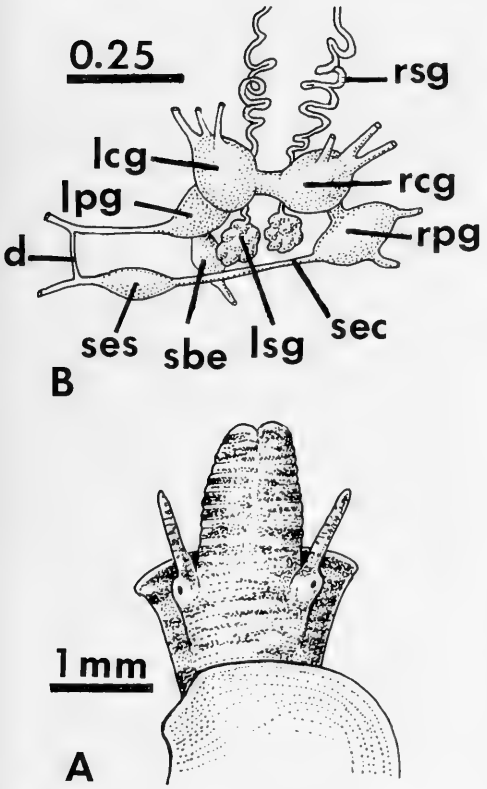

FIG. 14. Anatomical features of *Stylidium eschrichtii.* A, head and anterior foot, showing pigment pattern; B, position of salivary glands relative to nerve ring. d = left dialaneury; lcg = left cerebral ganglion; lpg = left pleural ganglion; lsg = left salivary gland; rcg = right cerebral ganglion; rsg = right salivary gland; rpg = right pleural ganglion; sbe = subesophageal ganglion; sec = supraesophageal connective; seg = supraesophageal ganglion.

at Carmel, California. According to Strathmann (1987), *Stylidium eschrichtii* has direct development. Spawn is deposited on the substrate in gelatinous masses (presumably comprising coiled strings) containing egg capsules measuring 0.2 μm diameter in which the embryos undergo direct development, passing through the veliger stage and hatching as small snails.

LIROBITTIUM BARTSCH, 1911

Lirobittium Bartsch, 1911: 384 (Type species by original designation, *Bittium catalinensis* Bartsch, 1907). Thiele, 1929: 211; Wenz, 1940: 757; Abbott, 1974: 106; Gründel, 1976: 54.

Diagnosis

Shell turreted, elongate, sculptured with axial riblets and spiral beaded cords. Protoconch with two spiral lirae. Varices not present on adult whorls. Operculum circular. Radular ribbon very small; radular teeth with many small denticles. Snout long; head with small cephalic tentacles and small eyes. Ovipositor and ciliated groove on right side of foot absent. Mantle edge with long papillae. Epipodial skirt very weakly developed. Osphradium vermiform, wide. Spawn comprising large egg capsules, each attached to long stalk and anchored together. Development direct.

Remarks

Bartsch (1911) divided *Bittium*-group species from the American west coast into four genera: *Bittium, Lirobittium, Semibittium,* and *Stylidium.* His groups were defined only on superficial shell characters, such as the presence or absence of varices, protoconch sculpture, and axial and spiral sculpture. Many of the species Bartsch (1911) included under his generic scheme have been ignored or referred by subsequent authors to different generic taxa.

The genus *Lirobittium* Bartsch, from the temperate eastern Pacific, was based on minor shell sculptural characters: Bartsch (1911: 384) noted that the defining characters of *Lirobittium* were a protoconch with two spiral lirae and the absence of varices from the adult whorls. These features were also mentioned by Gründel (1976: 54), who additionally noted that of the two primary spiral cords, the abapical one was inserted a little later. Gründel (1976: 54–56) assigned *Cacozeliana* and *Stylidium* (with a query) as subgenera of *Lirobittium.* He indicated that *Cacozeliana* differed from *Lirobittium* by the formation of varices, and *Stylidium* by the suppression or complete absence of axial ribs. It has been shown herein that the *Cacozeliana* is separated from *Lirobittium* by many significant characters.

The above history of *Lirobittium* shows that much of the confusion regarding the placement of the numerous California species stems from the original superficial generic descriptions based solely on shell morphology. It is obvious that the characters derived by these authors from minor sculptural details hardly seem to be of generic weight and have

resulted in poorly defined, ambiguous genera with broad or discordant limits, and that have been used in varying combinations. Although shell sculpture may have some value at the specific level, it is generally not useful at the generic level, especially in cerithiids. Not a single author has included radular or opercular characters and no mention is made of anatomical features in the definition of genera.

Abbott (1974: 106) considered both *Bittium catalinense* and *B. subplanatum* to be synonyms of *Lirobittium attenuatum* Bartsch, 1911, but gave no reasons for this decision. Hertz (1981: 40) showed that *Lirobittium subplanatum* (cited as *Bittium*) was a valid species. I have examined two species of *Lirobittium: L. catalinense* (one dried specimen) and well-preserved material of *L. subplanatum*. Observations on the poorly preserved, dried animal of *L. catalinense* are included because it is the type species of the genus, but the bulk of the descriptive anatomical characters of *Lirobittium* are derived from study of *L. subplanatum*. The two species are anatomically very similar, have similar radulae, and are undoubtedly congeneric. The above diagnosis and following specific descriptions represent an integrated analysis of generic characters, based on these two species.

Lirobittium catalinense Bartsch, 1907

Bittium catalinensis Bartsch, 1907: 28, pl. 57, fig. 13 (Holotype: USNM 165232, type locality: Santa Barbara, California [Pleistocene]); Abbott, 1974: 106, fig. 1013.
Bittium (Lirobittium) catalinense Bartsch, 1911: 402–403, pl. 51, fig. 1.

Remarks

The type species of this genus is a Pleistocene fossil, but Bartsch (1911) described many subspecies, some of which are Recent. *Bittium cataliense* is now regarded as a synonym of *"Bittium" attenuatum* Carpenter, 1864 (Abbott, 1974: 106).

Examination of a reconstituted, dried specimen of the type species of *Lirobittium, Bittium catalinense* (= *Bittium attenuatum*), showed that the animal is basically the same as *Lirobittium subplanatum*. It is relatively unpigmented, has a large, broad snout, bilobed at the anterior end and short cephalic tentacles, about half the snout length. The mantle edge has many long papillae along its dorsal and lateral sides, while the mantle edge forming the inhalant siphon has large paddle-shaped papillae. The buccal mass is small, and the radula minute, about one-thirteenth the shell length. The rachidian tooth has a triangular basal plate with a long glabrella and is as wide as tall; there is a deep concave indentation and a cutting edge with a long pointed central cusp flanked on each side by 4–5 small denticles. The lateral teeth are deeply concave on the top, have a wide basal plate with a large central buttress, and have numerous small denticles. The marginal teeth are slender, and serrated along their tips with many small pointed denticles (Fig. 15).

Lirobittium subplanatum (Bartsch, 1911) (Figs. 15–17)

Bittium (Semibittium) subplanatum Bartsch, 1911: 395–396, pl. 57, fig. 5 (Holotype, USNM 160076; type locality, Catalina Id., California); Oldroyd, 1927: 23: Ruhoff, 1973: 130.
Bittium subplanatum Bartsch. Dall, 1921: 146; Hertz, 1981: 40, figs. 23–27.
Bittium subplanatum Bartsch. Oldroyd, 1927: 23.
Bittium (Lirobittium) subplanatum (Batsch). Abbott, 1974: 106.

Description

Shell (Fig. 15): Shell elongate, turreted, comprising 8–9 moderately inflated whorls. Protoconch (Fig. 15) about 1.5 whorls, well rounded, smooth. Early whorls sculptured with two major spiral lirae, soon crossing over axial riblets (Fig. 15). Adult whorls sculptured with three major spiral cords crossed over by numerous thin axial ribs (24–26), forming cancellate appearance; small beads occurring at crossover points. Body whorl (Fig. 15) sculptured with four major spiral cords and numerous axial ribs; moderately constricted at base. Shell base with about 7 spiral cords. Aperture ovate with oblique columella and curved, thin outer lip. Anterior canal moderately developed; anal canal weak. Shell color white, covered with brown periostracum.

Animal (Fig. 16A, B): Animal pure white with pink buccal mass showing through snout. Head large with very large, wide, extensible snout, dorso-ventrally flattened, bilobed at tip; cephalic tentacles small, a little less than one-third snout length, each with small black eye adjacent to opaque white spot at tentacular peduncular base. Snout ringed with many

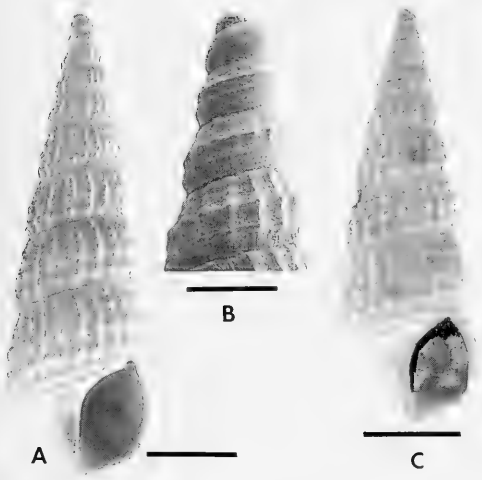

FIG. 15. SEM micrographs of shells of *Lirobittium subplanatum* from Palos Verdes, California (USNM 881021). A, bar = 1.8 mm; B, detail of protoconch and early teleoconch sculpture, bar = 0.6 mm; C, bar = 1.8 mm.

deep, transverse epithelial folds (Fig. 16B). Foot with very weak epipodial skirt and without papillae or distinctive operculiferous lobe. No ciliated groove on right side of foot; no ovipositor. Anterior of sole crescent shaped with deep transverse slit marking entrance to anterior mucus gland. No metapodial mucus gland. Mantle edge bilobed, fringed with many papillae emerging from ventral side of mantle edge.

Pallial Cavity: Osphradium brown, vermiform, without pectins, wide, about one-third the ctenidial width, nearly equaling ctenidial length. Ctenidium extending length of pallial cavity. Hypobranchial gland thick, comprising transversely ridged glandular tissue.

Alimentary System: Mouth at tip of snout, defined by pair of fleshy pads. Buccal mass (Fig. 16B, bm) pink, small, about one-third snout length.

Radular ribbon (Fig. 17) small, about one-ninth shell length. Rachidian tooth (Fig 17C) with large glabrella, long serrated central cusp and 6 small denticles on each side. Lateral tooth (Fig. 17 B,C) with broad basal plate; cutting edge has large denticle with 6 inner denticles and 15–17 outer denticles. Marginal teeth (Fig. 17D) long, curving; inner marginal tooth with 15–19 inner denticles, large central cusp and 5–6 outer denticles; outer marginal tooth same, but lacking outer denticles.

Stomach with central pad, gastric shield, short style sac and crystalline style; one opening to digestive gland.

Nervous System: Cerebral ganglia joined by short connective. Pleural ganglia close to cerebral ganglia; left pleural ganglion connected to subesophageal by very short connective. Supraesophageal connective about two-thirds length of right pleural ganglion.

Reproductive System (Fig. 16A): Testis white, producing dimorphic sperm; ovary cream-yellow containing large ova, 0.5 mm in diameter. Glandular portion of female pallial oviduct comprising many transverse folds, posterior opaque white portion comprising albumen gland (Fig. 16A, ag), and anterior, transparent greyish-white portion comprising capsule gland (Fig. 16A, cg). Anterior two-thirds of edge of medial lamina with large sperm gutter (Fig. 16A, sg) leading into deep slit containing two openings: anterior opening (Fig. 16A, osp) into large sperm bursa and posterior opening (Fig. 16A, osr) into small tubular sac-like seminal receptacle (Fig. 16A, sr). Lateral lamina less glandular than medial lamina and with short ciliated ridge tract (Fig. 16A, crt) leading into opening of spermatophore bursa (Fig. 16A, osb), adjacent to openings on medial lamina. Spermatophore bursa (Fig. 16A, sb) small, elongate, sac-like.

Discussion

Bartsch (1911) assigned this species to the subgenus *Semibittium,* and his assignment was followed by Dall (1921), Oldroyd (1927), and Hertz (1981). *Semibittium* is shown herein to comprise a group of Eocene fossils probably related to the extant Australian monotypic genus *Cacozeliana,* which differs considerably in anatomy from the California species. Abbott (1974) transferred this species, which he considered a synonym of *Bittium attenuatum* Carpenter, 1864, to *Lirobittium,* but gave no reasons for doing so.

The shell is of moderate size (Table 3) and has a large protoconch sculptured with two spiral lirae and lacking a sinusigeral notch. Although the shell of *Lirobittium subplanatum* does not resemble that of *Stylidium eschrichtii,* the anatomical features of the two species are quite similar. As far as can be seen in preserved material, *Lirobittium subplanatum* appears to have a very weak epipodial skirt, but closer examination of living animals may show that this character is com-

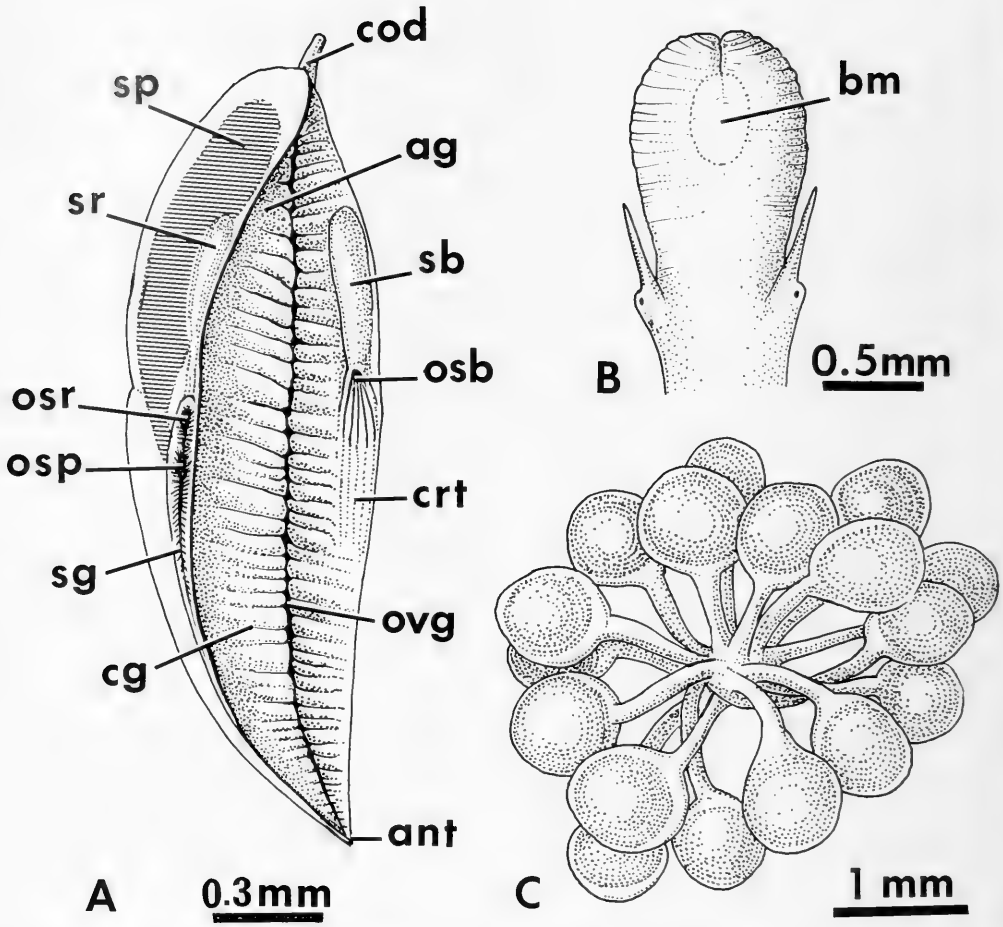

FIG. 16. *Lirobittium subplanatum.* A, pallial oviduct, spread open to reveal details; B, head, showing broad snout, short cephalic tentacles and small buccal mass; C, dorsal view of attached spawn mass, showing individual capsules with enclosed embryos and attachment strands. ag = albumen gland; ant = anterior of pallial oviduct; bm = buccal mass; cg = capsule gland; cod = coelomic oviduct; crt = ciliated ridge tract; osp = opening to sperm pouch; osb = opening to spermatophore bursa; ovg = oviductal groove; sb = spermatophore bursa; sg = sperm groove; sp = sperm pouch; sr = seminal receptacle.

pletely absent. The operculum also differs in being more typically rounded than that of *Stylidium.*

The radula of *Lirobittium subplanatum* (Fig. 16) is very similar to that of *Lirobittium attenuatum,* but differs in having many more denticles on the teeth. The exact dentition formula is given in Table 2.

There has apparently been some difficulty in identifying this species, as it has been considered synonymous with a number of other sympatric species, but Hertz (1981) has shown that it is a distinct, valid species. As mentioned above, the radula is distinct.

Lirobittium subplanatum lives offshore on sandy-rubble bottoms. The shell is frequently severly eroded and abraided.

Spawn morphology of *Lirobittium* is unique among Bittiinae (Fig. 17C) and is deposited on pieces of rubble or empty shells. It comprises clusters of large egg capsules, each about 0.5 mm in diameter and containing one embryo. Each egg capsule is connected by a strand to a central attachment point so that the spawn mass looks like a group of small balloons with their strings attached together. Embryos revolve slowly with their capsules, where they pass through the veliger stage,

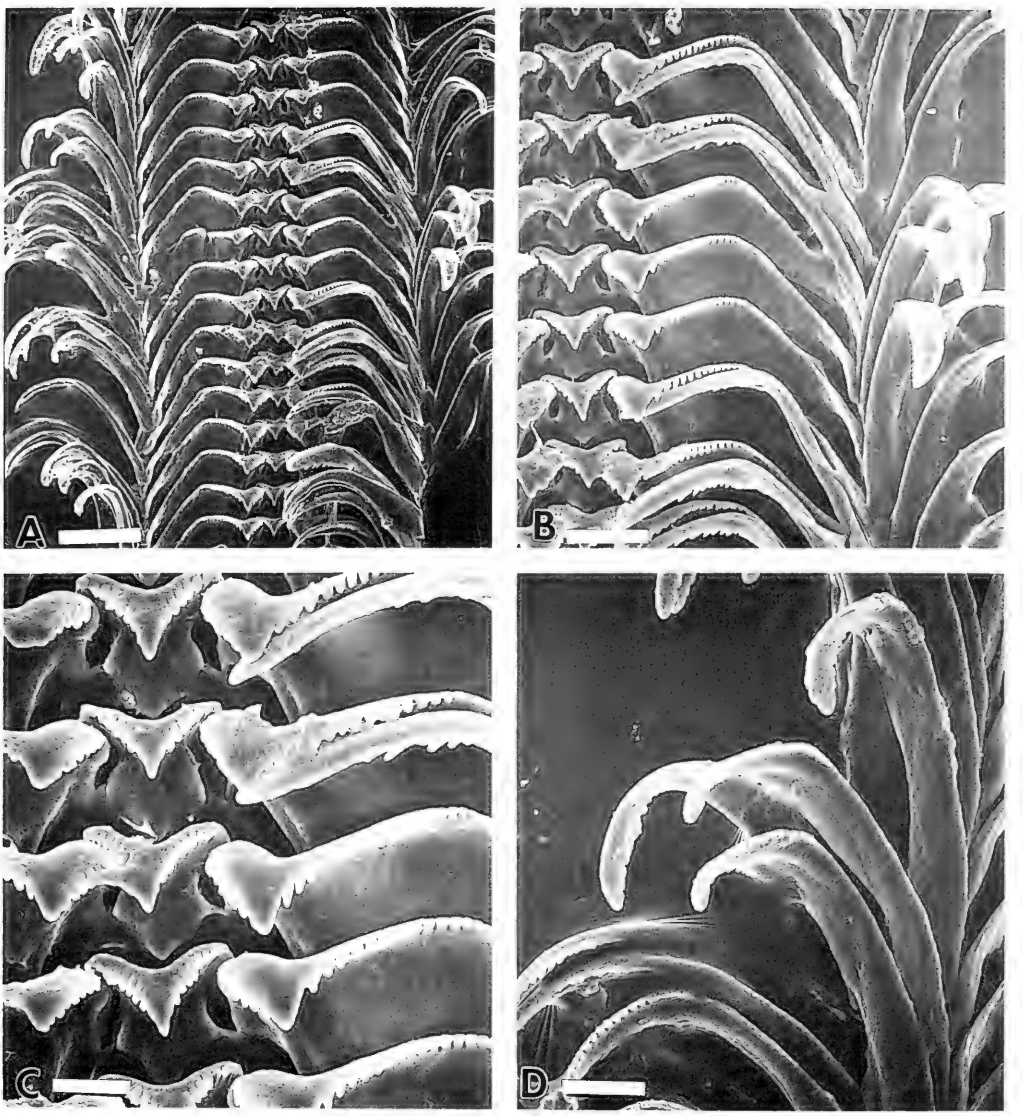

FIG. 17. SEM micrographs of radula of *Lirobittium subplanatum* (USNM 881021). A, radular ribbon with marginal teeth spread open, bar = 35 μm; B, half row showing rachidian and lateral teeth, bar = 19 μm; C, detail of dentition of rachidian and lateral teeth, bar = 10 μm; D, detail of dentition of marginal teeth, bar = 12 μm.

finally hatching out as small snails. Development is direct (pers. obs.).

CACOZELIANA STRAND, 1928

? *Semibittium* Cossmann, 1896: 29 (Type species by original designation: *Cerithium cancellatum* Lamarck, 1804; not *Semibittium* Bronn, 1831; nor Lea, 1842; nor Tuomey, 1848; nor J. de C. Sowerby, in Dixon, 1850). Thiele, 1929: 211; Wenz, 1940: 756; Gründel, 1976: 56–57.

Cacozelia Iredale, 1924: 246 (Type species by monotype: *Cerithium lacertinum* Gould, 1861); not *Cacozelia* Grote, 1878 [Lepidoptera]. Thiele, 1929: 211; Murray, 1969: 111.

Cacozeliana Strand, 1928: 66 (new name for *Cacozelia* Iredale, 1924). Wenz, 1940: 756.

Lirobittium (*Cacozeliana*) Strand. Gründel, 1976: 54–55.

Diagnosis

Shell large, elongate with many weakly inflated whorls, sculptured with four beaded spiral cords per whorl and having overall pustulose appearance. Protoconch unsculptured except for microscopic subsutural pustules, but large sinusigeral notch present (Fig. 18F). Operculum circular-ovate, paucispiral with subcentric nucleus and fringed edges. Epipodial skirt with smooth edges. Snout short, narrow. Opercular lobe lanceolate and with longitudinal median groove. Large ovipositor gland on right side of foot. Osphradium bipectinate. Salivary glands anterior to nerve ring. Rachidian tooth without glabrella. Openings to sperm bursa and seminal receptacle well separated. Seminal receptacle comprising several grape-like lobes.

Remarks

The genus *Cacozelia* was proposed by Iredale for *Cerithium lacertinum* Gould, a subjective synonym of *Cerithium granarium* Kiener. The living Australian species is thought to be congeneric with the Paris Basin Eocene species *Cerithium cancellatum* Lamarck, which is the type species of *Semibittium* Cossmann; however, as *Cacozelia* is a junior homonym, the name *Cacozeliana* was subsequently proposed by Strand (1928) as a replacement. The allocation of *Cacozeliana* as a subgenus of *Liocerithium* by Gründel (1976) was made on the observation that in *Cacozeliana,* the fourth primary spiral cord is initially weaker than the three formed earlier, whereas in *Liocerithium* all four are equally strong. Gründel (1976) also pointed out that varices are present in the subgenus, whereas they are absent in *Lirobittium.* These minor sculptural differences hardly seem appropriate as generic-level characters; furthermore, radular and anatomical characters of *Cacozeliana* show that it is far-removed from *Lirobittium.*

The type species of *Semibittium,* which is placed into synonymy with *Cacozeliana* with a query, is an Eocene fossil from the Paris Basin, *Cerithium cancellatum* Lamarck. This fossil species is conchologically very close to *Cerithium granarium* Kiener, the living type species of *Cacozeliana* from southern Australia redescribed herein; however, because the anatomy of the fossil is unknown, it is impossible to declare with confidence that the two species are congeneric. Gründel (1976: 56) considered the Eocene genus *Semibittium* to be separate from *Cacozeliana.* He noted that the shell of *Semibittium* species has a slight varix on the lip of the protoconch followed by an almost simultaneous insertion of the three primary spiral cords. The name *Cerithium cancellatum* Lamarck is preoccupied, and needs a replacement name. Moreover, the name *Semibittium* cannot be used because it is thrice preoccupied. The possibility that *Cacozeliana granaria* is a living survivor of the Eocene genus *Semibittium* represented by *Cerithium cancellatum* should be considered, because several other Tethyan Eocene cerithioidean genera survive among the living Australian molluscan fauna; e.g., *Diastoma* Deshayes, 1850; *Gourmya* Fischer, 1884; *Campanile* Fischer, 1884; and *Plesiotrochus* Fischer, 1878 (Houbrick, 1981b, 1981c, 1981d, 1990b, respectively). It is also notable that *Cacozeliana* falls out at the base of the cladogram (Fig. 1) as the closest taxon to the outgroup. Moreover, *Cacozeliana* is separated from all other *Bittium*-group genera by five non-homoplastic synapomorphies (Fig. 1), further demonstrating its distinctiveness. Gründel's (1976: 56–57) separation of *Semibittium* from *Cacozeliana* was based on the order of the insertion of spiral lirae on the early whorls, but this character has not been shown to be of generic weight, and therefore is not seriously considered herein. If *Cacozeliana* is truly congeneric with *Semibittium,* the genus would date from the Eocene, when the latter was common in the Paris Basin fauna (Cossmann, 1906: 138). *Cacozeliana* is today monotypic and confined to the temperate waters of southern Australia. The type species, *Cacozeliana granaria* (Kiener), undoubtedly has the largest shell of any representative of the subfamily Bittiinae and differs from other species of the group in several ways:

1. The short narrow snout (Fig. 20A) is distinctive, as is the fringed operculum (Fig. 18G).

2. The rachidian tooth of *Cacozeliana granaria* is unique, differing from other Bittiinae members in lacking a glabrella on the basal plate. Additionally, the rachidian tooth lacks concave sides and a strong pair of basal buttresses (Fig. 19B). Moreover, the lateral basal

extensions of the basal plate are nearly absent.

3. The pallial oviduct of *Cacozeliana granaria* (Fig. 20C), while having a typical layout, is unique among known pallial oviducts in the *Bittium*-group in having the seminal receptacle divided into several grape-like lobes (Fig. 20C, sr) and in having a highly developed, swollen anterior capsule gland (Fig. 20C, cg). As pointed out earlier, a grape-like seminal receptacle also occurs in some species of *Cerithium* Bruguière, 1789, *Rhinoclavis* Swainson, 1840, and in *Diala* A. Adams, 1861 (Houbrick, 1971, 1978, 1992, pers. obser.; Ponder, 1991), although this structure in *Diala* is not proven to be a seminal receptacle. This kind of seminal receptacle does not necessarily indicate relatedness among these groups: the bulging, grape-like morphology may be due to the swollen state of the filled seminal receptacle and may represent sexual "ripeness" rather than a distinct morphological character state of the seminal receptacle.

Cacozeliana granaria (Kiener, 1842)
(Figs. 18–20)

Cerithium granarium Kiener, 1842: 72–73, pl. 19, fig. 3 (Holotype MNHNP; type locality, "les côtes de Timor," in error, here corrected and restricted to Albany, Western Australia); G. B. Sowerby, 1855: 879, pl. 184, figs. 225–227; 1865: pl. 19, fig. 135; Kobelt, 1898: 249, pl. 23, fig. 9.

Cerithium lacertinum Gould, 1861: 368 (Holotype USNM 16571; type locality Sydney Harbor, New South Wales, Australia); 1862: 141; G. B. Sowerby, 1866: pl. 18, fig. 128; Tryon, 1884: 155, pl. 30, fig. 100; R. Johnson, 1964: 96, pl. 11, fig. 4.

Bittium granarium (Kiener). Tryon, 1887: 155, pl. 30, fig. 98; Wells, 1984: 30–31.

Synonymic Remarks

Kiener's (1842) name, *granarium,* predates Gould's (1861) *lacertinum.* Examination of the holotypes of both taxa leaves no doubt that the two are conspecific.

Description

Shell (Fig. 18): Shell large, elongate, turreted, reaching 24 mm in length comprising 12–13 nearly flat-sided whorls sculptured with four beaded spiral cords. Protoconch (Fig. 18F) comprising two smooth whorls with weak, microscopic subsutural pustules, no spiral lirae, and with deep sinusigeral notch. Early whorls (Fig. 18H) sculptured with 3 spinosely beaded spiral cords alined to form about 12–13 axial riblets. Adult whorls slightly beveled abapically, defining weak suture. Body whorl one-third shell length, having 6 spiral beaded cords and weakly constricted base. Aperture ovate, small, about one-fifth shell length. Columella concave with weak columellar callus and smooth, rounded outer lip. Anterior canal short, narrow, well defined. Shell color white to tan, blotched with pink to reddish brown and having brown spiral bands with white flecks (Fig. 18C, D). Beads sometimes white (Fig. 18A B). Periostracum light tan, thin.

Animal (Fig. 20): Head, snout and epipodium pigmented tan with chocolate blotches, tiny white spots, and irridescent green. Cephalic tentacles darkly pigmented, having many black spots, slender, elongate, about twice snout length. Snout narrow, short (Fig. 20A, sn) with flared bilobed tip. Mantle edge fringed with very small papillae each bearing white spot. Pair of ciliated strips emerging from mantle floor and running to base of cephalic tentacles on each side of headfoot. Deep ciliated groove running down right side of foot to edge, ending in small flap in males. Ciliated groove in females having thick glandular strips on each side of groove, comprising ovipositor. Epipodial skirt poorly developed, smooth along edge, forming short lanceolate opercular lobe with dorsal longitudinal furrow and without papillae along edge. Crescent-shaped propodial slit at edge of anterior foot leading into deep oval anterior mucus gland (Fig. 20A, amg). Longitudinal fold in middle of sole, but no metapodial mucus gland present. Operculum (Fig. 18G) circular-ovate, paucispiral, with subcentral nucleus. Opercular spiral fringed with thin lamella (Fig. 18G).

Pallial cavity: Osphradium bipectinate, with weak pectins. Osphradium equaling ctenidial length. Ctenidium comprising light tan elongate, triangular filaments. Hypobranchial gland thick, comprising irregular transverse glandular folds, secreting large amounts of mucus.

Alimentary system (Fig. 19B): Buccal mass large, filling snout cavity, having small jaws and short radula (Fig. 19A). Rachidian tooth (Fig. 19B) with rectangular basal plate lacking

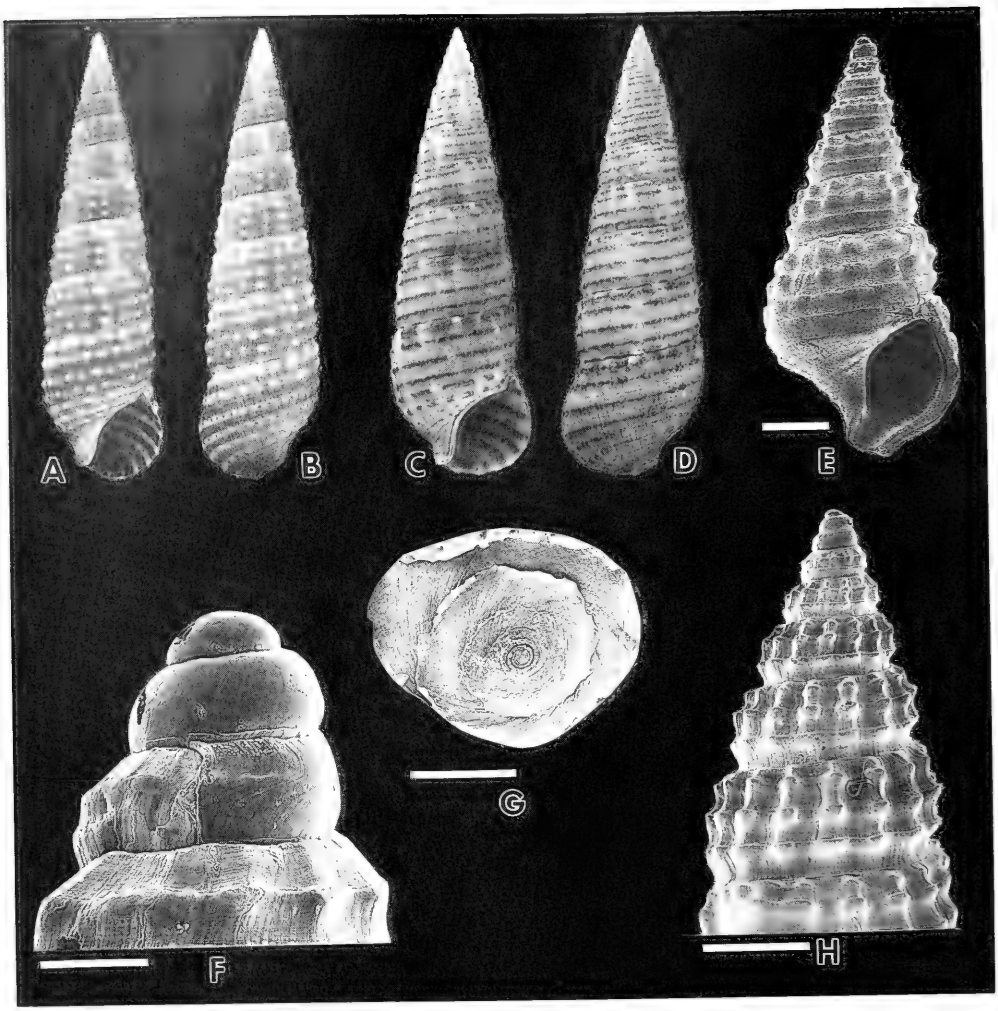

FIG. 18. *Cacozeliana granaria* from King George Sound, Western Australia (USNM 858551). A–D, two shells showing variation in color pattern and sculpture, length 22.4 mm and 20.2 mm, respectively; E, SEM micrograph of immature shell, bar = 0.6 mm; F, SEM micrograph of protoconch, bar = 16 μm; G, SEM micrograph of operculum, bar = 0.8 mm; H, SEM micrograph showing early sculpture, bar = 0.8 mm.

strong basal lateral buttresses, with straight base and equal in length to top of tooth; cutting edge with small central cusp flanked by two denticles on each side. Lateral tooth (Fig. 19B) with one inner denticle and 3–4 outer denticles. Inner marginal tooth with 5–6 inner denticles and 3–4 outer denticles. Outer marginal tooth (Fig. 19A) with 4 inner denticles. Salivary glands (Fig. 20B, lsg, rsg) paired, vermiform, coiled, lying anterior to nerve ring. Midesophagus expanded laterally having many transverse internal epithelial folds comprising esophageal gland. Stomach with one digestive gland opening to left of large central pad dividing left sorting area from right gastric shield complex. Style sac separated from intestinal opening by large typlosole fold.

Nervous System (Fig. 20, B): Cerebral ganglia joined by short connective, one-third the ganglion length. Subesophageal ganglion very close to left pleural ganglion.

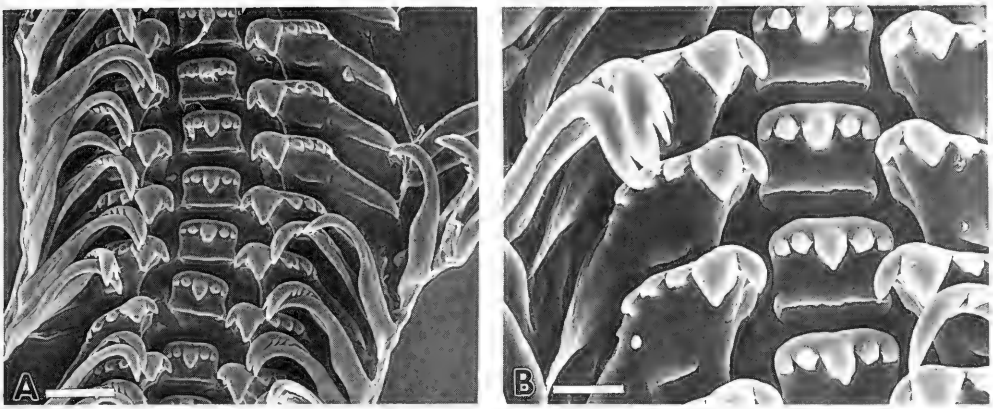

FIG. 19. Radula of *Cacozeliana granaria* from King George Sound, Western Australia (USNM 858551). A, mid-section of radula, bar = 60 μm; B, details of rachidian and lateral teeth, bar = 15 μm.

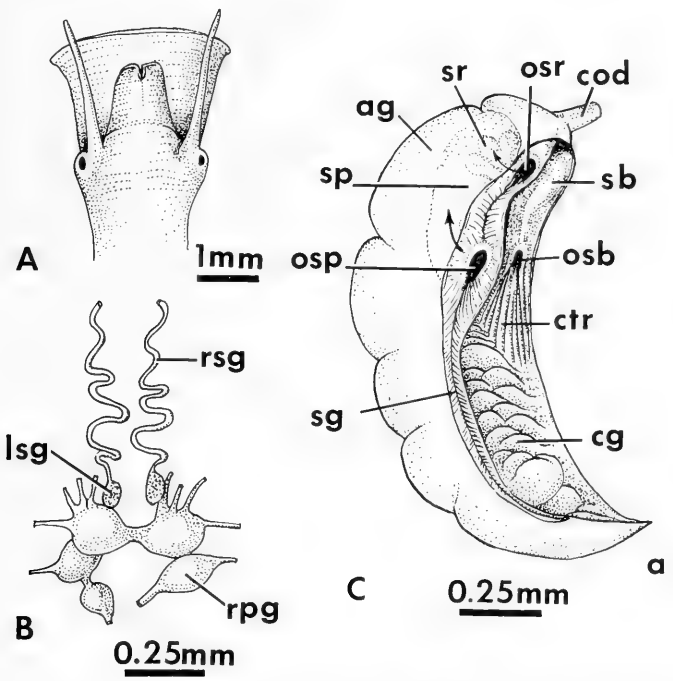

FIG. 20. Anatomical features of *Cacozeliana granaria.* A, head and foot anterior, showing narrow snout; B, position of salivary glands anterior to nerve ring; C, pallial oviduct, spread open to reveal interior details. a = anterior end of pallial oviduct; ag = albumen gland; cg = capsule gland; cod = coelomic oviduct; ctr = ciliated ridge tract; lsg = left salivary gland; osb = opening to spermatophore bursa; osp = opening to sperm pouch; osr = opening to seminal receptacle; rpg = right pleural ganglion; rsg = right salivary gland; sb = spermatophore bursa; sg = sperm groove; sp = sperm pouch; sr = seminal receptacle.

Reproductive System: Male pallial gonoduct thick, glandular, having wide transverse folds forming spermatophore organ in posterior half; anterior half of male pallial gonoduct less glandular, white but not opaque. Female pallial oviduct (Fig. 20C) having seminal recep-

tacle comprising several grape-like lobes in medial lamina (Fig. 20C, sr). Openings to the sperm pouch (Fig. 20C, osp) and seminal receptacle (Fig. 20C, osr) separated by long ciliated groove. Ciliated ridge tract (Fig. 20C, ctr) beginning behind anterior capsule gland (Fig. 20C, cg) comprising many swollen transverse elements. Opening to spermatophore bursa (Fig. 20C, osb) in lateral lamina adjacent to opening of sperm pouch in medial lamina. Spawn mass comprising a jelly string containing many encapsulated eggs, 0.1–0.13 mm diameter, wound into flattened coil about 20 mm wide. Eggs opaque, white, each within hyaline capsule. Development indirect with free swimming veliger stage.

Discussion

Although the shell of *Cacozeliana granaria* (Fig. 18) looks very much like those of some *Cerithium* species, the weak epipodial skirt, pallial oviduct, and other anatomical features are very typical of members of the Bittiinae. The protoconch, as indicated by Gründel (1976), differs from those of most other genera in being nearly smooth, and in lacking any spiral threads (Fig. 18F; Table 3), but it does have a deep sinusigeral notch, indicative of planktotrophy. *Stylidium* species also have a smooth protoconch. The operculum of *Cacozeliana* is unusual in having a thin lamellar-like fringe along its spiral (Fig. 18G). The shell of this species is undoubtedly the largest of any member of the *Bittium*-group (Table 3), but the aperture is very small in relation to the shell length. There is much color variation within populations.

The early life history of this species has been described by Murray (1969), who illustrated the spawn (1969: pl. 17). The spawn comprises a coiled gelatinous thread containing encapsulated eggs that hatch as planktotrophic veligers. Murray (1969) stated that 8–9 days after deposition, veliger-stage embryos hatched out and were maintained in sea water containers for up to 10 weeks.

Cacozeliana granaria is found in the shallow subtidal, temperate waters of southern Australia where it is common among *Posidonia, Zostera,* and other sea grasses. It also occurs on moderately exposed and sheltered shores, on sandy-muddy bottoms, under stones, and on rocky areas. I observed large populations of this species living on algal mats and on *Posidonia* grass blades in King George Sound, Western Australia, and in similar habitats in Sydney Harbor and Botany Bay, New South Wales.

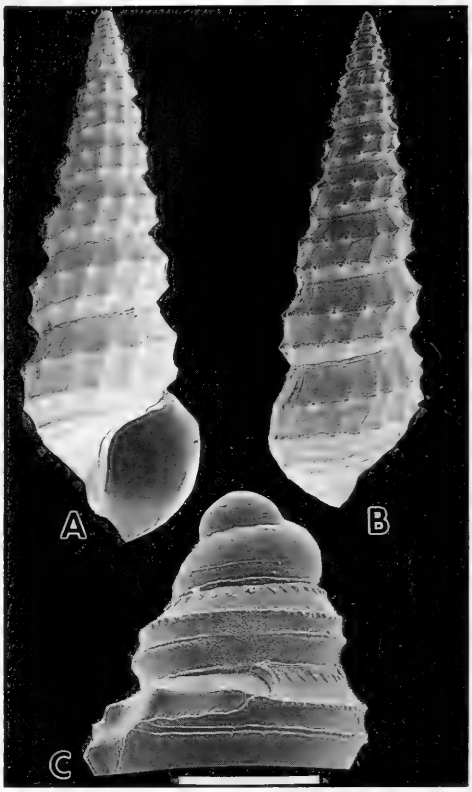

FIG. 21. SEM micrographs of shell of *Argyropeza divina* Melvill & Standen, from Refugio Id., Tanon Str., Philippines (USNM 302513); A, B, apertural and dorsal views of adult shell, 6.3 mm length; C, protoconch showing sculpture and sinusigeral notch, bar = 1 mm.

ARGYROPEZA MELVILL & STANDEN, 1901

Argyropeza Melvill & Standen, 1901: 371–372 (Type species by original designation, *Argyropeza divina* Melvill & Standen, 1901). Thiele, 1929: 212; Wenz, 1940: 757; Gründel, 1976: 44; Houbrick, 1980a: 2.

Diagnosis

Shell small, turreted, thin and vitreous, sculptured with axial and spiral elements, varices, and with many small nodules. Protoconch comprising three and a half whorls with deep sinusigeral notch; sculptured with two

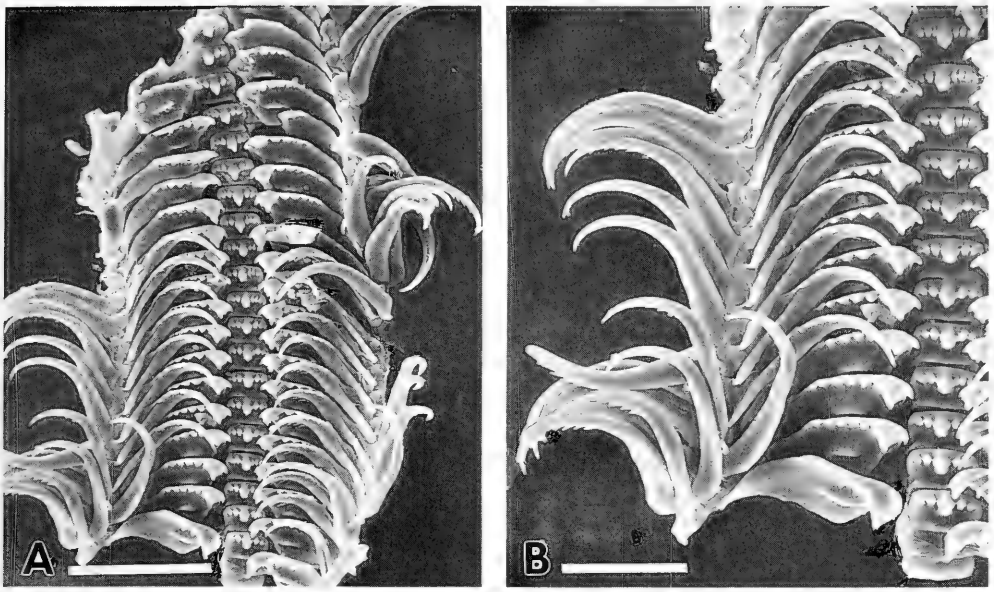

FIG. 22. SEM micrographs of radula of *Argyropeza divina* (USNM 302513), A, radular ribbon with marginal teeth spread open, bar = 100 μm; B, half row, bar = 50 μm.

spiral cords and many minute subsutural folds. Aperture ovate with well-developed, short anterior canal. Operculum corneous, subcircular, paucispiral, with subcentral nucleus. Snout broad with large cephalic tentacles and large eyes. Foot with anterior mucus gland. Mantle edge papillate. Pallial gonoducts open. Radula taenioglossate; rachidian tooth wider than tall; lateral tooth with transverse ridge on basal plate; marginal teeth slender, scythe-shaped.

Remarks

An alpha-level review of *Argyropeza* has been published by Houbrick (1980a), which should be consulted for details about taxonomy, morphology and geographic distribution. The genus comprises five described species and several undescribed ones (pers. obser.). Members of this genus live on fine-grained substrates of deep water shelves and slopes, and not much is known about their biology. All examined species have small shells and protoconchs sculptured with two spiral lirae, subsutural pleats, and a deep sinusigeral notch (Fig. 21C; Table 3) indicative of a planktotrophic larval stage. The anatomy of *Argyropeza* species is virtually unknown except for superficial observations made from reconstituted, dried specimens. The shell and radula of the type species, *Argyropeza divina* Melvill & Standen, 1901, are shown in Figures 21 and 22. I do not agree with Powell's (1979) suggestion that *Tasmalira* Dell, 1956, may be closely related to *Argyropeza,* because the shell morphology does not appear to fit the limits of the genus. *Argyropeza* is tentatively assigned to the Bittiinae until more complete anatomical information is available.

VARICOPEZA GRÜNDEL, 1976

Varicopeza Gründel, 1976: 46 (Type species by tautonomy, *Varicopeza varicopeza* Gründel, 1976). Houbrick, 1980b: 525; 1987: 85.

Diagnosis

Shell small, slender, turreted, vitreous, having impressed suture, and sculptured with strong spiral cords, weaker axial elements, and many nodules. Protoconch having three and one-half smooth whorls, with weak, median spiral cord, minute subsutural pustules, and sinusigeral notch. Aperture ovate with short, well-developed anal and anterior canals. Operculum corneous, ovate, paucispiral, with subcentral nucleus. Radula taenio-

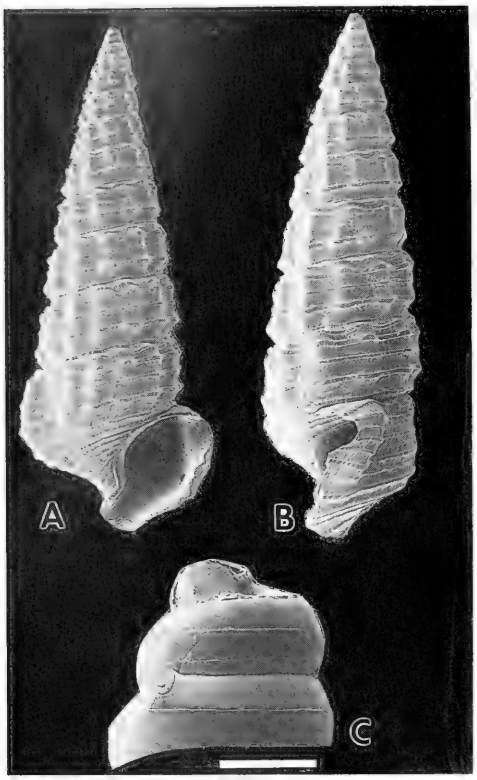

FIG. 23. SEM micrographs of shell of *Varicopeza pauxilla* (A. Adams, 1854) from Nagubat Id., E. Mindanao, Philippines (USNM 276898). A, B, apertural and side views of adult shell, 8.1 mm length; C, protoconch, bar = 100 μm.

glossate with hourglass-shaped rachidian tooth; lateral tooth with transverse ridge on basal plate; marginal teeth elongate, slender with denticulate sickle-shaped tips. Animal with large headfoot, elongate, wide snout, long cephalic tentacles and very large eyes. Deep ciliated groove on right side of foot. Mantle edge having short, thick papillae.

Remarks

The two known species of *Varicopeza* have been thoroughly described by Houbrick (1980b, 1987a). These publications should be consulted for specific information about taxonomy and a detailed description of the type species. The shell is of moderate length (Table 3) and has a protoconch sculptured with one spiral lira and a shallow sinusigeral notch (Fig. 23C). Although the shell and radula (Fig. 24) are well described, only a few external anatomical features are known. *Varicopeza* species occur at moderate subtidal depths on fine-grained substrates in the tropical Atlantic and Pacific. The shell sculpture of *Varicopeza* (Fig. 23A, B) is similar to that of *Argyropeza* species, differing chiefly in protoconch morphology. The aperture (Fig. 23A, B) is distinctive in having a large, flaring anal sinus. The radula (Fig. 24) has more denticles on the marginal teeth than in *Argyropeza* (Table 2).

Gründel (1976) suggested that *Varicopeza* was closely related to the extinct Jurassic genus *Cryptaulax* and considered it to be a Recent representative of the of the extinct family Procerithiidae Cossmann, 1905. The shell and radula of *Varicopeza pauxilla* (A. Adams, 1854) is shown in Figures 23 and 24. This genus is tentatively assigned to the *Bittium*-group until more complete anatomical information is available.

ZEBITTIUM FINLAY, 1927

Zebittium Finlay, 1927: 381 (Type species by original designation, *Cerithium exilis* Hutton, 1873); Wenz, 1940: 756; fig. 2191; Powell, 1979: 132, fig. 32:1.

Diagnosis

Shell very small, turreted, sculptured with beaded spiral cords, and weak axial riblets, having impressed suture. Aperture ovate with weak notch-like anterior canal. Protoconch two and a half whorls, bluntly rounded, unsculptured.

Remarks

This genus was proposed without any defining characters, and was apparently introduced only to accomodate the New Zealand species, *Bittium exile* Hutton and *Bittium vitreum* Suter. The shell of *Zebittium exile* (Hutton, 1873) is shown in Figure 25. *Zebittium* was assigned as a subgenus of *Bittium* by Wenz (1940), who noted that the genus occured from the Miocene to the Recent of New Zealand. The shell of the type species closely resembles those of *Bittium* and *Bittiolum* species and does not appear to have any distinguishing features of generic significance. The unsculptured protoconch (Fig. 25D) appears to indicate lecithotrophic development. No preserved material of this species was avail-

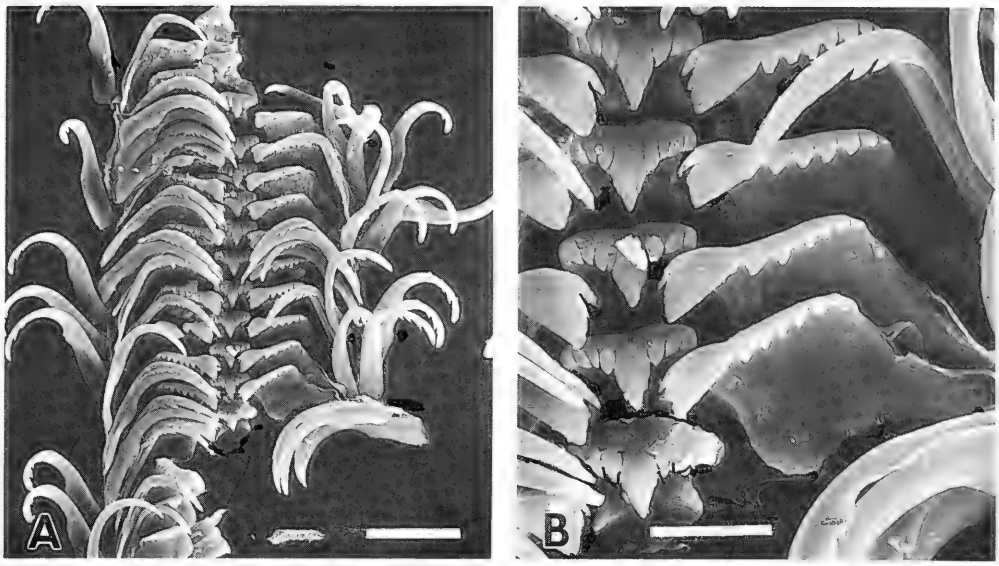

FIG. 24. SEM micrographs of radula of *Varicopeza pauxilla*. A, section of ribbon with some marginal teeth spread open, bar = 50 μm; B, detail of rachidian and lateral teeth, bar = 25 μm.

able for study; therefore, the genus *Zebittium* is included in this review only tentatively.

CASSIELLA GOFAS, 1976

Cassiella Gofas, 1987: 109 (Type species by original designation, *Cassiella abylensis* Gofas, 1987).

Diagnosis

Shell small, slender, turrited, sculptured with spiral cords, without varices and with impressed suture. Aperture ovate, without anterior canal and simple outer lip. Operculum corneous, ovate, paucispiral, with subcentral nucleus. Animal with bilobed snout and two elongate cephalic tentacles. Foot short and broad without ovipositor or ciliated groove on right side, and with large opercular lobe. Radula taenioglossate; rachidian tooth with squarish basal plate, moderately concave on each side with small median glabrella, and having cutting edge with large central cusp flanked by 3 smaller denticles on each side. Lateral tooth with large triangular cusp with one small inner denticle and 7–8 outer denticles. Marginal teeth elongate, spatulate with curved tips; inner marginal teeth denticulate on both sides; outer marginal teeth lacking outer denticles.

Remarks

This monotypic genus was recently proposed and described by Gofas (1987), and his publication should be consulted for descriptive details of the genus and figures of the type species. *Cassiella abylensis* does not fit easily into the *Bittium*-group, although there are some resemblances. The shell of *Cassiella abylensis* (Fig. 26) varies highly in color pattern and in spiral sculpture (Gofas, 1987: 111). The shell morphology is unlike those of other members of the *Bittium*-group. No vestige of an anterior canal is present, and the shell morphology strongly resembles those of some rissoids. The absence of an anterior canal is also a feature of *Cerithidium* Monerosato, a taxon I have excluded from Bittiinae.

The external anatomy of *Cassiella abylensis* was depicted by Gofas (1987: figs. 10, 14, 15). The animal does not have epipodial tentacles, although there is an inconspicuous groove around the foot, just above the edge of the sole, which may be homologous with the epipodial skirt found in members of Bittiinae. The opercular lobes are said to be "massive" (Gofas, 1987: 111), but they are not depicted or labeled in the figures of the external anatomy. The headfoot, operculum, and radula are not unlike those observed in other species

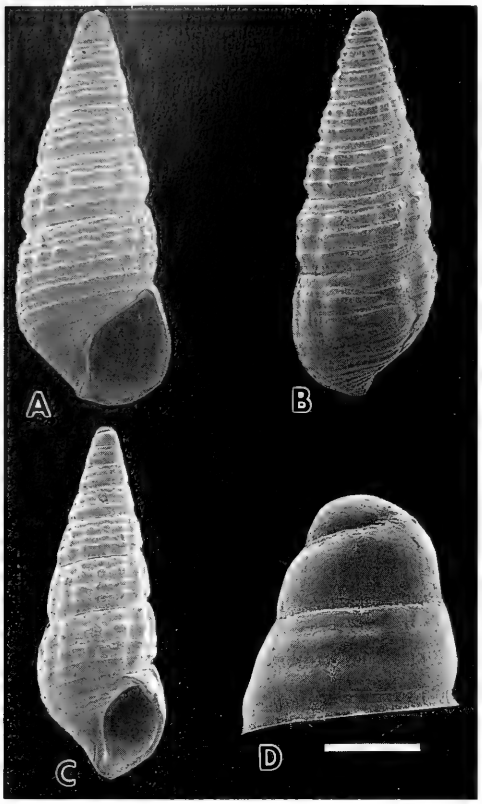

FIG. 25. SEM micrographs of shell of *Zebittium exile* (Hutton, 1873) from Long Bay, Auckland, New Zealand (USNM 681043); A, apertural view of adult shell, 4.7 mm length; B, dorsal view, 4.6 mm length; C, immature shell, 4.4 mm length; D, protoconch, bar = 0.25 mm.

of Bittiinae. There is no metapodial mucus gland, no ovipositor is indicated, and males are aphallate (Gofas, 1987: 111).

Pending further anatomical studies, the eastern Atlantic taxon *Cassiella* is tentatively assigned to Bittiinae with doubt.

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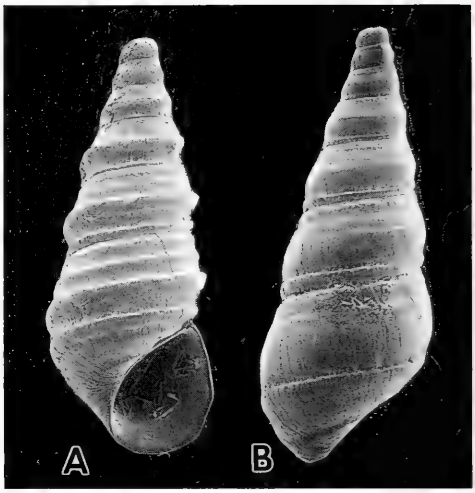

FIG. 26. SEM micrographs of shell of *Cassiella abylensis* Gofas, 1976, from Ceuta, Spain (USNM 869532); A, apertural view of shell, 2.3 mm length; B, dorsal view of shell, 2.5 mm length.

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SOME ASPECTS OF THE FUNCTIONAL MORPHOLOGY OF THE SHELL OF INFAUNAL BIVALVES (MOLLUSCA)

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ABSTRACT

Measures of streamlining, gapage, umbo position, and pallial sinus depth were taken from 632 species of Bivalvia in 13 families. Two types of gapage were measured: exchangeable gapage due to the rocking motion of the shells along a dynamic dorso-ventral axis, and permanent gapage, that portion of the gapage that could not be closed by the rocking movement. Models were given to predict changes in shell shape as an adaptation to infaunal life. Three stages occur in the sequence of shell shapes from shallow to deep infaunal dwellers for the families studied. The first stage is represented by unstreamlined, often sculptured shells with complete valve closure. The second, or intermediate stage, consists of an increase in streamlining, a loss of sculpture, central placement of the umbo, and temporary gapes in the shell for pedal and siphonal outlets. These gapes may be opened and closed by rocking the shells along a dorso-ventral axis (exchangeable gapage). Two paths are evident out of the intermediate stage into the third. The myid path results in unstreamlined shells with central umbos. The solenid path results in streamlined shells with a variable umbo position. Some families, such as the Mactridae, have members along both paths.

The entry into this sequence requires a particular set of pre-existing morphological conditions. The lack of these conditions in most species studied has resulted in a bottleneck, with few species in the deep infaunal zone. The constraints of bivalve shell geometry have limited the success of that group in otherwise favorable habitats.

Key words: Bivalvia, morphospace, functional morphology, ecology, phylogeny.

INTRODUCTION

The class Bivalvia of the phylum Mollusca is the most diverse group of organisms extant that principally have radiated into the deep infaunal zone. Nevertheless, the fossil record shows that this colonization required nearly 200 million years to become widespread, although the earliest known representatives of this class may have been shallow infaunal burrowers (Pojeta et al., 1973; Jell, 1980; but see Yochelson, 1981).

The deep infaunal habitat has several potentially positive adaptive features. Predation is reduced because of the general lack of burrowing molluscivores. The sediment acts as a buffer, ameliorating thermal, salinity, pH, and other environmental extremes. Desiccation is minimized. For these reasons, this habitat is advantageous to an organism associated with this niche.

Therefore why did so few members of the Bivalvia colonize the deep infaunal zone? It is probable that the changes required in evolving into the deep infaunal zone involve such considerable morphological modifications that members of few lineages have survived or ever began the transition. Burrowing in the substrate to greater depths must have occurred by degrees, where each modification was either adaptively or neutrally selective. Such intermediate morphological steps would have had their own immediate selective advantage.

The acquisition of shell structures and behaviors associated with deep burrowing has occurred in relatively few members of the bivalve families. This implies that characteristics that made for survival in this habitat served another function in another habitat, and that these particular characteristics were selected upon by natural factors or processes that resulted in deep burial. Members of lineages lacking these prerequisite characteristics could not attain a deep infaunal existence. These characteristics include the anatomy of the living individual, behavior, and the shape of the shell. This study is limited to a consideration of the shell.

Shell Shape

It is here hypothesized that bivalves associated with the deep infaunal habitat should

have a similar shell shape if there exists a suite of characteristics necessary to achieve this type of existence. The presence of homeoplasy (similar shell shapes by convergence, parallelism, or iteration) by individuals of deep infaunal species across suprageneric taxonomic levels would support this hypothesis. This study proposes to obtain measures of shell shape describing differences that may arise in a transition from a shallow to a deep infaunal existence. These measures are:

(1) degree of streamlining. This is a measure of the amount of surface area of the shell that is oriented perpendicular to the long axis of shell.

(2) relative position of the umbo. The placement of the umbo on the shell, standardized to remove size effects.

(3) relative depth of the pallial sinus. The depth of the pallial sinus, standardized to remove size effects.

(4) amount of permanent gape. Some bivalve shells do not close completely, leaving gapes anteriorly and posteriorly. These shells may open and close along a dorso-ventral axis to close much of the gape, but some portion may remain open. These are permanent gapes. The amount of permanent gapage is the sum of the anterior and posterior gapes in the commissure of the shell that cannot be closed by rocking the shells along a dorso-ventral axis (Fig. 1: $g_1 + g_2$).

(5) amount of exchangeable gape. The amount of gape created by rocking the shells along a dorso-ventral axis minus the amount of permanent gape (Fig. 1: $pg + sg - g_1 - g_2$).

These parameters are discussed in detail under "Methods."

Shell shapes form a predictable sequence among individuals that inhabit the shallow to deep infaunal habitats because a necessary suite of shell characteristics is needed to succeed in a deep infaunal habitat. This sequence is defined by the distribution of each measurement specified for representatives of the species in this study. The existence of a sequence could explain the rarity of deep infaunal bivalves and the degree of homeoplasy present in burrowing bivalves in general. In may be that few Recent representatives of bivalve lineages are deep infaunal burrowers because ancestral members of the lineage lacked the shell characteristics necessary to enter the sequence.

The sequence may be divided into three phases. The shallow infaunal phase contains bivalves that do not have exchangeable gapage. The deep infaunal phase contains forms with permanent gapage. These individuals often are deep burrowing or sedentary forms. The intermediate phase connects these two phases and contains forms having exchangeable gapage. Homeoplasy would be the expected result if only a few sequences of shell shape morphologies existed among those individuals that occur in these phases.

It has long been known that there is convergence in shell characteristics in bivalves. Seed (1980b: 32) stated that "perhaps one of the most striking features concerning the evolution of such a diverse group as the bivalves has been the repeated appearance of a comparatively restricted number of very successful shell morphologies." Linnaeus, Cuvier, Bruguière, and Lamarck placed bivalves in only a few genera. They based their criteria for classification primarily upon shell form and a consideration of hinge dentition, but little internal anatomy. This is in contrast to a recent classification (Vaught, 1989) that lists nearly 1,000 genera. Taxa not known to be related may possess similar shells when internal anatomy, dentition, and larval types are also examined. This has been a major obstacle to the study of fossil forms.

Two hypotheses may be formed to explain this convergence, and they are not mutually exclusive. The first states that similar shells have arisen in response to similar environmental pressures. Convergence has occurred because of natural selection "favoring" a specific shell shape. However, evolution may only act upon available morphological material. Pre-existing structures may be co-opted for a different use or an improved original function if the genetic program can be modified in such a fashion. This is the basis behind the second hypothesis of convergence in shell shapes: bivalve shells may be similar because there is only a limited range of values for shell geometric parameters that occur in nature. Convergence may be expected because of this restriction if there are few viable alternative shell shapes.

The results of this study suggest that the cause of convergence in bivalve shell shape may be explained as the consequence of a sequence of morphologies. This sequence represents a compromise between natural selection and morphological constraints. Evolution is conditional and the changes at any step in a phylogeny depend upon the characteristics of the previous step. Such "trends"

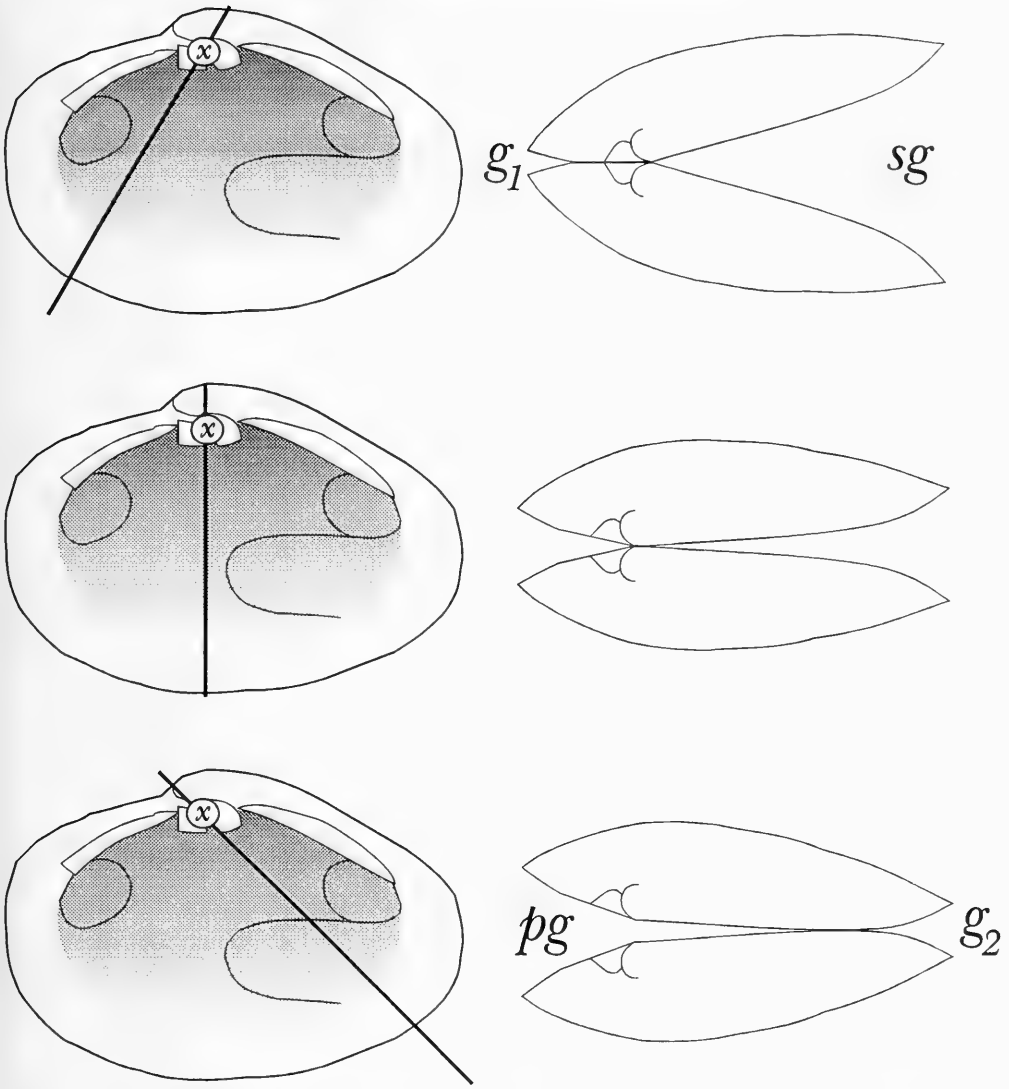


FIG. 1. Rocking of shells along a dorso-ventral axis. Heavy line: Axis. x: Fixed pivot at cardinal teeth. Top: Shells rocked forwards to open siphonal gape (sg). Middle: Shells at neutral position. Bottom: Shells rocked backwards to open pedal gape (pg). g_1: Non-closable permanent anterior gape. g_2: Non-closable permanent posterior gape.

have been modeled satisfactorily by a Markov process or random walk (Bookstein, 1987). As an example, Cope's Law of Phyletic Size Increase has been shown to be stochastic (Stanley, 1973). The convergence of bivalve shell shapes may be such a stochastic process.

The molluscan shell has long been recognized as a geometric form, at least in the artistic sense. Examples of this geometry, as a by-product or necessity of biological design, were not popularized until Thompson (1942) published *On Growth and Form*. The further study of shell geometry did not progress past this recognition stage for many years. The computations were time consuming and the results difficult to visualize as three-dimensional shapes. Recently, geometric studies of

this type have been facilitated by computers. Raup (1961, 1962, 1963, 1966, 1967) identified the basic parameters of spiral coiling and generated simulations of molluscan shells by computer emulation. He demonstrated that a simple gastropod or cephalopod shell design could be modeled with few variables. Savazzi (1987) produced an even more realistic computer generated model, and the recent work of Fowler et al. (in press) has produced amazing simulations. The science of "theoretical morphology" (Raup & Michelson, 1965) and, more specifically, "conchyliometry" (coined by Naumann, 1840), became a discipline belonging as much, if not more, to computer programmers and mathematicians as to biologists. The course of these studies culminated in Bayer's (1978) and Illert's (1992) purely mathematical analyses of shell shape using morphogenetic programs. The emphasis of these studies had shifted from the biological aspects of shell geometry to a consideration of the biometrics as the sole purpose of the investigation.

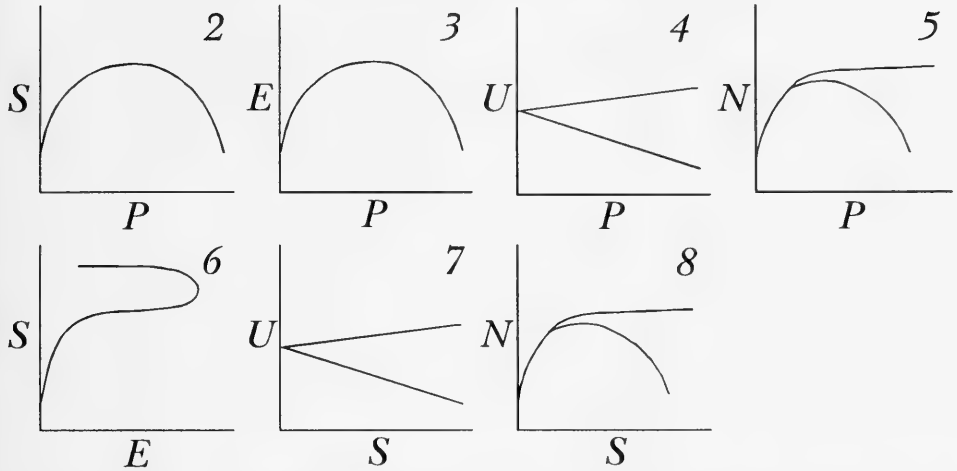
In 1970, Stanley published a study on marine bivalves that marked a turning point in molluscan morphometrics. He presented a synthesis of shell geometry, systematics, ecology, and field observation. For the first time, on a comprehensive scale, explanations were advanced for why shells were shaped like they were, rather than how they were shaped. Following the studies of Trueman et al. (1966a) and Nair & Ansell (1968) on the dynamics of bivalve burrowing, Stanley's work showed that members of such diverse groups as the solecurtines, the solenids, the cardiids, and the mactrids had highly convergent shells because of similar habitats. From his results, I have inferred the possibility of analogous, predictable shell shapes in equivalent niches despite phylogenetic position.

Stanley (1969, 1970, 1972, 1975, 1977b, 1981) documented the probable function of many types of marine bivalve sculpture. I believe that the single most important conclusion of these works was the concept of "composite sculpture," the exaptation (*sensu* Gould & Vrba, 1982) of pre-existing sculpture for vicarious multiple tasks. Gould and Vrba coined this term for previous adaptations or nonadaptations that have been co-opted for a new function. For example, radial ribs may have originated as sculpture strengthening the shell in individuals of the Cardiidae (Stanley, 1981). That sculpture has been exapted to function as a burrowing device in many members of the trachycardiinine cockles. As aspects of the function of shell sculpture have been discussed elsewhere, they generally will not be addressed in this study.

Of central importance to this analysis is the concept of the theoretical morphospace: the array of potential shapes that an organism may possess. This space usually is limited to a few parameters, such as size, coiling rate, or color, for experimental studies and represents the possible range of values of that parameter. The theoretical morphospace may be contrasted with the actual morphospace. The actual morphospace is the observed values of that parameter, or in a broader sense, the form in which the organism is found in nature. The actual morphospace is always a subset of the theoretical morphospace. In its simplest form, this methodology addresses the question: why are things shaped the way they are? Or conversely, why aren't they shaped like something else? It is the latter question that may be the most insightful, for it implies a limitation of form and a constraint on possible morphologies. The cause of this constraint may be fundamental to understanding the organism in question. The idea of the theoretical morphospace has been applied to the morphological features of several groups, most notably coiling in cephalopods (Raup, 1967).

Convergence is most apparent in a morphospace scenario. Phylogenetically unrelated groups that consistently occupy the same morphospace have converged toward the same values of the morphospace parameters. In this study, the sum of overlapping regions is shown to lie along a sequence of shell shapes.

Rudwick (1965) is usually given credit for advancing the use of the paradigm approach in biology, although this method of analysis may have been in use for many years. The term is from the Greek *paradeigma*, meaning "example" or "model." The methodology allows the worker to form hypotheses concerning the potential characteristics of an organism possessing a certain life style or behavior, given information on the necessities of the organism's life and its general morphology. For example, given the morphological characteristics of a small dinosaur, what changes are necessary to metamorphose it into a bird? The result is a model having parameters describing the organism in that life style as dictated by the logic of the investigator and the presumed efficiency of those characteristics.



FIGS. 2–8. Models of shell shape. 2. Model for interaction between permanent gapage (P) and streamlining (S). 3. Model for interaction between permanent gapage (P) and exchangeable gapage (E). 4. Model for interaction between permanent gapage (P) and position of umbo (U). 5. Model for interaction between permanent gapage (P) and depth of sinus (N). 6. Model for interaction between exchangeable gapage (E) and streamlining (S). 7. Model for interaction between streamlining (S) and position of umbo (U). Fig. 8. Model for interaction between streamlining (S) and depth of sinus (N).

The value of the model is in its degree of resemblance to the actual organism. What are the discrepancies, if any, and how are they significant?

The paradigm model is similar to the theoretical morphospace. Both analyses compare actual and hypothetical characteristics of an organism. The model represents a region of the theoretical morphospace that has a high probability of being the actual morphospace, based on outside inferences. Both form a consistent pattern against which to compare the results of analyses.

Models of Shell Shape

It is possible to predict sequences in the values of shell shape parameters using the paradigm methodology. These parameters may be taken as a whole to describe the overall shell shape. The models are understood most easily as pairwise comparisons of the parameters.

Permanent Gapage and Streamlining: Streamlining would be expected first to increase into the intermediate phase with increasing depth of burrowing, and then decrease as permanent gapage becomes pronounced (Fig. 2). Increased streamlining occurs as bivalves become more suited to burrowing in the shallow infaunal zone. At a critical depth, which varies from sediment to sediment and depends upon the size of the bivalve, the weight of the substrate limits the depth of burial. Deeper burrowing can occur in a lineage only by the formation of exchangeable gapage. This is the beginning of the intermediate phase. The increasing degree of exchangeable gapage should begin to diminish the amount of streamlining. As exchangeable gapage is modified into permanent gapage, streamlining should decrease continuously as the life style shifts from efficiently moving in the shallow substrate to a deeply buried sedentary existence.

Permanent Gapage and Exchangeable Gapage: As with streamlining, levels of exchangeable gapage should rise and then fall with increasing permanent gapage and deeper infaunal existence (Fig. 3). The peak of exchangeable gapage lies within the intermediate phase. Streamlining is modified into exchangeable gapage, which in turn is modified into permanent gapage.

Permanent Gapage and Relative Position of Umbo. The model suggests that the umbo, as a relative measure of the position of the cardinal teeth, should become centralized to allow maximum exchangeable gapage as a lineage enters the intermediate phase (Fig. 4). The position of the umbo in individuals

past the intermediate phase may depend upon the type of life style. The location of the umbo may be unimportant in sedentary forms that lack both a functional foot and rocking of the shell along a dorso-ventral axis. The umbo may become placed anteriorly in tube-dwelling forms, which have large muscular feet, because of its associated pedal muscle insertions. Thus two paths are expected out of the intermediate phase.

Permanent Gapage and Relative Depth of Sinus. As burrowing depth increases, so must the length of the siphons in non-tube dwelling forms. This entails an increase in sinus depth to accommodate them. The depth of the sinus will be high within the intermediate phase (Fig. 5). Two paths are predicted as the lineage passes into permanent gapage. Siphons in tube-dwelling species do not increase if they remain permanently exterior to the shell, as in members of the solenaceans. Siphons may remain retractile in other forms, requiring a deep pallial sinus.

Exchangeable Gapage and Streamlining. Streamlining is expected to increase into the intermediate phase until exchangeable gapage becomes more evident (Fig. 6). As exchangeable gapage is modified into permanent gapage, both exchangeable gapage and streamlining should decrease. Thus, there should be both a path out and in along the exchangeable gapage axis.

Streamlining and Relative Position of Umbo. The relative position of the umbo should become centralized for maximum exchangeable gapage as streamlining passes into the intermediate phase (Fig. 7). As previously mentioned, the fate of the position of the umbo depends upon factors not accounted for in this model, and two paths are expected out of the intermediate phase.

Streamlining and Relative Depth of Sinus. With increasing streamlining, the relative depth of the sinus should increase into the intermediate phase (Fig. 8). Past this point the sinus depth may remain constant or decrease.

METHODS AND MATERIALS

Taxa Used in the Study

Representatives of 632 Recent species and subspecies of bivalves were used in this study. Specimens were acquired from the following repositories and collections: Museum of Comparative Zoology, Cambridge, Massachusetts; National Museum of Natural History, Washington, D. C.; Ohio State University Museum of Zoology, Columbus, Ohio; and the author's private collection. The identification of museum specimens was taken from collection records, with the following exceptions at Ohio State University. Individuals of southeastern United States in the genus *Elliptio*, and a few members of other genera from that region, were identified by the author, as were all marine species from that collection. These identifications may not reflect the views of systematists at that institution. The higher systematic levels are taken from Vaught (1989).

Members of 15 families were selected for study, representing most of the living infaunal bivalve groups. These families, and the number of species or subspecies used in this study for each in parentheses, are: Mactridae (41), Cardiidae (56), Myidae (6), Psammobiidae (25), Solenidae (8), Cultellidae (9), Tellinidae (42), Semelidae (7), Donacidae (18), Veneridae (103), Petricolidae (1), Unionidae (276), Hyriidae (16), Mycetopodidae (13), and Mutelidae (11). Many families were chosen because they displayed a wide range of shell forms: streamlined vs. rotund, sculptured vs. unsculptured, etc. Others, such as the Solenacea, were chosen because their unique forms offered insight into this study. Some families subsequently were divided into subfamilies, and others grouped into orders better to indicate functionally alike groups. The Unionaceans, which have been omitted from most studies of this sort, were represented by the most taxa. They were included because no other group of Recent bivalves encompasses such a wide range of shell shapes. Other infaunal bivalve groups were not included, for the following reasons. Individuals of the anomalodesmaceans generally are too rare to obtain a reasonable sample. The Arcidae, Mytilidae, and Pinnidae have infaunal members, but most are sessile and byssate, and thus different from the free living infaunal groups chosen for study (Newell, 1969; Rosewater, 1961; Soot-Ryen, 1955, 1969). Members of other groups, such as the Astartidae, are too homogeneous to warrant repetitive measurements. Individuals of the Lucinidae are infaunal and have a wide range of shell shapes, and members of many species are common. However, the mode of circulating

water of the lucinids is quite different from the groups included here (Allen, 1958). The differences are sufficient to eliminate it from this study of infaunal groups. Because this study deals only with Recent species, otherwise interesting groups such as the largely extinct Trigoniacea were excluded.

Measurements and Derived Values

The following measurements, all in mm, were taken on individuals for each of the 632 species.

Length—the greatest length along an anterior-posterior line (Fig. 9a). This line usually was parallel to the hinge axis.

Height—the greatest dorsal-ventral height, perpendicular to the line for length (Fig. 9d). This line often extended through the umbo.

Width—the greatest lateral width, with both valves closed (Fig. 9c).

Position of umbo—the distance from the anterior margin to the umbo, along the length line (Fig. 9b).

Depth of pallial sinus—maximum depth of the sinus measured out to a curve that follows the pallial line (Fig. 9e).

Anterior permanent gape—the maximum width of any anterior space between the valves when the valves are closed and rocked forward, if possible (Fig. 9f). All measurements of gape were made on dry shells with separated ligaments and no commisural periostracum. The values obtained therefore may be overestimated uniformly to some degree.

Posterior permanent gape—the maximum width of any posterior space between the valves when the valves are closed and rocked backwards, if possible (Fig. 9h).

Anterior exchangeable gape—the total anterior gape is the maximum width of any space created anteriorly between the valves when the valves are rocked backwards (Fig. 9g). The anterior exchangeable gape is the total minus the permanent anterior gape.

Posterior exchangeable gape—the total posterior gape is the maximum width of any space created posteriorly between the valves when the valves are rocked forwards (Fig. 9i). The posterior exchangeable gape is the total minus the permanent posterior gape.

The following derived values were calculated from the above measurements.

Streamlining (S)—a univariate estimate of the relative amount of surface area exposed perpendicular to the direction of maximum length. The algorithm was devised for this study to permit the simple quantification of a parameter that has been expressed historically as a multivariate construction. The metric is dimensionless, independent of size, and has a finite range of values. Its derivation, characteristics, and application will be treated in detail.

Workers in bivalve morphometrics have realized that some shells are more elongate than others and should offer less resistance to the substrate in burrowing activities. Stanley (1970) and subsequent authors (notably Morton, 1976) have attempted to illustrate this shape by graphing ratios of shell measurements against one another and delineating a region of the theoretical morphospace as "streamlined." The difficulty with this approach is that it requires two dimensions to describe elongation. If one wishes to investigate the relationships between elongation and any other parameter, one must use multivariate correlations (at least three variables). This has not been attempted, except in the study of Thomas (1975) on glycymerid bivalves.

Streamlining in a different sense has been mathematically defined and quantified by engineers working with fluid and aerodynamics, and several attempts have been made to treat organisms in the same manner as ships and planes. These studies generally focus on optimum shapes for maximum speed, or the reverse, maximum speeds given a certain shape. One study calculated swimming speeds of extinct marine reptiles (Massare, 1988). She calculated the total drag on reptiles using an estimate of surface area, water velocity, density of the medium, and the Reynolds number (a function of body shape in lamellar or turbulent flow). Such an analysis is not applicable to bivalves burrowing through a mixed substrate.

It must be emphasized that the use of the term "streamlined" by malacologists working with bivalves is not that of Massare. That expression is used here as a descriptive variable, crudely measuring only the relative amount of surface area normal to the long axis of the shell, generally coinciding with the direction of burrowing. It carries no connotation of, or resemblance to, fluid dynamic theory. Neither is it a dynamic value dependent on burrowing speed, current velocity, or substrate type. Although univariate, the quantification of streamlining put forth in this study is identical with the sense of that term used in describing bivalve shell shape by Trueman et

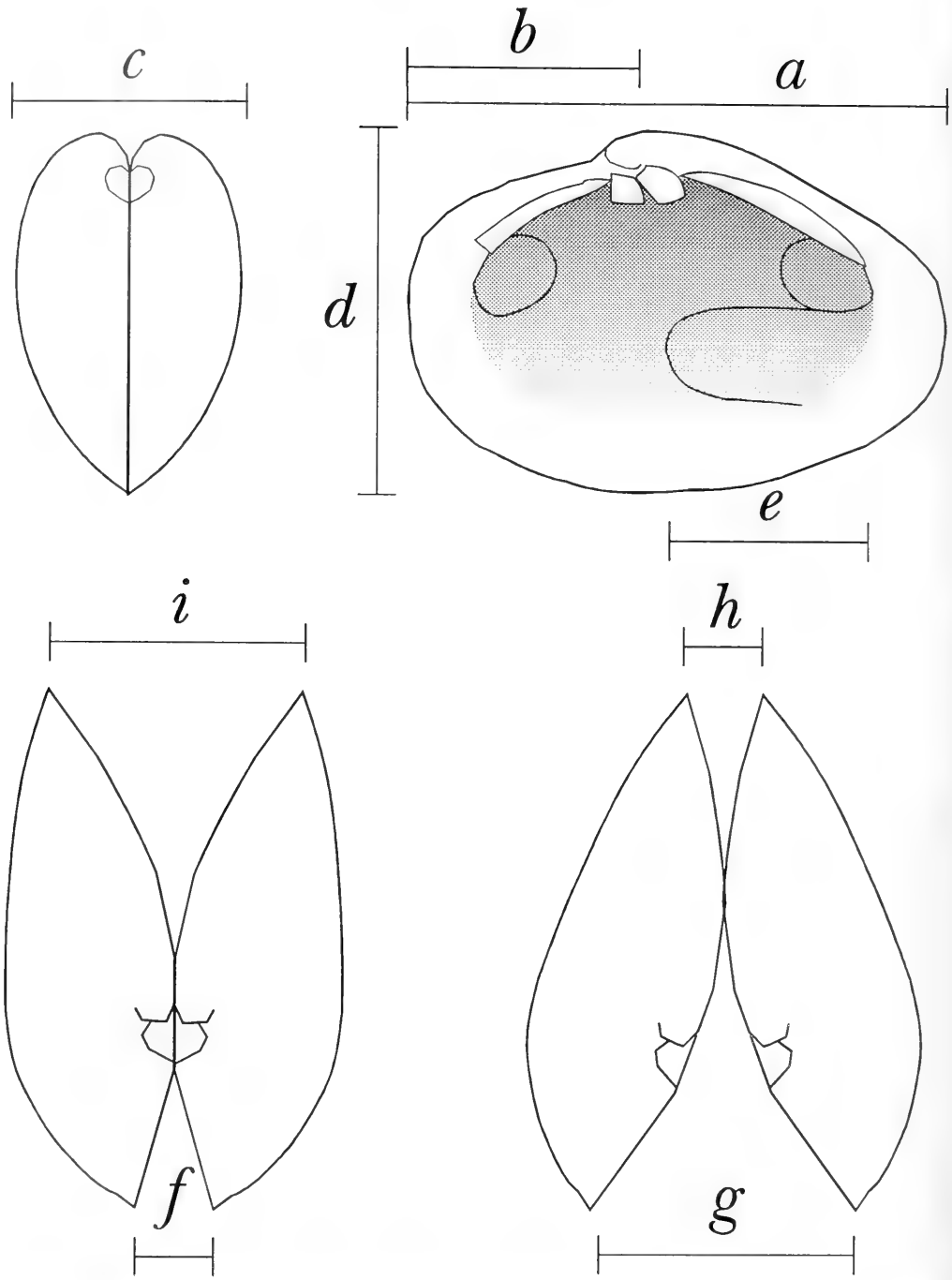


FIG. 9. Measurements used in study. a: Length. b: Distance of umbo from anterior margin. c: Width. d: Height. e: Depth of pallial sinus. f: Permanent anterior gape. g: Total anterior gape. h: Permanent posterior gape. i: Total posterior gape.

al. (1966b), Stanley (1970), Alexander (1974), Eagar (1974, 1978), Thomas (1975), Morton (1976), and Seed (1980a, b).

The calculation of streamlining (S) in this study estimates the shell shape as a rectangular solid of dimensions Length × Width × Height. The value of S lies between two hypothetical limits, interpreted as the minimum and maximum amount of streamlining for the rectangular model. At the theoretical minimum, Height and Width equal a unit measure (Height and Width = 1), and Length = 0. Movement is in the direction of Length, perpendicular to Height and Width. The model resembles a sheet of paper moving perpendicular to the face of the page. This is the minimum amount of streamlining. The theoretical maximum is achieved when Length = 1 and Height and Width both = 0. This model resembles a line of no thickness moving parallel to itself. Bivalves lie between the two extremes. The calculation is dependent on the relationship between Length and the remaining descriptors. This has the effect of standardizing data by size by removing any influence of Length. The equation can be written as:

$$S = (\text{Width}/\text{Length})(\text{Height}/\text{Length})(\text{Length}/\text{Length}) \quad (1)$$

When Height and/or Width is very small relative to Length, S approaches 0. Conversely, when Length is very small relative to Height and/or Width, S approaches infinity (∞). It is possible to limit these theoretical boundaries by raising the natural logarithm (e) to the exponent S and taking the inverse. Removing the cancelled expression (Length/Length), and raising e to the remaining parameters yields the equation:

$$S = e((\text{Height}/\text{Length})(\text{Width}/\text{Length})) \quad (2)$$

Now as Length/Height or Length/Width → 0, S → ∞, and as Height/Length or Width/Length → 0, S → 1. Taking the inverse of the function has the following effect. As Length/Height or Length/Width → 0, S → 0; as Height/Length or Width/Length → 0, S → 1. The equation has the final form:

$$S = 1/(e((\text{Height} \times \text{Width})/(\text{Length})^2)) \quad (3)$$

The resulting parameter is independent of original size, unitless, and ranges from a value of 0 for no streamlining to a value of 1 for maximum streamlining. Although the values resemble percentages, they are not. As S is univariate, it may be compared with other morphometric parameters without the necessity of multivariate analysis. The function is nearly rectilinear within the biological range of its values. In this study, a maximum S of 0.99 was encountered in several members of the solenid genus *Ensis*; a minimum of 0.01 was found in individuals of the epifaunal cardiid *Corculum cardissa* (Linnaeus, 1758).

The choice of length as the direction of motion was necessitated by the lack of knowledge of the actual life positions of most bivalves used in this study (Stanley, 1970). The use of this metric is considered a normalizing method. Arguments may be raised against its use based upon the well-known fact that maximum length does not always correspond to burrowing direction. This particularly is true of such groups as the lucinids not treated here (Allen, 1958). This discrepancy between length and direction of movement exists primarily in individuals of very shallow infaunal species, having a low S and no gapage. It can be shown that as S increases, the angle of offset diminishes, for the few species for which data are available (Fig. 10). Most of the species discussed here have an S value > 0.8. Thus, for most the forms covered, the incongruity between length and direction of movement is small. Even at large offset angles the discrepancy is overestimated. The species at this level of S are generally circular in outline, or nearly so. The line of greatest length is a secant through the shell outline, as would be the direction of movement. Both approximately would be equal in length. Height would differ little between the two lines, and Width not at all. The calculation of S may therefore be accurate even at low levels of S.

Relative position of umbo (U)—the measurement of the position of the umbo was divided by total length to standardize this variable. The metric is a percentage of the total length.

Relative depth of pallial sinus (N)—calculated as for U, using depth of pallial sinus.

Relative permanent gape (P)—standardized with the formula:

$$(\text{anterior permanent gape} + \text{posterior permanent gape})/(2 \times \text{width}) \quad (4)$$

Relative exchangeable gape (E)—standardized with the formula:

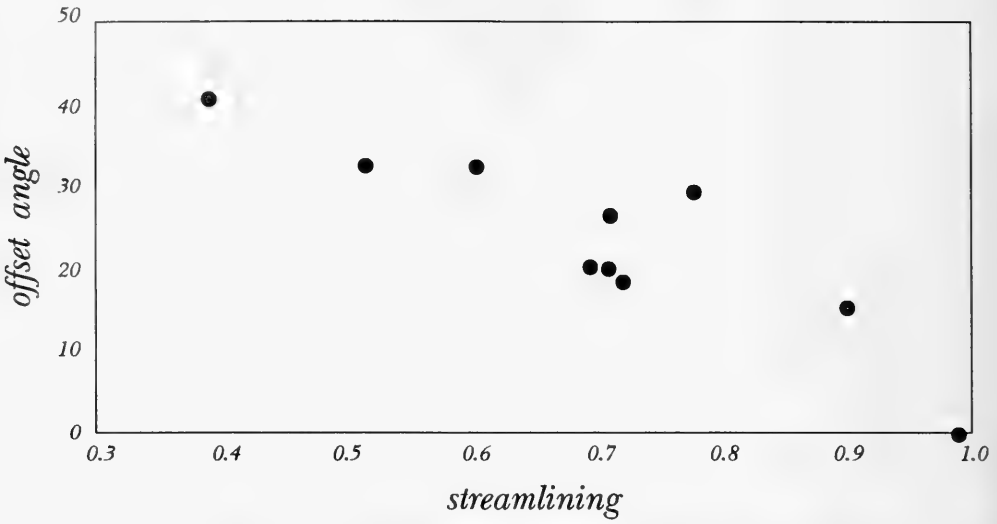


FIG. 10. Offset angle (burrowing angle relative to greatest length) vs. streamlining.

(anterior exchangeable gape + posterior exchangeable gape)/(2 × width) (5)

RESULTS

Comparison of Shell Shapes With Models

Permanent Gapage and Streamlining: A comparison with the results reveals that although streamlining initially does increase as permanent gapage increases, past the intermediate phase the degree of streamlining becomes constant rather than decreases in many individuals (Fig. 11). There are two paths out of the intermediate phase, although the numbers of individuals in that region are so few that it is difficult to make such a claim with certainty. Individuals of the Tellinidae and Myidae conform to the predicted model given above. Deep burrowing forms have lost streamlining and may be sedentary as adults. Members of the solenaceans and some solecurtine psammobiids have maintained high levels of streamlining despite pronounced permanent gapage. This is due in large part to the ability of many of these forms to construct tubes in which they move (Drew, 1907, 1908). The highest degree of streamlining is found in the tube-dwelling members of *Solen.* Levels of permanent gapage and streamlining are both high in these forms because these bivalves no longer burrow through the substrate, but rather move within water filled tubes.

Permanent Gapage and Exchangeable Gapage: The results support the model, but two paths are suggested (Fig. 12). Members of the solenaceans and some solecurtines occupy one path, but the individuals of the Myidae and other members of the Solecurtinae occur on the other path. The first path contains forms having high levels of exchangeable gapage and permanent gapage as the result of their tube-dwelling behavior. It is important to note that members of the Solecurtinae have participated in both paths, and that forms of the mactrids also are diverging. This suggests that members of a single family may not follow a single morphological path. This result occurs in several families.

Permanent Gapage and Relative Position of Umbo: Two paths are evident out of the intermediate phase (Fig. 13). The model predicts 0.5 for maximum exchangeable gapage, but most bivalves have the umbos placed slightly anterior to act as a source of attachment and a buttress for pedal muscles. The intermediate phase average relative position of the umbo is approximately 0.4. From that point (and perhaps before), the umbo may be placed either anteriorly or slightly posteriorly. The forms with anteriorly positioned umbos are those that use the foot either as an anchor

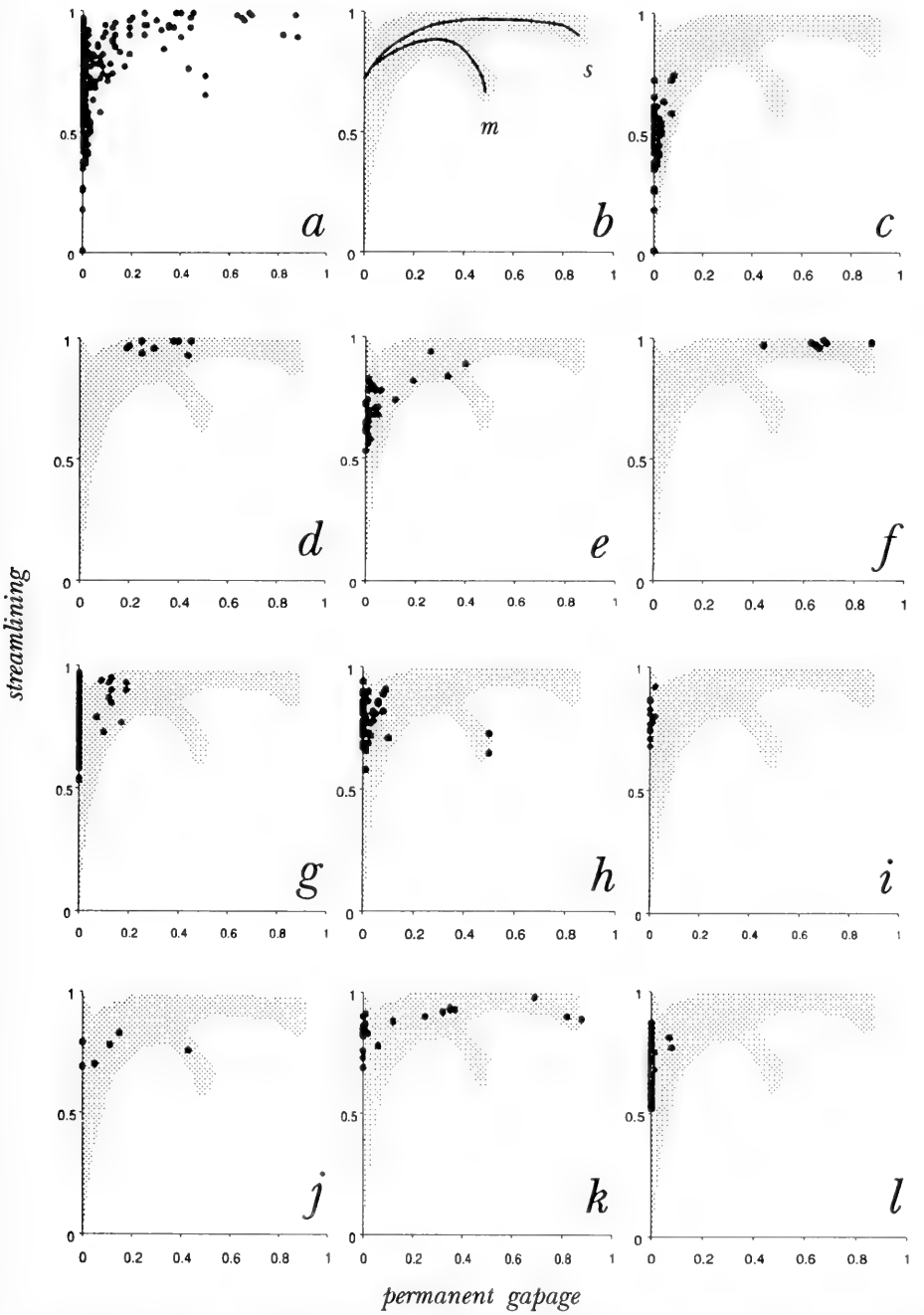


FIG. 11. Permanent gapage vs. streamlining. a: All data. b: Hypothesized paths. c: Cardiidae. d: Donacidae. e: Mactridae. f: Solenidae. g: Unionoida. h: Tellinidae, Semelidae. i: Cultellidae. j: Myidae. k: Psammobiidae. l: Veneridae, Petricolidae. Shaded area: Actual morphospace. m: Myid path. s: Solenid path.

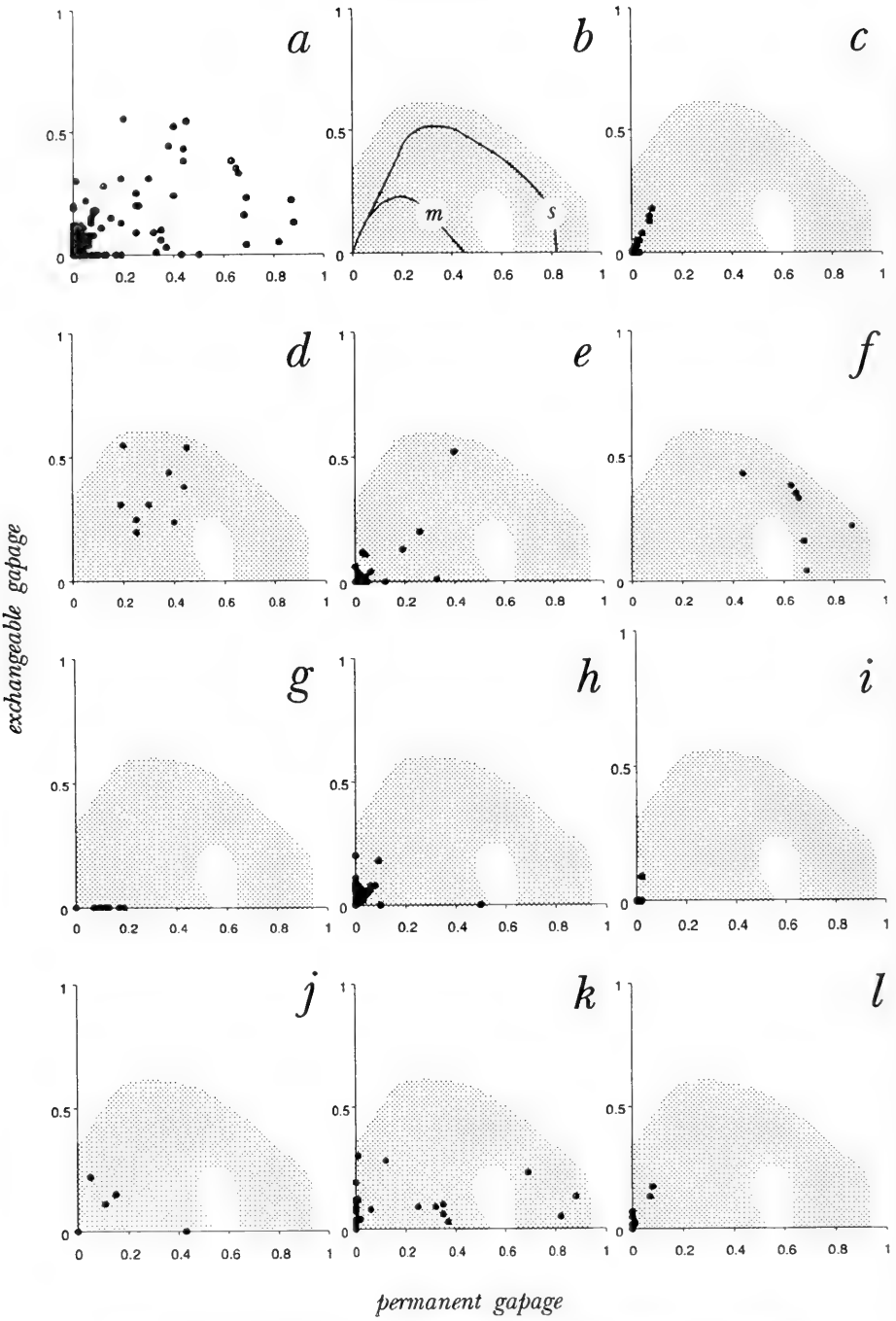


FIG. 12. Permanent gapage vs. exchangeable gapage. See Fig. 11 for details.

(Unionoida) or a wedge within a burrow (solenaceans, cultellids), not as a device for active burrowing. The second path tends toward the theoretical value of 0.5, indicating the emphasis on active burrowing and exchangeable gapage in most of its members (Tellinidae,

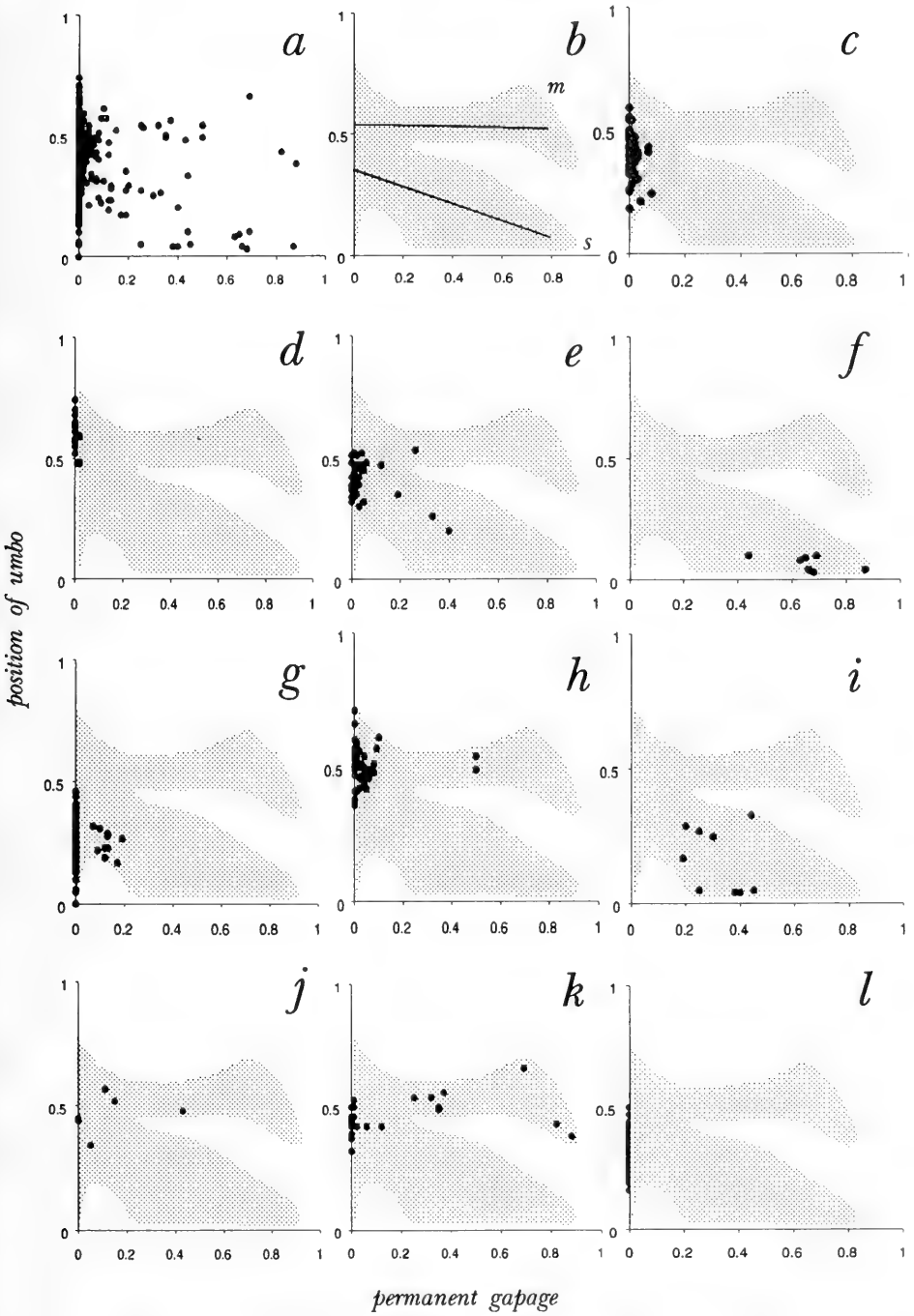


FIG. 13. Permanent gapage vs. position of umbo. See Fig. 11 for details.

Solecurtinae, and others). The families Cardiidae and Mactridae have morphologies tending toward both directions.

Permanent Gapage and Relative Depth of Sinus: The results seem to suggest two ill-defined routes away from the intermediate

phase. One toward slightly increased sinus depth and the other toward greatly reduced depth (Fig. 14). Within members of a family, both paths may be found (Solecurtinae, Tellinidae, and Mactridae). Members of the solenaceans have reduced the sinus to a minimum despite their deep infaunal habitat. This is due to a reduction in siphon length. Individuals of solenaceans live in water-filled tubes and may dwell at the surface, only retreating to the bottom of the burrow to escape.

Exchangeable Gapage and Streamlining: Streamlining is expected to increase into the intermediate phase as exchangeable gapage becomes more evident. The results support this prediction (Fig. 15). Members of all families lie upon a fairly narrow region of the theoretical morphospace. This is unexpected in view of the original prediction: as exchangeable gapage is exapted into permanent gapage, both exchangeable gapage and streamlining should decrease. Thus, there should be a path out and in. However, the parameters used could not differentiate these paths.

Streamlining and Relative Position of Umbo: Two paths are apparent out of the intermediate phase (Fig. 16). The first is toward a slightly more posterior position and contains members of the Tellinidae, Donacidae, Solecurtinae, and Myidae. The second, toward a more anterior placement, contains forms of the solenaceans and the Unionoida. The Mactridae and Veneridae have members in both paths.

Streamlining And Relative Depth Of Sinus: The relative depth of the sinus is predicted to increase into the intermediate phase. Two paths are possible beyond the intermediate phase and this pattern is supported by the results (Fig. 17), along with an unexpected result. Members of the order Unionoida do not participate in this path but reach a high level of streamlining with no appreciable sinus (or siphons). The presence of individuals of the Myidae so far back on the path suggests that the sequence is reversible along its path.

DISCUSSION

Family Accounts

Cardiidae. The cockles are a large family of shallow infaunal dwellers with heavy composite sculpture. Anti-scouring, anchoring, and burrowing sculptures may exist in the same species (Stanley, 1981). These sculptural devices are suited particularly to a shallow infaunal existence. Few members have colonized the deeper infaunal zone.

However, three of the five subfamilies have members that have entered the intermediate phase. None have evolved beyond it. In the Protocardiinae, containing the most primitive living cockles, members of the genus *Lophocardium* are in the intermediate phase. This is a rarely encountered group of perhaps three species. The Laevicardiinae contains the intermediate phase members in the genus *Fulvia*. This genus also is composed of very few species. The Trachycardiinae includes the genus *Papyridea*, containing seven or eight species.

The premier example of a group in the intermediate phase is members of the cardiid genus *Papyridea*. One must know something about their ancestral stock to appreciate their remarkable modifications. *Papyridea* is a genus of the trachycardiinine cockles, which is a widespread group of tropical and sub-temperate species. The members of the subfamily are characterized by: (1) strongly, radially ribbed shells, ornamented with complex composite sculptures used for burrowing and anti-scouring (Stanley, 1981); (2) short siphons, limiting them to a shallow infaunal existence; (3) central, or nearly so, umbos; and (4) a short hinge plate with simple interlocking lateral teeth and centrally located cardinals. The pronounced ribs apparently act as strengthening devices and on the shell margin tend to interdigitate to form a "ventral hinge" (Carter, 1968).

Members of *Papyridea* have these shell characteristics modified into features predicted for exchangeable gapage. The dorso-ventral axis of shell rocking employs the following changes: (1) the central umbo and cardinal teeth become the static dorsal pivot; (2) the interdigitation of the ribs on the ventral margin becomes a dynamic pivot as the sculpture functions like the teeth on two intermeshed gears; and (3) the lateral teeth disengage in the resting position, but alternately mesh as the shells are rocked along the dorso-ventral axis forward or backward. The shell has become more streamlined (S = 0.74) than most other cockle shells. The ribbed sculpture is minimized on the disc of the shell, although the composite sculpture is retained. The ligament is shortened and po-

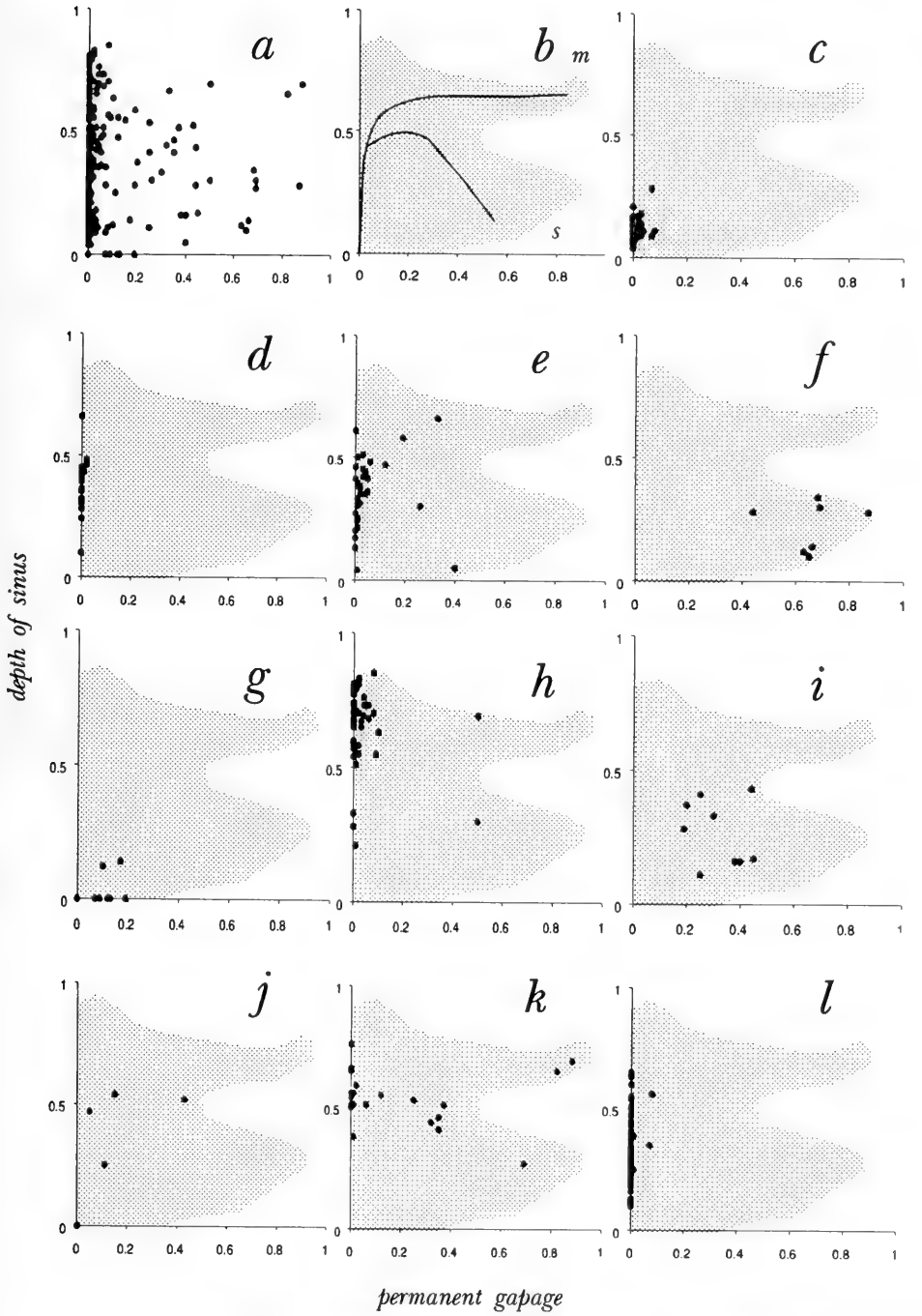


FIG. 14. Permanent gapage vs. depth of sinus. See Fig. 11 for details.

sitioned near the umbo where it does not interfere with the rocking movements. The short siphons have become more elongate (Stanley, 1970). Unlike the shallow infaunal habitat of other members of the Trachycardiinae, members of *Papyridea* are known to burrow

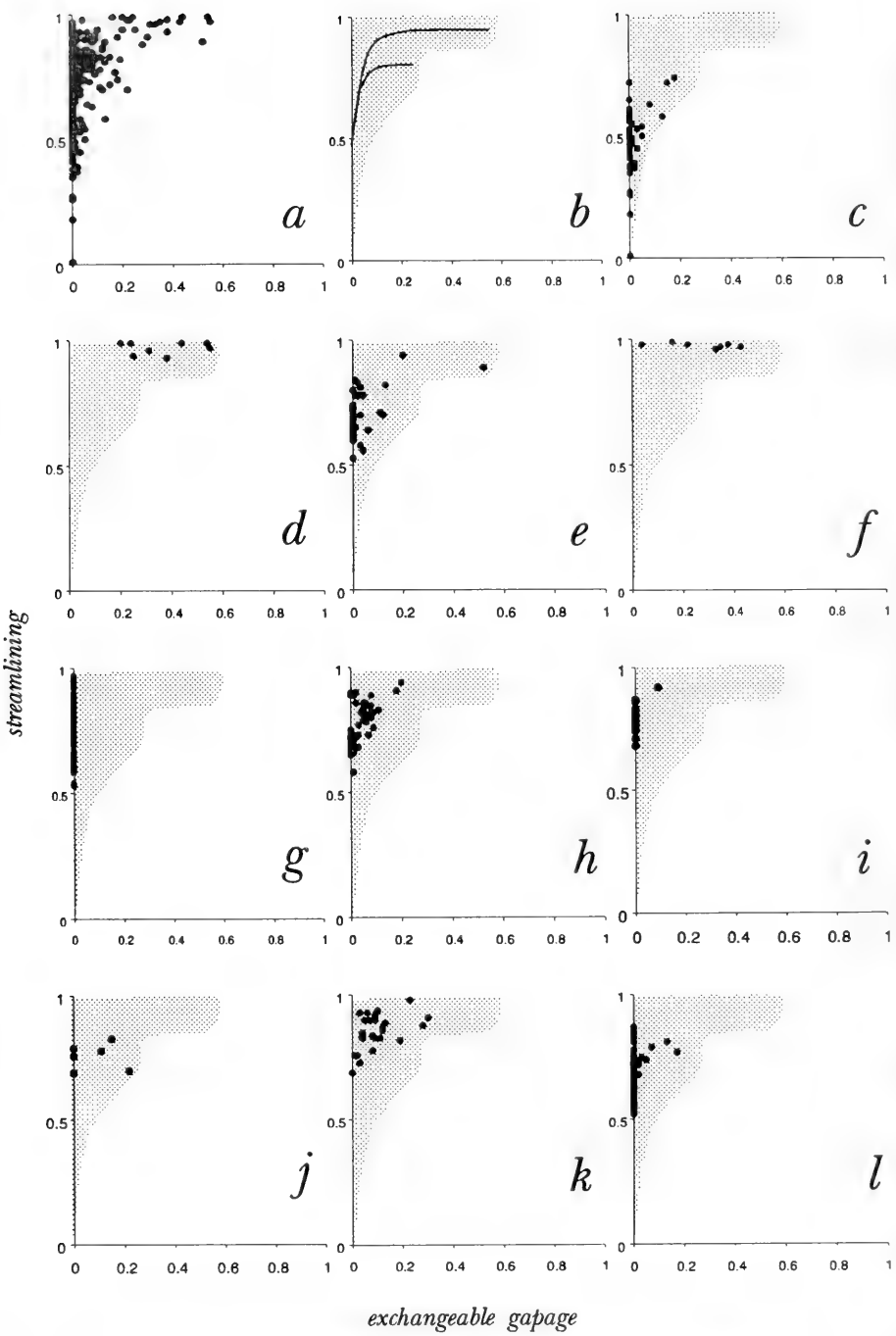


FIG. 15. Exchangeable gapage vs. streamlining. See Fig. 11 for details.

to approximately one half their length and are moderately rapid burrowers. Stanley (1970: 158) stated that an individual of *P. soleniformis* (Bruguière, 1789) "has longer siphons and lives at a greater depth than other cardiids studied."

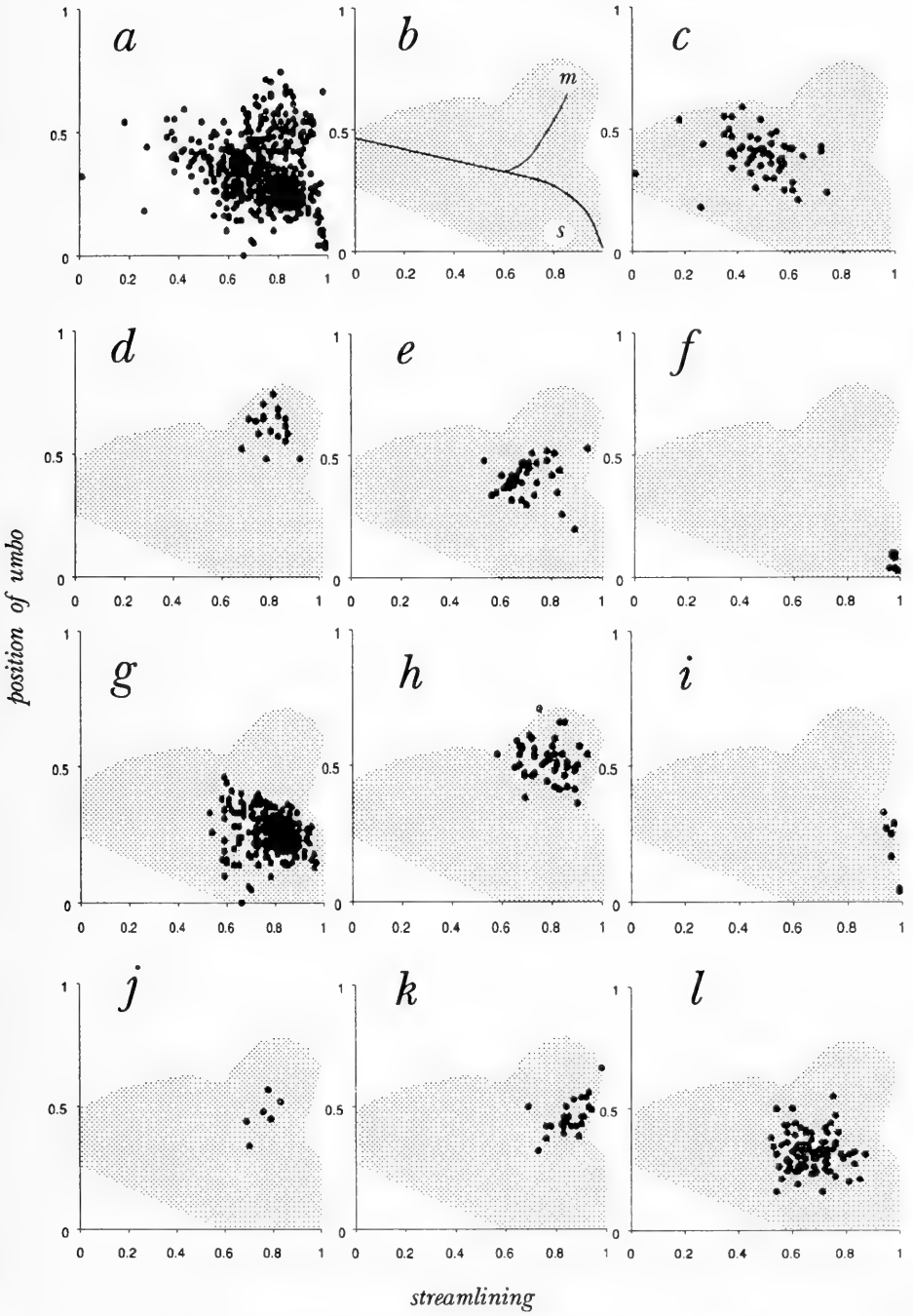


FIG. 16. Streamlining vs. position of umbo. See Fig. 11 for details.

Members of the *Papyridea* lineage are in the process of colonizing the deeper infaunal habitat. It is one of the few modern groups in the intermediate phase. Most bivalves are either bottlenecked behind this position (including most of the members of the Cardiidae), or

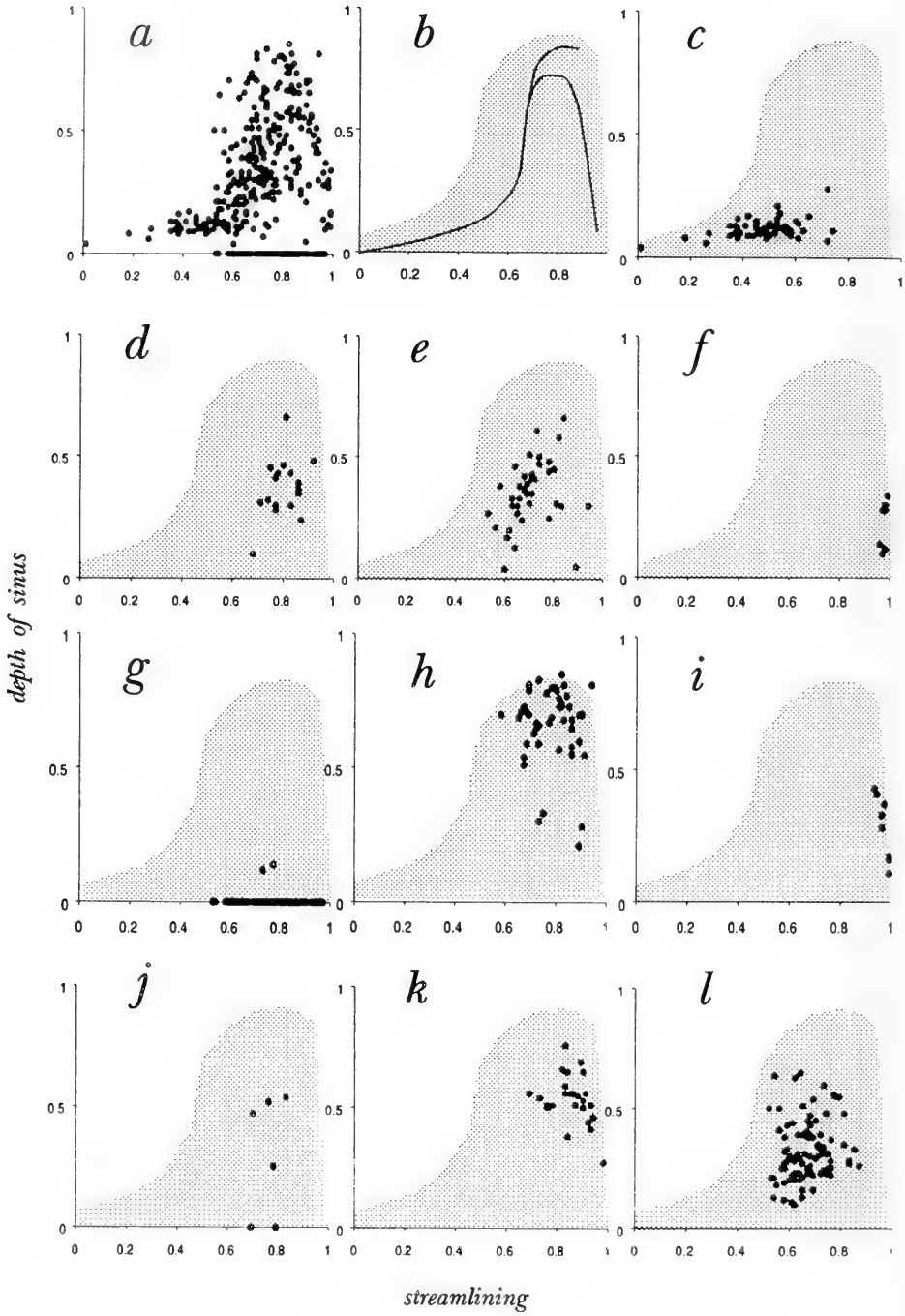


FIG. 17. Streamlining vs. depth of sinus. See Fig. 11 for details.

have advanced into the permanent gapage phase (members of the solenids, cultellids, and solecurtines).

Members of *Papyridea* stand out from the few groups in the same level of transition because of their high degree of modification of

pre-existing shell characteristics. The central position of the umbo, the short central ligament, and the simple lateral teeth all are prerequisite to enter the intermediate phase. It must be emphasized that entry into this phase depends upon the chance alignment of several shell characteristics, therefore the great number of shallow infaunal species bottlenecked behind this morphological barrier.

Veneracea (Veneridae and Petricolidae). The true, or venus, clams comprise the largest single family of living bivalves. Ansell (1961) categorized individuals of this family as soft substrate-dwelling with few burrowing modifications. They successfully have exploited the shallow infaunal zone with little invasion of the deeper infaunal zone. None have achieved a streamlining coefficient greater than 0.9 or a permanent gapage of greater than 0.15. None have entered the intermediate phase. This is because venerids have not achieved the suite of characteristics necessary to enter that part of the sequence. Ansell (1961: 514) remarked that "[in members of the genus *Petricola*], well developed hinge teeth and the long ligament make rocking movements of the shell valves . . . impossible." Yet the members of the group have already begun to diverge along the streamlining/relative position of the umbo paths (Fig. 16). Members of the Meretricinae are tending toward a more central umbonal position. Individuals of the Tapetinae and some elements of the Pitarinae (forms in *Macrocallista*) and the Chioninae (members of *Protothaca*) are on the path toward an anteriorly positioned umbo.

Mactridae. The surf clams encompass more morphological forms than any other family in this study. The group contains venerid-like shallow infaunal forms as well as deep infaunal dwelling individuals reminiscent of some members of the solenaceans. Stanley (1972, 1977a) has pointed out the convergence in morphology of mactrids with that of individuals of such other families as the Myidae, Veneridae, and Tellinidae.

A singular shell design is prevalent in this family and has been modified for the intermediate phase. The ligament has been partially internalized and positioned beneath the umbo in a resilifer, where it serves as a fulcrum during rocking as well as providing the opening moment of the valves (Yonge, 1982). The result is a central ligament independent of streamlining (Seilacher, 1984) and offering little resistance to exchangeable gapage.

Two paths may be taken out of the intermediate phase. Members of four genera have entered the intermediate phase and/or exceeded it into the area of permanent gapage. As in the Cardiidae, the species within each genus are very few. These groups are members of the lutrariinine genera *Lutraria* and *Psammophila*, both of European seas, and the Indo-Pacific zenatiinine genera *Zenatia* and *Resania* [Beu (1966) places the latter in its own subfamily, the Resaniinae]. Members of *Resania* tend toward the path to a centrally located umbo. Members of the other three all lie on a path toward an anterior umbo (Fig. 13). For the relative depth of the sinus, members of *Lutraria* and *Psammophila* are tending toward a deep sinus, whereas those of *Resania* and *Zenatia* are approaching a very shallow sinus reminiscent of that found in members of the solenaceans. For exchangeable gapage, individuals of *Psammophilia* are on the path of the myids, whereas the members of the remaining three genera are on the solenacean path.

Individuals of *Lutraria* and *Tresus* have a reduced foot as adults (Yonge & Allen, 1985), indicative of diminished burrowing ability. Members of *Tresus* may live at substrate depths of 50 cm, where they are sedentary as adults (Yonge, 1982). Cotton (1961: 297) gave this account of an individual of *Lutraria rhynchaena* Jonas, 1844, a species in intermediate phase (note the modifications for exchangeable gapage):

> [It] burrows deeply in sandy mud . . . siphons reaching upwards to the surface. . . . The short ligament allows considerable movement at the ends without opening the shell throughout. With the valves in their ordinary positions the shell gapes equally at each end, but the arrangement of teeth and ligament is such that the front of the shell may be entirely closed.

That members of *Lutraria* lie on the solenacean path is not surprising. Beu (1966) described their life habits as tube dwelling in the manner of individuals of *Solen*.

Beu (1966) also noted the exchangeable gapage of members of *Resania* and *Zenatia*. He believed the former to be an active burrower in sand in the wave zone, and the latter to be a sedentary burrower offshore.

Lineages of the mactrids are evolving (in the sense of the variables studied here) in diverse directions, more so than any other family covered in this study. The family has members in all possible paths and in all three morphological phases.

Tellinacea (Tellinidae and Semelidae). The tellins and semelids are large groups of active, streamlined, shallow to moderate depth burrowing bivalves. Most are unsculptured, and the few groups that are (some members of *Scutarcopagia* and *Strigilla*, for example) have composite burrowing sculptures. They are within the intermediate phase and are on the path of the myids. They have extensive siphons and a pronounced sinus, also a central umbo, and the shell of many forms has some degree of exchangeable gapage. Members of a few species can burrow to moderate depths (Hughes, 1969).

Yonge (1949) believed that forms of the Tellinidae, Solecurtinae, and Donacidae were derived independently from members of the Psammobiinae resembling individuals of *Gari*. Pohlo (1982) offered a different phylogeny, making members of the Tellinidae the end of the sequence Donacidae → Solecurtinae → Psammobiinae → Tellinidae. The present study does not support this contention, and suggests a phylogeny more similar to that of Yonge. Members of the donacids may be an offshoot of the tellins specialized to the high-energy environment of the sandy intertidal zone.

Most, if not all, tellins, also some forms of the psammobiids, have a unique "X"-shaped muscle, the cruciform muscle, connecting the ventral margins of the shells. Yonge (1949) noted that this muscle occurs at the ventral base of the siphonal attachment and believed that it functioned to anchor the siphons at this margin during protraction and retraction. This muscle group also could serve as a ventral connection during a rocking motion, limiting the ventral pivot to a specific point. This differs from the dynamic ventral pivot of most other groups in the intermediate phase.

Psammobiinae and Sanguinolariinae (Psammobiidae). Members of these subfamilies are the morphological precursors of the solecurtine psammobiids, and occupy the intermediate phase for this family. They are morphologically the analog of the tellins. But unlike them, members of the Psammobiidae have a permanent gapage group, the Solecurtinae. Members of the family lie upon the myid path.

Solecurtinae (Psammobiidae). Individuals of this subfamily are a fairly small group that resemble the razor clams in many shell characteristics. Members of the Solecurtinae, except forms of *Tagelus*, do not construct tube-like burrows, and have extensive siphons (and deep sinuses). The members of *Tagelus* are similar ecologically and behaviorally to those of the solenaceans (Stanley, 1970). They occupy many of the same paths as that group. The major difference is the position of the umbos, which are central in members of *Tagelus* and anterior in solenaceans. Other groups of solecurtines are on different morphological paths.

Solenaceans. The razor clams have diverged from most infaunal bivalves in behavior and habitat. They construct tube burrows in which they move horizontally. This habit has produced a distinct alternative path out of the intermediate phase. Siphons and sinus may be greatly reduced because the animal may dwell at the surface, becoming deep infaunal in the sense of this study only to avoid danger. Because they can retreat into the deep substrate, permanent gapage is available. As tube dwellers, the highly streamlined shape is retained at maximum permanent gapage. This combination of characteristics has led to two paths out of the post-intermediate phase morphologies. Yonge (1951c: 429) recognized the important principle that shell and anatomy are separate entities: "There is the fundamental, though largely unrecognized, fact that throughout the Mollusca the growth of the body and the growth of the shell must be considered separately."

Myidae. The myids are few in species number but quite variable in morphology and ecology. Members of the genus *Cryptomya* live at depths of up to 50 cm, have only short siphons, and "tap" into the water filled cavities of burrowing crustaceans and echinoderms (Yonge, 1951a). Members of *Platyodon* bore into soft stone (Yonge, 1951b). These specializations aside, the members of the genus *Mya* illustrate the expected result of the modeled path. All exchangeable gapage has been modified into permanent gapage, streamlining is reduced, teeth are non-functional, and the sinus is shallow as the siphons become increasingly non-retractable. Like forms in the Mactridae, the myids have a central, internalized ligament carried within a resilifer (Yonge, 1982). Analogs in the Hiatellidae (not included in this study), are individuals of *Panopea*, the geoduck clams.

Order Unionoida. Members of the four families of the freshwater unionoids participate in few of the paths discussed here. This seems attributable to their lack of fused mantle tissue, necessary to form siphons. Without siphons, deep burrowing is not obtainable un-

less tubes are constructed, as in the solenaceans, a behavior unknown in members of the Unionoida. Although the members of the unionoids achieve a high level of streamlining, this type of shell form appears to function in quick reburial rather than in efficient movement while buried (Watters, in prep). Individuals of the unionoids lie upon the solenacean path rather than upon the path of the other groups studied for streamlining and the relative position of the umbo. This is not to imply that unionoids are following the solenaceans in morphology. Individuals of unionoids have no true siphons (with the possible exception of members of *Leila*), usually cannot burrow far below the substrate/water level, and do not construct burrows.

Pholadacea. Although not used in this study, the shipworms and relatives briefly are discussed here because of their novel use of exchangeable gapage. The antero-posterior rocking motion of the shells is used not only to protrude foot and siphons, but as a mechanical rasping device to excavate burrows in wood, shell, and stone. The shell and musculature have been reorganized to maximize this movement. These innovations have been discussed by Röder (1977) and Hoagland & Turner (1981). A recent study (Fuller & Castagna, 1989) also documents the complicated ontogeny of individuals of one species of this group.

Underlying Assumptions and Paradigms

The fundamental assumption of this study is that there is a definite selective advantage to becoming deep infaunal. The underlying question, then, is why aren't there more deep infaunal bivalves? The reason is related to the possible ways that a bivalve shell can be modified for this habitat. These modifications require a particular suite of characteristics, and only bivalves having this prerequisite suite can colonize the deep infaunal region. If the morphology of the lineage cannot be modified, that group cannot succeed in that habitat. Entry into this sequence would be rare if there was little or no adaptive significance to the lineage possessing the suite, or if another suite had high selective value. In the former case, the acquisition of the suite would depend on random fluctuations in the characteristics of the morphology. In the latter, there may be no impetus to move from one adaptive peak to another. A paucicity of deep-dwelling forms would be the expected result if either of these factors occurred in the evolution of the bivalves. Convergence also would be the expected result if only a few viable sequences of morphologies were available.

These constraints are due in part to the interactions between sediment and shell with increasing depth of burial. For simplicity, I will consider the substrate to be homogeneous. The addition of heterogeneous and stratified sediment variables, while a much more realistic scenario, cannot adequately be accounted for in this model. It is suggested that the simpler model may be extrapolated to the more complex.

The mechanics of burrowing in shallow infaunal bivalves have been documented by Trueman (1966), Trueman et al. (1966a), and Stanley (1970, 1975). However, the members of all groups studied, such as *Mercenaria mercenaria* (Linnaeus, 1758) in Stanley (1975), have low S values, no exchangeable gape, and no permanent gape. The steps in burrowing in such forms may be given briefly:

(1) The foot probes the substrate.

(2) The siphons are closed.

(3) Adductor muscles close the valves, raising pressure in the haemocoel, which is transferred to the foot, forming an anchor.

(4) Simultaneously, water is ejected from the mantle cavity, which momentarily loosens the immediately surrounding substrate.

(5) The anterior pedal retractor contracts, pulling the animal forward against the anchored foot.

(6) The posterior pedal retractor contracts, returning the shell to the original burrowing position.

(7) The adductor muscles relax, diminishing haemocoel pressure and redirecting fluid out of the anchored foot. The siphons are opened.

This process continues until the animal is buried. Other factors also may be involved. Sculpture may assist burrowing, as may the presence of a prosogyre shape and a lunule (Stanley, 1969, 1975, 1981). But the focus of this study is deep-dwelling bivalves. The burrowing model given above may work for only a few of the groups in this study. The rocking motion around a dorso-ventral axis becomes impossible to accomplish as shells become more elongate (S increasing; Stanley, 1970). The foot must protrude from the anterior gape and is often as large in cross-section as the shell in streamlined forms. It appears, by its larger size, to be much stronger than the foot

of shallow infaunal burrowers of the same shell size. Eagar (1978) reported that the force of the pedal retractors may be equal to 100 times the weight of the shell in water in individuals of deep dwelling *Ensis*, but equal to only one-quarter the weight in members of shallow infaunal *Mercenaria*. These factors may be necessary in these groups to offset the lack of burrowing assistance that is found in shallow-dwelling forms afforded by the burrowing movement, shell sculpture, and lunule. Expulsion of water to loosen sediment appears still to be important. Many deep-dwelling forms have ventrally fused mantle tissue that presumably directs water forward during a burrowing cycle.

The ability to enter efficiently the substrate is a function of shell shape. Nair & Ansell (1968) found that elongate shells offer the least resistance to burrowing. In this study, the design most suited to burrowing is found in the entity having the highest S value, all other factors being equal. This often takes the form of a laterally compressed, antero-posterior elongated blade-like shape. Sculpture typically is lost, and Stanley (1970) has shown that coarse-sculptured species are slow burrowers. In members of a species that have both infaunal and epifaunal individuals, the infaunal morphs are more elongate (Seed, 1980a). Within the same genus, deep-burrowing members are more streamlined than are shallow-burrowing ones (Alexander, 1974; Eagar, 1974), although Agrell (1949) made a correlation between shell morphology and the trophic level of the water body.

The sediment load pressure increases with increasing depth of burial (Nair & Ansell, 1968). The animal must exert a force to open and maintain open the shells (Stanley, 1970). In bivalves this is accomplished typically by the ligament and/or haemocoel pressure. The shells must be opened to allow protrusion of the foot and siphons. Trueman et al. (1966a, b) have shown that the sediment pressure may exceed the opening moment of the ligament at critical depths, effectively limiting burial depth. One solution to this problem is the incorporation of permanent shell gapes into the morphology. The foot and siphons may be protruded through these openings or permanently left exposed. But the primary function of the shell is defense, and therefore the vast majority of epifaunal or shallow infaunal forms have complete closure of the valves. But a selective advantage is to be gained by penetrating the substrate further, including a concomitant decrease in predation and an increase in habitat stability.

A solution to this problem requires having the shells retain their function as protective devices, while allowing the foot and siphons to protrude in a manner independent of the ligamental opening moment. Such a suite of characteristics does exist, and apparently represents the only compromise found in living bivalves. I have termed this unique morphology the intermediate phase, between the shallow and deep infaunal existence phases. It has a suite of predictable and testable characteristics that may be compared with actual forms.

The key innovation is exchangeable gapage (Fig. 1). The shells rotate along a dynamic dorso-ventral axis rather than along the dorsal hinge axis. Movement is effected by the adductor muscles rather than by the weaker ligament or haemocoel pressure. Contraction of the anterior adductor muscle closes the anterior (pedal) gape and opens the posterior (siphonal) gape. Contraction of the posterior adductor muscle has the opposite effect. Several important morphological requirements must be met for this mechanism to work.

First, the umbo must be approximately central. This orientation allows the maximum amount of exchangeable gapage at both ends. Second, the ligament also must be central and reduced. A long opisthodetic ligament would not allow rocking along a dorso-ventral axis. Third, cardinal teeth must be retained to act as the dorsal pivot of the axis. Lateral teeth may or may not be present, but if present, they must be able to disengage smoothly as the rocking movement takes place. Forth, the valve commissure must be open anteriorly and posteriorly, creating a gape when the shells are rocked.

This morphology may have an adverse side effect. The simultaneous contraction of the adductor muscles may split the valves at the umbo along a line of structural weakness if the shell is sufficiently thin. This is known to happen in all members of the anomalodesmacean genus *Laternula* and some *Periploma* (Morton, 1976). Individuals of other species, all within or past the intermediate phase, may have an internal rib or buttress at this position to counteract the stress: *Nuculites* (Nuculidae); *Capistrocardia* (Saxicavidae); *Cleidophorus* (Ledidae); *Siliqua, Cultellus*, and *Phaxus* (Solenacea); *Sanguinolaria*, *Nuttallia*, *Solecurtus*, and *Tagelus* (Psammobiidae); among others (Gill & Darragh, 1964, and this study). In other

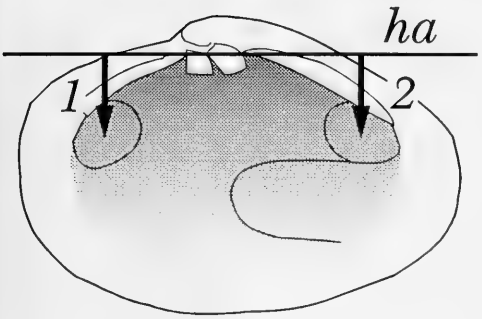


FIG. 18. Opening moment of movement around hinge axis (ha). 1: Anterior torque arm. 2: Posterior torque arm. Magnitudes of torque arms do not change during movement.

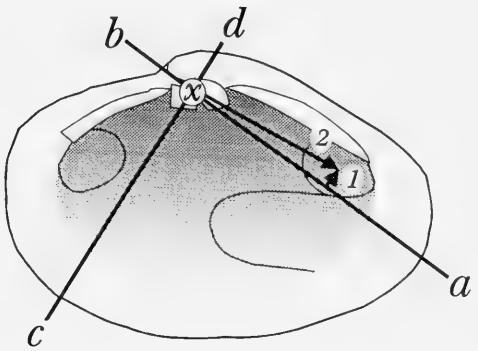


FIG. 19. Opening moment of movement around dynamic dorso-ventral axis. x: Fixed pivot at cardinal teeth. 1: Posterior torque arm at minimum posterior closure with axis along ab. 2: Posterior torque arm at maximum posterior closure with axis along cd. Magnitude of torque arm changes during movement. Anterior torque arm would behave in the opposite manner.

species, additional buttresses may be present.

The presence and the position of these buttresses are not simply the result of adductor muscles contracting within a shell with anterior and posterior gapes during normal closure (around the hinge axis). Factors influencing the disposition of internal buttresses are tied to the mechanics of exchangeable gapage. In most shells, the valves rotate along an axis determined by the hinge line, particularly the line through the ligament. The insertions of the adductor muscles on the valves remain the same distance from that axis throughout contraction and the adductor muscles work in concert (Fig. 18). The situation is different during the process of exchangeable gapage. The dorsal pivot of the axis is anchored, usually by the cardinal teeth. But the ventral pivot moves along the ventral margin of the shell, sweeping out an angle defined by the anterior-and posterior-most positions of the axis (Fig. 19). The distance from the adductor muscles to this dynamic axis changes in a linear fashion during this rocking motion. The adductor muscles are antagonistic during this motion.

Thomas (1975) estimated the amount of force generated during valve closure, the adductor moment, by:

$$(\text{cross-sectional area of adductor}) \times (\text{distance to axis}) \qquad (6)$$

The cross-sectional area is an estimate of force. The distance to the axis represents the torque arm. In his calculations, which involved no exchangeable gapage, the adductor moments are constant during closure. The moments during exchangeable gapage are not (Fig. 20). The lines of adductor moments may or may not cross, depending on the location of the adductor muscles and the shape of the shell. If the shell is thin, a buttress generally will occur near the angle at which the moments are equal. This angle represents the point during an exchangeable gapage rocking motion that the anterior and posterior adductor forces are equal, thereby placing maximum strain on the shell between them if they are contracted simultaneously (Fig. 21). The buttress reinforces this region. Buttresses also may occur at the beginning and end of the exchangeable gapage angle. These may counteract the forces generated by the adductor muscles attempting to contract beyond the limit of the allowable angle. The central buttress may be placed at the bisection of the angle, but other evidence suggests that it is dependent on the point of equal moments. For the individual in Figure 22, the lines do not cross and the central buttress is absent, although the two flanking ones limiting the angle are prominent. Figure 23 illustrates the moment lines for a form in which the lines cross only at the end of the angle. The formation of internal buttresses is a modification for forces generated on the shell by the adductor muscles during exchangeable gapage.

Past the intermediate phase, the deeply buried bivalve may take on equally predictable characteristics. Movement within the sub-

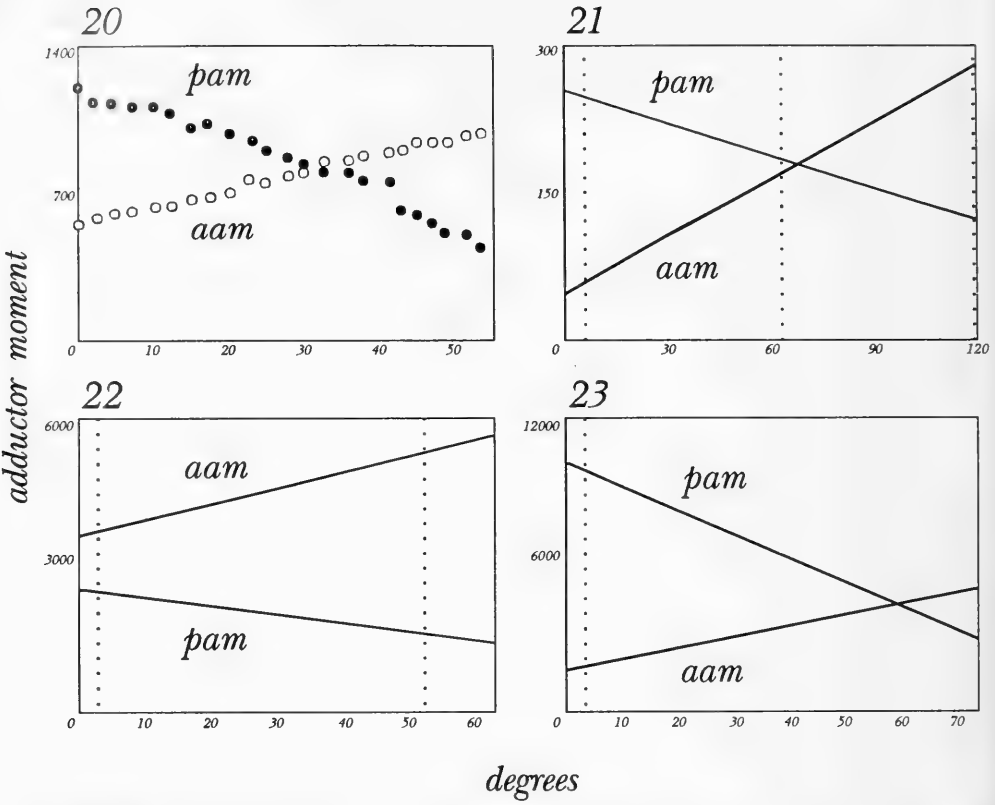


FIG. 20. Anterior (aam) and posterior (pam) adductor moments for *Tresus nuttali* (Conrad, 1837) through entire angle of exchangeable gape.
FIG. 21. Anterior (aam) and posterior (pam) adductor moments for *Tagelus divisus* (Spengler, 1794), through entire angle of exchangeable gape. Dotted lines indicate angles at which buttresses are positioned.
FIG. 22. Anterior (aam) and posterior (pam) adductor moments for *Resania lanceolata* Gray, 1862, through entire angle of exchangeable gape. Dotted lines indicate angles at which buttresses are positioned.
FIG. 23. Anterior (aam) and posterior (pam) adductor moments for *Siliqua patula* (Dixon, 1789), through entire angle of exchangeable gape. Dotted lines indicate angles at which buttresses are positioned.

strate is minimized as exchangeable gapage is modified into less streamlined permanent gapage. Shell shape may return to a non-streamlined form reminiscent of the shallow infaunal stage. Sculpture, lost in the transition, remains absent as the substrate becomes the primary protective device (Stanley, 1970). Shell thickness, also originally protective, may be minimized (Stanley, 1970; Morton, 1976). The teeth, reduced or weakly meshed in the intermediate phase, may become rudimentary as all shell/shell movement is lost (both along the horizontal hinge line and along the dynamic hinge of exchangeable gapage). The siphons may become partially or wholly non-retractable, resulting in a decrease of the sinus depth. Members of some species have been shown to possess an atrophied foot as an adult, suggesting a sedentary habit. Individuals of *Panopea abrupta* (Conrad, 1855), a hiatellid, may live immotile in burrows 90 cm deep (Yonge, 1949).

Evolutionary Considerations

Most forms studied are uniform for the calculated parameters. The position of the umbo is distributed about a mode of 0.3. The depth of the sinus is generally less than 0.1 (reflecting the large numbers of members of the Unionoida in the study). Streamlining is quite high, with a mode of 0.9, indicating that most bivalves, even shallow infaunal ones, are somewhat streamlined. But high levels of ex-

changeable gapage and permanent gapage are rare. This suggests that most forms are still in the streamlining phase of the sequence. Few have made the transition to the intermediate phase. Why is this the case?

To enter the intermediate phase requires a specific set of shell characteristics. The umbo and cardinal teeth must be central, the laterals must be able to disengage, and the ligament must be short and central. Presumably, this suite of morphological characteristics is not met in most bivalves. This has resulted in a bottleneck at the intermediate phase. Species occurring before this stage are numerous. It is hypothesized here that the acquisition of the necessary combination of characteristics needed to continue in the sequence may be determined by chance. Like billiard balls thrown at random on the table, one may drop in the pocket, but most continue rolling.

Once in the intermediate phase, morphological change may be rapid. The change from intermediate phase to exchangeable gapage phase may be brief on a geological time scale. Radiation usually is rapid after a morphological or ecological innovation (Hoagland & Turner, 1981). Of the several hundred species of Mactridae, members of fewer than a dozen are in the intermediate phase, and the percentage is less for forms in the Cardiidae. Although members of the Mactridae have been in existence since at least the late Cretaceous, the groups now in the intermediate phase are no older than the Miocene. But within that small group, speciation may be high. Beu (1966) has recognized three distinct lineages within the members of the genus *Zenatia*.

Geary (1987) found that slow rates of change in the lineage of species of *Pleurocardia* are punctuated with quick major changes. Stanley (1977a) and Stanley & Yang (1987) also found low levels of phyletic change in members of the Veneridae and Tellinidae, two families with members still predominantly in the streamlining phase. The bottlenecking of morphologies has created a steady, but low rate of evolution in these taxa. Even so, as stated by Stanley (1979: 118), "there is no evidence that a limit [to diversity] is being approached even after more than 400 My of radiation." But the acquisition of the intermediate phase must be seen as a major morphological step opening a new area of the morphospace.

Within and after the intermediate phase, members of lineages would be expected to radiate to fill the new morphospace. As an example, the Anomalodesmata is a large, diverse group, with many of its members tending toward deep-dwelling, sedentary habits (Morton, 1977). The Solenacea also is a large group of species, the members of most in the permanent gapage phase. They are recognizable as solenaceans as far back as the Cretaceous, suggesting that they had passed through the intermediate phase prior to that time. Most of the basic adaptive radiation of the Bivalvia had occurred by the Cretaceous (Nicol, 1986), though 96% of the species, and 52% of the families became extinct during the Permo-Triassic extinction (Raup, 1979). This suggests that the sequence of morphologies discussed here is an ongoing process, taking place asynchronously in different lineages as the necessary morphological prerequisites are obtained.

No clades have been defined in this study of Recent species. The phylogeny of most bivalves is too insufficiently known to allow the concepts developed here to be tested by the fossil record. If the sequences of shell shape change are reversible, then the precursors of modern groups may have assumed a wide variety of forms. While some obvious trends within clades exist, such as those culminating in *Papyridea*, others are too ambiguous. The trends in shell shape described here are trends between clades acting simultaneously on unrelated taxa.

Is the evolution of these groups predictable? To a certain extent the answer may be yes. If continued studies show that other groups of bivalves lie along these paths, then we may assume that bivalve lineages entering a path may evolve toward the shell shapes of individuals already on the path. The great degree of convergence in bivalves supports this hypothesis. Several groups, such as the mactrids and venerids, have members in both the myid and solenacean paths. Members of *Resania* look remarkably like those in its solenacean counterpart, *Phaxus*. They occupy the same place in the path. Will there eventually be a mactrid counterpart to *Solen*? Members of *Lutraria* already have adopted the tube dwelling habit of that genus.

SUMMARY

A hypothesis is advanced to explain: (1) the changes in shell shape in individuals of spe-

cies as a continuously deeper infaunal habitat is colonized; and (2) the degree of convergence in shell shapes among infaunal bivalves. A maximum depth of burrowing for streamlined morphologies will be reached as sediment weight becomes significant. Up to this point, forms will adopt streamlined shapes for more efficient penetration of and movement in the substrate.

To achieve a deeper infaunal existence requires that the shell possess gapes through which the foot and siphons may extend. This would make the animal susceptible to predation and other immediate environmental dangers because the shell functions as the main defensive mechanism. Only one morphological "solution" has been adopted by the bivalves. This entails the antero-posterior rocking of the shell such that a pedal or siphonal gape alternately may be opened and closed. Because this action is caused by the adductor muscles, rather than by the much weaker ligamental or haemocoel opening mechanisms, the problem of sediment weight has been bypassed at this depth. The acquisition of exchangeable gapage requires several preexisting morphological conditions. These conditions must be modified to new functions in this stage of development, termed here the intermediate phase.

The cardinal hinge teeth must still function as a dorsal pivot, but on a dorso-ventral axis. These teeth must be located centrally to maximize exchangeable gapage. The laterals must be able to disengage (or no movement along that axis could take place). The hinge must be centralized to avoid interference with the rocking motion of the shells. This may be accomplished by a shortening of the ligament or the internalizing of it in a resilifer ventral to the umbo.

Movement into a deeper infaunal position may be possible once the intermediate phase is reached. This entails a further decline in predation and environmental extremes. At this point, exchangeable gapage may be modified into permanent gapage. The animal may be sedentary, with a reduced foot and externalized siphons. Shell thickness may decrease as the result of the reduced dependency on the shell for defense.

Comparisons between these models and the actual shell shapes of the individuals of the species studied show a general agreement. The morphologies are found in the predicted morphospace. The hypothetical suite of specialized characteristics does occur in real species in the intermediate phase. Members of lineages follow a specific path, a sequence of body shapes, as they increasingly become infaunal. This results in unrelated species sharing the same general morphological pattern because they are at the same point on this path. The constraints of this sequence are such that some paths may move in both directions, whereas in others a separate course may exist for each direction.

Two paths occur out of the intermediate phase, termed here the solenacean and the myid paths after the typical member of each route. The solenacean path differs because of the behavior of its members, which construct tube burrows, allowing the shell to retain its streamlining along with exchangeable gapage. The unionoids appear to lie on this path but the convergence is superficial. The members of that group lack the fused mantle tissue necessary to form true siphons.

That so few forms exist in the intermediate phase or in the exchangeable gapage phase supports the idea that the specific suite of shell characteristics necessary to enter the intermediate phase has not been attained by most groups. Shallow infaunal species, though high in diversity, are bottlenecked at this point. The entry into the intermediate phase may allow a new morphological radiation. This passage may be quick in geological time and be largely the product of chance.

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A CLADISTIC REASSESSMENT OF OCTOPODID CLASSIFICATION

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ABSTRACT

Octopodid classifications have been traditionally, and are currently, based on a few readily apparent characters. In this analysis, I examine methods that have contributed to octopodid classifications from a cladistic perspective that emphasizes the recognition of monophyletic groups, and I apply parsimony algorithms to the data set reported by Voss (1988a) for the Octopodidae. I reject current and previous subfamily classifications of the Octopodidae as having created paraphyletic groups. Use of the category subfamily should be avoided, as it implies our knowledge of octopodid evolution has reached level that is as yet unattained.

To further our knowledge of octopod phylogeny, we must define primitive and derived characters states by objective criteria, consider only monophyletic species groups in our analyses and expand the range of characters considered. Analysis of the data set compiled for cladistic analysis reveals that characters of the radula, anterior digestive system and skin change in concert. These associated character changes may indicate underlying functional relationships that have been unsuspected.

Key words: Octopodidae, parsimony analysis, Graneledoninae, Eledoninae, Bathypolypodinae, Octopodinae, systematics, radula.

INTRODUCTION

Taxonomic treatments intended to identify astonishingly different, or to separate overtly similar, specimens have produced the current classification of coleoid cephalopods. This scheme, similar to Naef's (1923) reconstruction of ancestor-descendent relationships, groups taxa based on morphological similarity, with primitive characters contributing as much as derived characters. That comparatively few characters support subfamily groups in octopodids have been cited as evidence of the family's chaotic evolution (Robson, 1932). Whether these formally recognized morphologically distinct groups constitute monophyletic lineages that share a common evolutionary history is unknown.

Phylogenetic reconstruction through phylogenetic or cladistic analysis seeks to recognize only monophyletic groups. The possession of shared derived characters (synapomorphies) is the criterion on which monophyletic groups are recognized. Neither shared primitive characters (symplesiomorphies) nor character states unique to a single taxon (autapomorphies) provide information concerning relationships.

Cladistic analysis considers as many presumed synapomorphies as possible. Homoplasy (whether due to parallelism, convergence or reversal) affects some character changes, but these are assumed to be fewer than the character changes that reflect unique modification with descent from a common ancestor. Cladistics uses the absolute criterion of parsimony to evaluate alternate hypotheses of relationships; parsimony dictates that the hypothesized relationship that requires the fewest number of character changes is the most likely to reflect history.

In this paper, I test the extent to which octopodid classification is supported by cladistic analysis. I apply parsimony analysis to the characters reported by Voss (1988a). My intent is to introduce a cladistic perspective to octopodid systematics, to examine implicit assumptions that may have affected earlier treatments of the group and to assess the information contained in traditional characters.

THE OCTOPODS

Among octopods, the bathypelagic taxa of the suborder Cirrata are unified by the presence of fins, cirri and internal shells, all primitive characters (Naef, 1923; Robson, 1932; Voss, 1988a). Members of the suborder Incirrata, which occur throughout the water column and in benthic habitats, are united by the absence of these characters, and by egg care by the female, and associated characters (Boletzky, 1992). Among the incirrates, male reproductive characters and pelagic habitats

TABLE 1. Octopodid classifications of Grimpe (1921, 1922), Robson (1932), Thiele (1934) and Voss (1988a). Listed are the subfamilies and their diagnostic characters; in addition to these characters, geographic and depth distribution are also cited in subfamily definitions.

Reference	Subfamilies	Sucker rows	Ink sac	Other characters
Grimpe	Octopodinae	2	±	small eggs
(1921, 1922)	Eledoninae	1 or 2	±	large eggs
Robson (1932)	Octopodinae	1 or 2	±	typical
	Bathypolypodinae	1 or 2	−	reduced crop, gills, radula; large eggs, spermatophores, squat body; double funnel organ; narrow mantle aperture
Thiele (1934)	Octopodinae	1 or 2	+	generally small eggs
	Bathypolypodinae*	1 or 2	−	reduced crop; large eggs & spermatophores; short arms; narrow mantle aperture
	Ozaeninae (Eledoninae)	1	+	large eggs
Voss (1988a)	Octopodinae	2	+	
	Bathypolypodinae	2	−	
	Eledoninae	1	+	
	Graneledoninae	1	−	

*Including *Benthoctopus* and *Teretoctopus*, despite the large crop of *Teretoctopus*.

define membership in the argonauts; multicuspid radular teeth and adaptation to the mesopelagic zone define members of the Ctenoglossa. The Octopodidae, with the most recognized species, contains the benthic octopuses. Prominent among the few characters that have contributed to octopodid classification (Table 1) are the number of sucker rows and the presence or absence of an ink sac.

Members of the Octopodidae range from the intertidal zone to over 3500 m depth and from the equator to the polar ice caps (Voss, 1988b). I follow taxonomic tradition in assuming that the Octopodidae represent a monophyletic group. Although Naef (1923) suggested the pelagic Argonautida are derived from *Octopus s. s.*, I assume here that the characters cited as uniting these groups (e.g. double sucker rows, ink sac) are better attributed to convergences and symplesiomorphies than to synapomorphies (Robson, 1932; Voight, 1990).

Based on similarities in their radulae, the monotypic taxon, *Vitreledonella*, has been suggested to be an octopodid derived for the mesopelagic habitat (Robson, 1932). Although *Vitreledonella* lacks the multicuspidate radula that has defined the Ctenoglossa (an apparent clade of the meso- and bathypelagic octopods), this taxon and the ctenoglossid *Amphetritus* share a rotated digestive system unique in the Cephalopoda (Thore, 1949). I tentatively consider *Vitreledonella* to be a ctenoglossid (Voight, 1990) and exclude it from this analysis.

METHODS

Taxa that serve as the operational taxonomic units (OTUs) in this analysis are octopodid genera. Genera that Toll (1991) recently revitalized are not included, pending complete diagnoses. The characters Voss (1988a) cited as diagnosing nonoctopodine genera and his polarity assessments are summarized on Table 2. For genera not included by Voss (1988a), data were gathered from specimens and literature accounts. Octopodine genera other than *Scaeurgus* and *Pteroctopus* (i.e., *Robsonella, Hapalochlaena, Cistopus, Enteroctopus, Euaxoctopus*), however, do not differ from *Octopus* in the characters considered (Robson, 1929; Roper & Hochberg, 1988; Hochberg et al., 1992). These taxa were excluded, as autapomorphies cannot contribute to the analysis.

The data matrix (Appendix 1) was analyzed by PAUP (Version 3.0) using subtree pruning-regrafting and the MULPARS option (Swofford, 1989). The specified ancestor (Appendix 1) served to root the analysis. Characters with polarities defined by Voss (1988a; Table 2)

TABLE 2. Characters, character state definitions, and stated reasoning behind polarity definitions (Voss, 1988a).

0 = ancestral character state; 1 = derived state.
1. Number of sucker rows: 0 = one; 1 = two (after Naef).
2. Ink sac: 0 = present; 1 = absent (known in fossil cephalopods).
3. Crop: 0 = with diverticulum; 1 = with dilation. (Loss of diverticulum is a modification to small prey.)
4. Posterior salivary glands: 0 = large; 1 = small; 2 = vestigial. (Large is normal in shallow-water forms.)
5. Rachidian lateral cusps: 0 = present; 1 = absent (commonality).
6. Lateral tooth: 0 = present; 1 = absent (commonality).
7. Marginal plates: 0 = present; 1 = absent (commonality).
8, 9. Funnel organ: 00 = W-shaped; 01 = VV; 10 = IIII (commonality).
10. Gill lamellae per demibranch: 0 = 9 or more; 1 = less than 9. (Reduction assumed to be adaptive in the deep sea.)
11. Egg length: 0 = less than 11 mm; 1 = 12–13 mm; 2 = over 15 mm (polarity rationale unclear).
12. Spermatophore size: 0 = small; 1 = medium; 2 = large (commonality, also small in cirrates).
13. Mantle aperture width: 0 = narrow (A or B); 1 = wide (C) (polarity rationale unclear).
14. Skin texture: 0 = smooth; 1 = papillose; 2 = tubercles (polarity rationale unclear).
15. Supra-ocular cirri: 0 = absent; 1 = present (polarity rationale unclear).

were entered as ordered; characters with uncertain polarities (egg length, mantle aperture width, skin texture, supra-ocular cirri; Table 2) were entered unordered.

States of functionally related characters were examined to assess whether characters changed independently, or in concert. If associated changes were identified, characters were recoded as a single, multistate character.

RESULTS

Analysis of the data set (Appendix 1) resulted in at least 1999 equally parsimonious trees (35 steps, consistency index 0.514). The strict consensus tree, which depicts groups supported by all equally parsimonious trees, revealed two groups, one containing *Pareledone, Eledone, Octopus, Benthoctopus* and *Teretoctopus*, and the other containing the remaining nine genera. None of the 1999 equally parsimonious topologies (Fig. 2) are consistent with Voss' evolutionary tree (Fig. 1). Voss' tree, when analyzed by cladistic methods requires 49 steps, i.e. 14 steps (40%) more than the most parsimonious solution.

Relaxation of the strict consensus constraint illustrates relationships supported by some (in this case by at least 60%) but not all, of the alternate trees (majority rule consensus n = 60%). *Bathypolypus* is suggested to be more closely related to *Graneledone, Thaumeledone* and *Bentheledone* than to any taxon with which it shares biserial suckers. Of

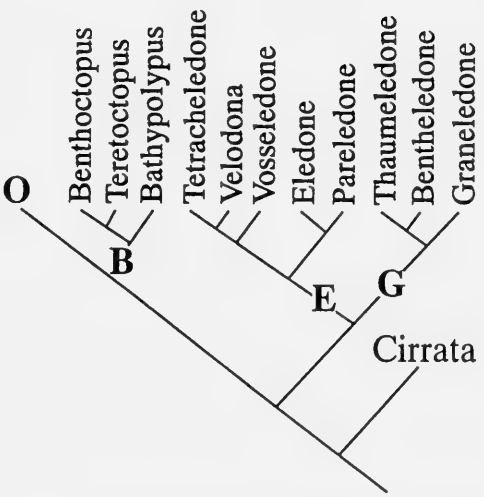

FIG. 1. The evolutionary tree presenting subfamily and generic relationships of the benthic Octopodidae, rooted to the Cirrata, excluding oceanic forms (after Voss 1988a: 274). 0, Octopodinae; B, Bathypolypodinae; E, Eledoninae; G, Graneledoninae.

Voss' generic relationships (Fig. 1), close relationships between *Benthoctopus-Teretoctopus* and *Thaumeledone-Bentheledone* are supported at the indicated levels. The strict consensus tree requires the number of sucker rows to change and the ink sac to be lost at least twice. The majority rule consensus arrangement requires these changes, and an additional change in the number of sucker rows.

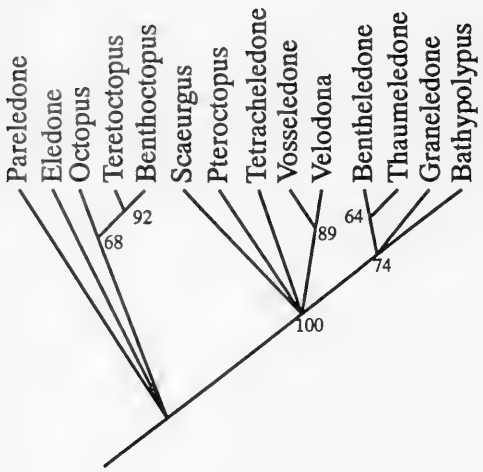

FIG. 2. Diagrammatic results of the cladistic analysis of data set in Appendix 1, rooted to the hypothetical ancestor. Numbers at the nodes indicate the proportion of the 1999 equally parsimonious trees discovered that support that node. The node indicated by 100 is the limit of resolution supported by all equally parsimonious trees.

Examination of the data matrix (Appendix 1) reveals that several functionally related characters change in concert. All taxa that lack marginal plates (character 7) also lack lateral teeth (character 6); all taxa that lack lateral teeth also have a homodont rachidian (character 5). These changes in the radula appear to occur in a cascade pattern. A similar suite of changes is also seen in the anterior digestive system (no taxon with small posterior salivary glands, character 5, has a crop diverticulum, character 4) and between skin texture and supraocular cirri (characters 14, 15). Recoding associated characters as single multistate characters maintains the information in the original data matrix, reflects the associated nature of the changes and condenses the number of characters from 15 to 11 (Appendix 2).

DISCUSSION

Cladistic analysis (Fig. 2) of characters traditionally used in octopodid classification indicates that the octopodid subfamilies are, and have been, paraphyletic (Table 1). Although these subfamilies have been defined on comparatively obvious differences, they cannot be held to share evolutionary histories.

The uncertain status of octopodid subfamilies has been a subject of earlier discussion. In Robson's original (1928) definition, the Bathypolypodinae (two sucker rows and no ink sac) included *Bathypolypus, Benthoctopus* and *Teretoctopus*. In 1932, Robson redefined the group (Table 1) to include *Bathypolypus, Graneledone, Thaumeledone* and *Bentheledone*, with *Benthoctopus* and *Teretoctopus* assigned to the Octopodinae. Robson (1932: 49–56) apparently recognized that, although his original definition of Bathypolypodinae created a morphologically distinctive and cohesive group, the presence of multiple characters refuted monophyly of the Eledoninae and a close relationship between *Bathypolypus* and *Benthoctopus*.

Robson stated that his (1932) definition of the Bathypolypodinae may have made the Octopodinae paraphyletic; Figure 2 supports this suggestion. Because *Scaeurgus, Pteroctopus, Tetracheledone, Vosseledone* and *Velodona* appear to share a more recent common ancestor with members of the Bathypolypodinae than do *Pareledone, Eledone, Octopus, Teretoctopus* or *Benthoctopus* (Fig. 2), including them in the Octopodinae creates an unnatural group that exists only in the classification. Voss (1988a), rejected Robson' subfamilies, in essence, to return to those erected earlier.

As we appear to be unable to define subfamilies that are even arguably monophyletic, use of the taxonomic category of subfamily should be avoided. The presence of an artificial category implies a level of knowledge that we have yet to achieve; in doing so, it impedes the discovery of evolutionary histories. Octopodid groups may best be defined for discussion by ecological or ontogenetic criteria, for example, holobenthic (Boletzky, 1992).

Among the major problems octopod systematics faces is how to define ancestral states. In this analysis, the definition of the hypothetical ancestor as nearly identical to shallow-water taxa ensures that deep water taxa will be found to be derived. This traditional view (Naef, 1923; Robson, 1925, 1932; Voss, 1967) may be an artifact of the taxonomic need to distinguish comparatively rare specimens of deep water taxa from familiar, normal octopuses.

That the common ancestor of the incirrate octopods was a benthic octopod, based on

the rationale that the loss of the fins would not be adaptive in pelagic forms (Boletzky, 1992), has canalized the way we think of the group. Young (1977) attributed the absence of the supra-branchial commissure in the ctenoglossan *Japetella* to loss associated with adaptation to a pelagic habitat from a benthic ancestral state. In that evolutionary scenario, the possibility that the suprabranchial commissure is a synapomorphy shared by octopodids and argonauts is eliminated from consideration.

To ensure alternate octopodid relationships are considered, primitive states must be defined by objective criteria such as outgroup analysis or ontogeny (see discussion by Bryant, 1991). Whether a given character state is widely distributed, occurs in the most common species, or characterizes the most diverse taxon, does not demonstrate that it is ancestral.

Systematic studies of octopodids are also hindered by our inability to define monophyletic species groups. Taxonomy succeeds if specimens can be assigned to genera; systematics fails if genera do not share a common history. Members of the genus *Pareledone*, for instance, are separable from those of *Eledone* and *Graneledone*. Whether they represent divergent octopodid lineages that lack the diagnostic synapomorphies, or are united by a unique history is unknown and cannot be discovered with the available characters. The taxon Eledoninae of Voss (1988a), and the genus *Octopus* itself are affected by the same problem. These taxa are the leftovers after the removal of those with synapomorphies. Incorrectly assuming monophyly for species groups obscures patterns of character change, and can undermine the analysis.

Too few characters of uncertain (or uncontested) homology also limit phylogenetic reconstruction of the octopodids. Characters of loss and reduction dominate this data set. Although Begle (1991) showed reductive characters to be as informative as character gains, and Voss & Voss (1983) found losses as informative as gains in their cladistic analysis of the cranchiid squids, in this analysis too few positive characters are available to test this statement. Perhaps because taxonomy has focused on differences between deep-sea and shallow-water octopuses, several of the characters used here (e.g. ink sac, crop, posterior salivary glands, gill lamellae, egg size, mantle aperture) are losses and reductions that may be under direct selection in deep-water habitats (Robson 1925, 1932; Voss, 1967, 1988a).

Every opportunity must be used to increase our knowledge of octopod biology. Because cladistic analysis requires explicit definition of the characters and character states considered in the analysis, the data set documents associated change in characters (Appendices 1, 2). The presence of associated change may indicate the existence of a functional relationship among characters that might otherwise be undetected; it can provide insight into the biology of the animals.

The radular reductions among the octopodids that have been viewed as independent (characters 5–7, Appendix 1) show unexpectedly orderly character change (Appendix 2). Only taxa in which the rachidian is homodont lose the first lateral tooth; only taxa without the first lateral teeth lose the marginal plates. This sequence suggests that the radulae of taxa with homodont rachidians differ functionally from those with a multicuspid rachidian, in which the radular teeth may function as a mutually supporting bracing mechanism (Solem & Roper, 1975). Similar changes in the digestive system, that only taxa without a crop diverticulum have small posterior salivary glands, suggest that these taxa allocate digestive enzymes differently. The changes appear to be neither independent nor random, although we must demonstrate that they are functionally associated. Defining each of these conditions as separate inflates the number of characters without increasing the information entered into the analysis. Eleven characters cannot resolve relationships among 14 taxa.

It may be argued that these data were not intended for parsimony-based methodology, and that cladistic analysis violates the premise and rationale behind their collections and initial analyses. Other, undocumented characters may have contributed to the recognition of these taxonomic groups. Group definitions relying on subtle, inexpressible similarities, however, only further support that morphological cohesiveness defines the groups. Explicit reliance on these few characters, and on paraphyletic groups they have created, has limited our knowledge of octopod evolution. We must recognize and eliminate artificial taxonomic divisions to begin modern systematic treatments of this cosmopolitan marine group. Shedding preconceived notions may free us to discover the monophyletic groups that evolution has produced.

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APPENDIX 1. Reported are the data matrix, including for each OTU, characters coded as indicated on Table 2 (9 = character absent, or polymorphic within genus), the total number of characters coded as derived and the estimated mean depth distribution of each genus (Voss, 1988b).

	CHARACTER NUMBER									1	1	1	1	1	1		
OTU	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	Σ	Depth
ANCESTOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
OCTOPUS	1	0	0	0	0	0	0	0	0	0	9	0	0	0	0	1	46
ELEDONE	0	0	0	0	0	0	0	0	9	0	9	0	9	1	0	1	157
PARELEDONE	0	0	0	0	0	0	0	0	9	0	0	0	9	9	0	0	481
TERETOCTOPUS	1	1	0	9	0	0	0	1	0	0	9	9	9	0	0	4	907
BENTHOCTOPUS	1	1	0	0	0	0	0	0	9	0	1	9	0	0	0	3	1060
SCAEURGUS	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	4	275
TETRACHELEDONE	0	0	0	0	1	0	0	1	0	1	0	1	0	2	1	6	364
PTEROCTOPUS	1	0	1	1	0	0	0	0	1	0	0	0	9	1	1	6	410
VOSSELEDONE	0	0	0	0	1	1	1	0	1	1	1	1	1	1	9	9	105
VELODONA	0	9	0	0	1	0	0	0	1	0	9	1	1	2	1	6	588
GRANELEDONE	0	1	1	1	9	9	0	0	1	1	1	2	0	2	1	9	1721
BATHYPOLYPUS	1	1	1	1	1	0	0	0	1	1	0	2	0	1	1	10	790
THAUMELEDONE	0	1	1	2	1	1	0	0	1	1	0	2	0	1	0	9	1388
BENTHELEDONE	0	1	1	2	1	1	1	0	1	1	1	2	0	1	9	11	3354

APPENDIX 2. Data matrix recoded to reflect associated (cascading) changes in character states, and thus the reduction in the number of characters from 15 to 11. Characters defined as in Table 1, except 3, 5 and 14, below.

	CHARACTER NUMBER										
							1	1	1	1	1
OTU	1	2	3*	5*	8	9	0	1	2	3	4*
OCTOPUS	1	0	0	0	0	0	0	9	0	0	0
ELEDONE	0	0	0	0	0	9	0	9	0	9	1
PARELEDONE	0	0	0	0	0	9	0	0	0	9	9
TERETOCTOPUS	1	1	0	0	1	0	0	9	9	9	0
BENTHOCTOPUS	1	1	0	0	0	9	0	1	9	0	0
SCAEURGUS	1	0	0	0	0	0	0	0	1	0	2
TETRACHELEDONE	0	0	0	1	1	0	1	0	1	0	3
PTEROCTOPUS	1	0	1	0	0	1	0	0	0	9	2
VOSSELEDONE	0	0	0	3	0	1	1	1	1	1	1
VELODONA	0	9	0	1	0	1	0	9	1	1	3
GRANELEDONE	0	1	1	9	0	1	1	1	2	0	3
BATHYPOLYPUS	1	1	1	1	0	1	1	0	2	0	2
THAUMELEDONE	0	1	2	2	0	1	1	0	2	0	1
BENTHELEDONE	0	1	2	3	0	1	1	1	2	0	1

3*. 0 = crop diverticulum; 1 = crop dilation; 2 = crop dilation and posterior salivary gland reduction.
5*. 0 = radula with 7 teeth; rachidian multicuspid; 1 = radula with 7 teeth, rachidian non-cuspid; 2 = rachidian non-cuspid and lateral teeth absent, 3 = rachidian non-cuspid, lateral teeth and marginal plates absent.
14*. 0 = smooth skin; 1 = papillose skin; 2 = papillose skin with supra-ocular cirri; 3 = tubercles and supra-ocular cirri.

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THE ARRANGEMENT OF SUCKERS ON OCTOPODID ARMS AS A CONTINUOUS CHARACTER

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ABSTRACT

Studies of octopodid taxonomy and classification have cited the number of longitudinal sucker rows on octopus arms as if it were a purely dichotomous character. This character, however, has been suspected to be continuously distributed and associated with increased sucker density (Hoyle, 1886; Berry, 1914). This study tests that hypothesis by comparing the relationship between the mean number of suckers per arm to mean arm length among octopodid genera occurring above 500 m depth. Specimens of genera typified by a single sucker row but with suckers arranged in a zigzag pattern are also included.

Most specimens with two sucker rows and with suckers arranged in zigzags have more suckers at a given arm length than do specimens with suckers arranged in a single row, supporting the hypothesis. Most specimens with one sucker row are separated from those with two rows by a curve on the plot of the number of suckers versus arm length, although four specimens of *Pareledone* spp., preserved with their arms straightened into a swimming position rather than recurved, and the holotype of *Aphrodoctopus schultzei* are exceptional. The number of suckers on the arms of these specimens predict that they will be arranged in one row. The zigzag arrangement seen on the specimens may be due to preservation artifact in the case of the specimens of *Pareledone* and in *A. schultzei* by the 6–8 enlarged suckers on each arm. Variation in the number of suckers within groups defined by the number of sucker rows is greater than that between groups, suggesting that the number of sucker rows is a continuous character. Evidence provided here indicates that *A. schultzei* should be included among the species of *Eledone*.

Key words: Octopodidae, sucker rows, classification, continuous character, *Eledone*, *Aphrodoctopus*.

INTRODUCTION

Octopodid taxonomy and systematics is entering a dynamic period; preliminary attempts to reconstruct evolutionary relationships among members of the Octopoda (Voss, 1988; Voight, 1990) have lead to a reassessment of our assumptions about the group (Voight, 1991, 1993; in press). One such assumption, expounded by Voss (1988), is that the number of longitudinal sucker rows on the oral surface of the octopus arm is a dichotomous character that accurately reflects evolutionary relationships.

Whether suckers on an octopus arm form one or two longitudinal rows has featured prominently in diagnoses of octopod families (Rochebrune, 1884; Joubin, 1918), subfamilies (Voss, 1988), and genera (e.g. Robson, 1932; Roper & Mangold, 1991). Statements such as in young *Eledone* "as suckers are added they never form two rows" (Hochberg et al., 1992: 265; similarly, Rochebrune, 1884) reflect the degree to which the character is thought to be dichotomous. Yet, the arms of specimens of *Eledone* and *Pareledone* sometimes carry suckers arranged in double rows, or in a zigzag pattern where the number of rows is arguable (Hoyle, 1904; Joubin, 1905, 1918; Gravely, 1908). Preservation may contribute to the formation of double sucker rows in these genera (Guérin, 1908), but live animals also show sucker arrangements considered to be anomalous for their taxon (Chadwick, cited by Gravely, 1908; Naef, 1923).

Whether the number of sucker rows on an octopus arm is a valuable character for reconstructing phylogenies has been questioned (Owen, 1881; Hoyle, 1886; Berry, 1914; Naef, 1923). Based on his discovery of only slight differences in the sucker musculature between specimens of *Octopus*, with two sucker rows, and those of *Eledone*, with one sucker row, Guérin (1908) doubted that sucker arrangement was an adequate basis on which to distinguish the genera. Berry (1914) suggested that octopus suckers are inherently organized in a single row and that only because of crowding are suckers displaced alternately to the side. He felt that this displacement created the appearance of a double sucker row.

The biological significance of this character had yet to be evaluated despite this alternate hypothesis.

This paper tests the hypothesis that sucker crowding is associated with the formation of double sucker rows by examining the relationship between the number of suckers on an arm and arm length among octopodid genera typically occurring above 500 m depth. Specimens of taxa characterized by one sucker row that have suckers in a zigzag arrangement are predicted to show the same pattern as taxa with two sucker rows. The phylogenetic significance of sucker arrangement is assessed.

MATERIALS AND METHODS

To test the hypothesis that the formation of double sucker rows is associated with sucker crowding, the number of suckers on octopus arms with one sucker row was compared to that with two sucker rows as a function of arm length. The hypothesis predicts that more suckers will occupy arms with two rows than with one row at the same arm length. Specimens of taxa typified by one row with suckers arranged in a zigzag pattern will reflect the pattern shown by specimens with two sucker rows.

Specimens included in this analysis (n = 142) were from the California Academy of Sciences, San Francisco; Field Museum of Natural History, Chicago; Rosenstiel School of Marine and Atmospheric Science, University of Miami; the United States National Museum, Washington, D.C.; and University of California Museum of Paleontology, Berkeley. Octopuses with suckers arranged in a double row were represented by specimens of *Octopus*, *Hapalochlaena* and *Macrotritopus* and the type specimen of *Macrochlaena* (Robson, 1926). Data from Toll (1988) for *Cistopus*, *Pteroctopus*, *Robsonella* and *Scaeurgus* and from Roper & Mangold (1991) for *Aphrodoctopus* increased the number of genera with two sucker rows included. Data from Toll (1988) also increased the data available for species of *Octopus*.

Representing octopuses with suckers arranged in a single row were typical specimens of the genera *Eledone*, *Pareledone*, *Vosseledone*, and *Tetracheledone*. To ensure complete and unbiased representation of the taxa, eight data points for *Pareledone* were taken from reports of Joubin (1905), Berry (1917), Adam (1941), Taki (1961) and Kubodera & Okutani (1986); seven points for *Eledone* were from Massy (1916), Rees (1956) and Adam (1951, 1984). Three specimens of *E. cirrhosa* and data from the type of *P. turqueti* (Joubin, 1905), all with suckers in a zigzag arrangement, were included. Only taxa with mean depth distributions above 500 m were included to avoid the effects of decreased sucker size associated with increased depth distribution (Voight, in press).

Suckers were counted as described by Toll (1988), using a combination of macroscopic and microscopic techniques. Suckers on right arms I-IV were counted; left arms were used if the right were damaged. Only normal arms were used for data analysis; injured arms or those with incomplete regeneration were excluded. Hectocotylized arms of males (one of the third pair of arms specialized for spermatophore transfer) were considered separately from normal arms.

The analysis requires that each datum be independent, that is, free of any correlations or association with other data in the analysis. Because all non-hectocotylized arms of an individual specimen are subject to identical genetic and environmental variables or controls, they are not independent. Statistical tests of the working null hypothesis, that each normal arm of an individual specimen has the same number of suckers, were prohibited by the small sample size within an individual, inevitable errors in counting, and errors in regeneration that may have failed to restore all suckers. This hypothesis was rejected if the number of suckers on different arm pairs varied consistently in all available specimens of a given species.

Only male specimens of *Eledone caparti* were available, and only in this species was the null hypothesis rejected, as indicated by Adam (1950). Typical of *Eledone*, these males have sucker-derived modifications at the arm tips (Haas, 1989: Fig. 2). When the number of modifications and suckers were summed, the result was virtually invariant within an individual (Table 1). Because within individual specimens of all other species examined, the number of suckers was essentially equal among the arm pairs, data taken from only one or two arms were considered representative and were included.

Despite the anomalous pattern seen on arms of *E. caparti*, sucker counts of males with heteromorphic arm tips were represented in the analysis by mean sucker num-

TABLE 1 Sucker counts, heteromorphic arm tip counts and arm lengths for normal arms and hectocotylized arms (R3) of males of *Eledone caparti*.

Specimen	ARM	Suckers	Modif.	Total	Arm Length (mm)
A.	R1	98	35	133	193
	R2	97	34	131	143
	R3	41	—	41	76
	L3	59	82	141	111
	R4	60	73	133	106
B.	R1	89	36	125	174
	R2	72	63	135	115
	L3	59	77	136	94
	R3	43	—	43	65
	R4	57	80	137	95
C.	R1	85	45	130	179
	R2	54	47	101	104
	R3	41	—	41	64
	L3	REGENERATING			
	R4	41	68	109	78

ber, rather than by the sum of suckers and modifications. Because the modified suckers at the arm tips are very strongly reduced in size, e.g. over 14 can occupy 1 mm in males of *E. caparti*, including them would have biased the results against the hypothesis being tested.

The number of suckers on, and the lengths of, the normal arms of each individual specimen were meaned. To compare the number of suckers on normal arms of octopuses with one sucker row to those with two sucker rows independent of differences in size, the mean number of suckers was plotted versus mean arm length for each individual.

Using arm length as the univariate proxy of size carries with it liabilities. Voight (in press a) hypothesized that the different parts of the muscular octopus body respond to preservation equally, allowing measurements within a preserved specimen to be compared without net preservation bias, as shown by Voight (1991). Because preservation-linked changes affect arm length but not the number of suckers, such biases affect only the x-axis in this analysis. The arms of flaccid specimens may appear abnormally long with comparatively few suckers; contracted arms may appear short with many suckers. To moderate the effect of this bias, a large size range of specimens was included. Arm length rather than a multivariate size measure was used here because it is easily determined, requires no statistical expertise, and is a biologically realistic measure by which to compare the number of suckers.

Data from hectocotyli were analyzed directly. The number of suckers versus hectocotylus length was plotted for male specimens of each species.

RESULTS

On the normal arms of the octopuses considered, virtually all specimens with suckers in double or zigzag rows have more suckers at a given arm length than do those with one row. With few exceptions, points representing specimens with one sucker row can be separated from those representing specimens with two sucker rows by a curve on the plot of sucker number versus arm length (Fig. 1). Specimens of *Eledone cirrhosa* and the type of *Pareledone turqueti*, both with suckers arranged in a zigzag pattern, have more suckers at the same arm length than do congeneric specimens of comparable size with suckers arranged in a single row; they fall on the two-rowed side of the curve.

Four specimens of *Pareledone* and the holotype of *Aphrodoctopus schultzei* violate this pattern. Suckers on these five specimens were arranged in double rows or in zigzags, despite plotting with specimens with a single sucker row (Fig. 1).

Most specimens of *Pareledone* have fewer than 50 suckers on an arm, however, specimens of *P. senoi* (Taki, 1961; Kubodera & Okutani, 1986) diagnosed as the genus *Megaleledone* based on their large size, appear to have up to 65 suckers (Fig. 1). Arms

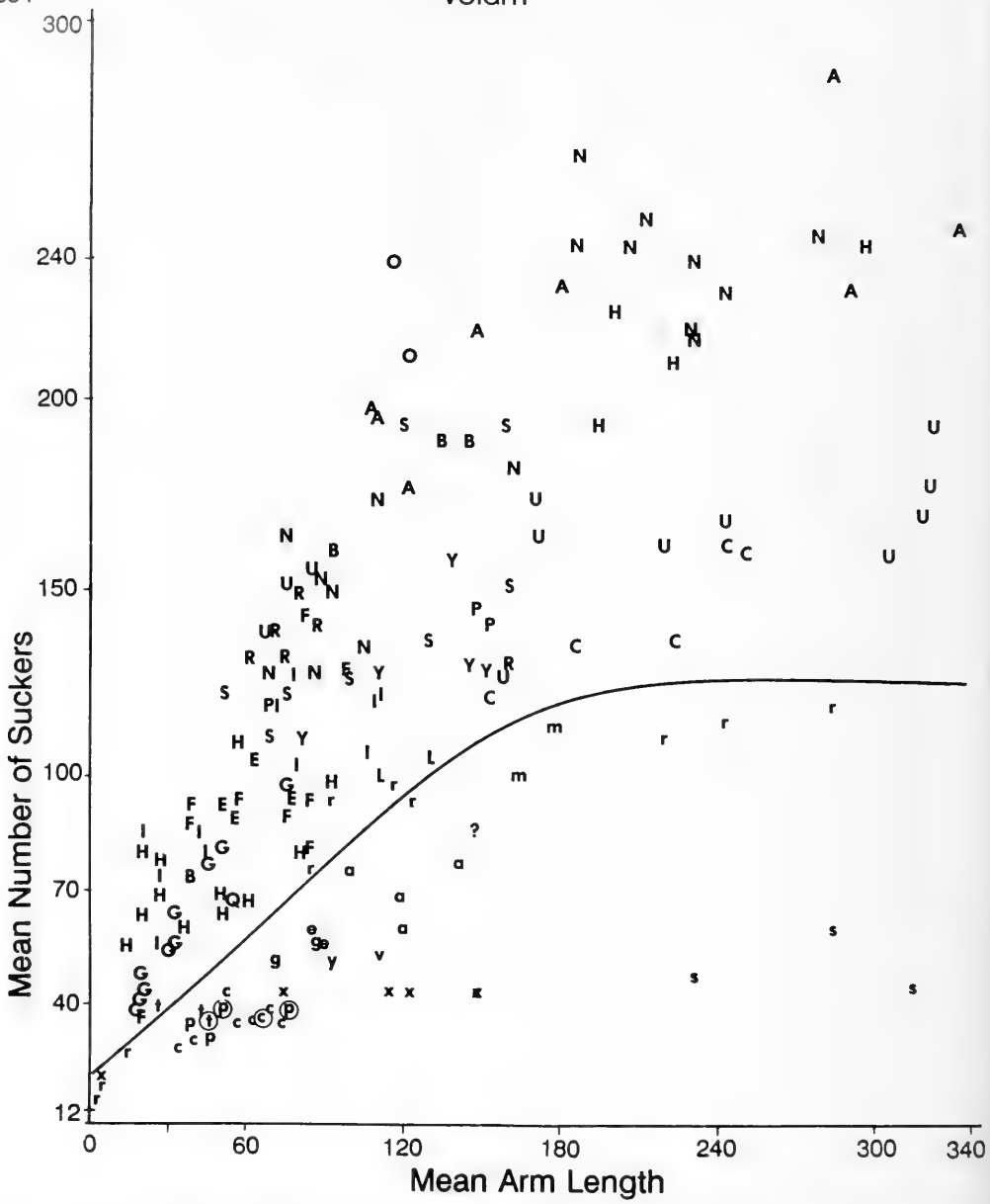

FIG. 1. Plotted for the normal arms of each specimen are the mean number of suckers versus the mean arm length. Upper case letters represent specimens with a double sucker row: A, *Octopus bimaculatus*; B, *O. briareus*; C, *Cistopus indicus*; E, *O. selene*; F, *O. fitchi*; G, *O. chierchiae, O. penicilifer* and *O. stitiochrus*; H, *O. hubbsorum* and *Hapalochlaena* spp., I, *O. digueti*; L, *O. californicus*; N, *Macrotritopus defilippi/horridus*; O, *O. macropus/ornatus*; P, *Pteroctopus tetracirrhus*; Q, *Octopus (Macrochlaena) winckworthi*; R, *Robsonella fontanianus*; S, *Scaeurgus unicirrhus/patagiatus*; U, *O. bimaculoides*; V, *O. vulgaris*; X, *O. filosus*; Y, *O. burryi; ? Aphrodoctopus schultzei*. Lower case letters represent specimens of taxa with a single sucker row: a, *Eledone caparti*; c, *Pareledone charcoti*; e, *Tetracheledone spinicirrus*; g, *E. gaucha*; m, *E. moschata*; p, *P. polymorpha*; r, *E. cirrhosa*; s, *P. (Megaleledone) senoi*; t, *P. turqueti*; v, *Vosseledone charrua*; x, *P. adelieana, P. aurorae P. harrissoni* and *P. nigra* (one specimen each); y, *E. massyae*. The curve, which was fitted by eye, generally separates specimens with a single sucker row (below) from those with two sucker rows and suckers in a zigzag arrangement (above). The points within circles represent specimens of *Pareledone* with suckers in zigzags below the curve.

of specimens of *Eledone* can carry at least 135 suckers; specimens of *Octopus* can have up to 300 suckers on an arm. The number of suckers on an arm of *E. cirrhosa* and *E. moschata* approaches that of some specimens with two sucker rows. The number of suckers on the arms of the type of *P. turqueti* (Joubin, 1905) cannot be distinguished from that of octopuses of equal size with two sucker rows.

Although most octopuses with one sucker row are separated from those with two sucker rows by a very narrow margin (Fig. 1), within each group the average number of suckers borne on an arm of a given length varies considerably. At arm lengths near 200 mm, specimens with one sucker row average from 46 (*P. senoi*) to 112 (*E. moschata*) suckers on an arm, specimens with two sucker rows average from 135 (in *Cistopus indicus*) to 247 (in *Macrotritopus* spp.) suckers on an arm. Literature-based and specimen-based data report a comparable number of suckers on arms of similar length within a taxon.

On the plot of the number of suckers on the hectocotylus versus hectocotylus length (Fig. 2), most males of taxa typified by a single sucker row have fewer suckers on the hectocotylus than do specimens with two sucker rows. On the hectocotyli of two males of *E. cirrhosa*, one with one sucker row and one with zigzag sucker arrangement, however, the number of suckers equals or exceeds that on hectocotyli of octopuses with two rows. The male type of *A. schultzei* with two sucker rows, has as few suckers on the hectocotylus as do males with one sucker row. Hectocotyli with one sucker row, other than those of *Eledone*, always plot beneath the curve that separates normal arms with one from those with two sucker rows; hectocotyli with two sucker rows plot on both sides of the curve.

DISCUSSION

The hypothesis that sucker crowding is associated with the formation of double sucker rows is supported. In most of the octopus specimens considered, if the number of suckers exceeds a critical limit dependent on arm length, the suckers form double rows. The consistency of this limit, or threshold (Fig. 1), among the octopuses considered suggests that a physical constraint affects each of the taxa considered; the five exceptional specimens reveal the effect of other factors.

In four specimens of *Pareledone*, the suckers arranged in zigzags despite being few in number. These specimens may violate the pattern because their arms were preserved straight, in a swimming position, as recommended by Roper & Sweeney (1983). The arms of comparable specimens that are recurved in preservation carry a single sucker row.

In fixation, unrestrained arms recoil, apparently due to contraction of the web. On a recurved arm, the oral, suckered surface on the outer curve of the arm is in tension; the aboral surface, forming the inner curve, is compressed. Artificially straightened arms are subject to different forces, which may invalidate comparisons between straight and recoiled arms. When straight arms are flexed aborally, the space between the suckers increases and their arrangement can approach a single row.

That a curve rather than a line separates most taxa with one sucker row from those with two rows (Fig. 1) illustrates that sucker size also influences the relationship between suckers. On the short arms of young octopuses with small suckers, each small sucker at the arm tip occupies a large proportion of the total space. On longer arms with larger suckers, small suckers at the arm tip occupy proportionately less space, the large suckers already in place dominate. The threshold curves with increasing size as a result of growth.

Sucker growth may also explain why some hectocotylized arms violate the pattern seen in normal arms (Fig. 2). Hectocotyli develop as normal arms up to a point; if more than the critical number of suckers recruit, double sucker rows form. Small hectocotyli plot as predicted by normal arms (Fig. 2), and they are directly comparable; the comparison, however, becomes invalid with growth. The hectocotylus carries an apparently species-specific number of suckers, often many fewer than on normal arms (Toll, 1988; Villanueva et al., 1991). Although hectocotyli are shorter with fewer suckers than are other arms, the arm and suckers continue to grow, as evidenced by within species variation in hectocotylus length (Fig. 2; Toll, 1988; Villanueva et al., 1991). If the suckers on the hectocotylus become larger than those on normal arms, their size may maintain the double sucker rows, despite their reduced number.

If a double sucker row is associated with sucker crowding, and large suckers occupy more space than small suckers, then a comparatively few very large suckers could form

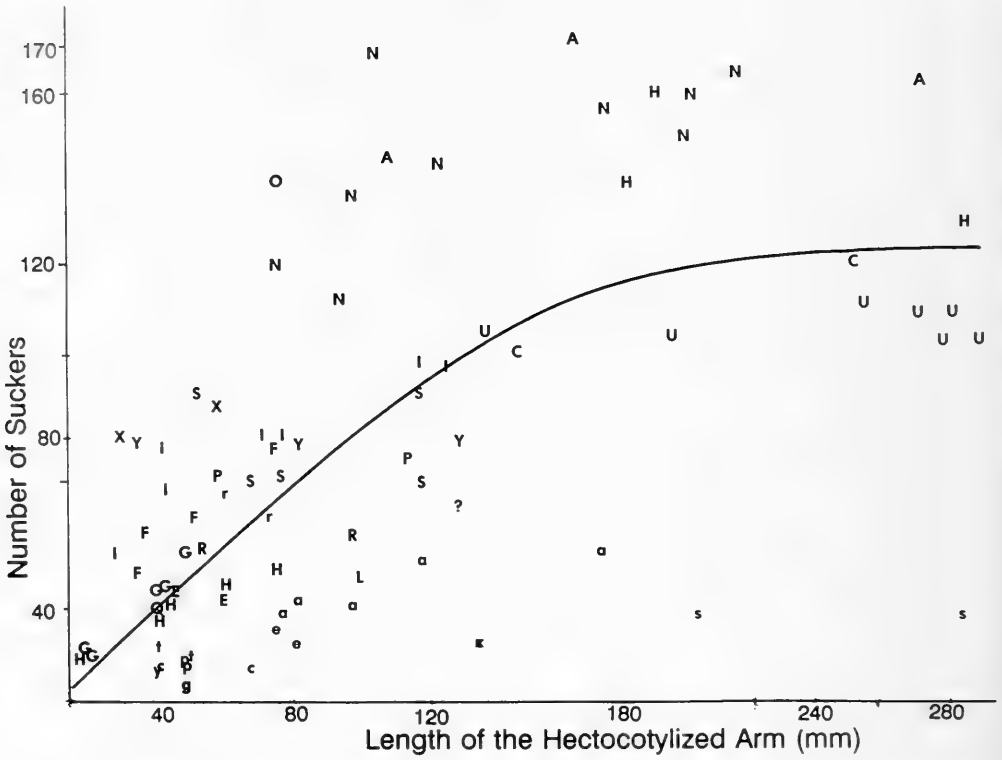

FIG. 2. Plotted are the number of suckers on the hectocotylus versus hectocotylus length. Symbols defined as in Figure 1. The curve separates normal arms with two rows from normal arms with one sucker row.

double rows. This mechanism has been suggested to create double sucker rows in male specimens of the cirrate octopods *Opisthoteuthis depressa* and *O. japonica* (Sasaki, 1929; Taki, 1963). I suggest that this mechanism also produced the double sucker rows on the type of *A. schultzei*. The number of suckers on the arms of the type predicts that it will have a single sucker row, but the 6–8 dramatically enlarged suckers on each arm of *Aphrodoctopus schultzei* (Roper & Mangold, 1991) may occupy enough space that most suckers occupy more than one row (Hoyle, 1910: plate Va, fig. 1; Roper & Mangold, 1991: fig. 4).

Sucker number varies more within groups sharing the same number of sucker rows than it does between groups. Such groups may thus be arbitrary units. Three lines of evidence support this statement. First, although the genera *Eledone* and *Pareledone* are defined by having a single sucker row, specimens of both can have suckers arranged in two rows or in zigzags (Joubin, 1905; Gravely, 1908). *Octopus*, defined by having a double sucker row, contains specimens with suckers arranged in zigzags or nearly single rows (Robson, 1932). That exceptions occur in diverse genera suggest that the character is artificial.

Second, the muscles attaching the suckers to the arms are very similar in specimens of *Eledone* and *Octopus* (Guérin, 1908; Kier & Smith, 1990). Guérin (1908: 59) predicted that eliminating some of the suckers and elongating the axis of the arm, that is reducing sucker crowding, would shift the sucker arrangement from two rows to one. The present results support his prediction and indicate that these genera differ only superficially in this character. Detailed studies of other genera and of developmental series have yet to be accomplished.

Third, the distribution of points relative to the critical limit separating specimens with a single row from those with double suckers

rows (Fig. 1) reflects the arrangement of suckers on most specimens. Points lying just above the curve (Fig. 1) represent specimens of *Cistopus indicus* that have suckers arranged diagonally, or nearly in a single line (Robson, 1929), as predicted by the plot. Specimens of *Eledone* are just below the curve if the suckers form a single rows; specimens of this species with suckers in a zigzag are just above it. The continuous distribution of points reflects the continuous nature of the character.

If, as suggested here, the spatial relationship among the suckers determines their arrangement, different strategies may serve to influence that relationship. Chief among these strategies may be differentiation of sucker sizes along the arms.

If octopuses have dramatically more than the critical number of suckers required to form double sucker rows, why do the suckers only form double rows? Although individuals with three sucker rows per arm are currently considered developmental anomalies (Toll & Binger, 1991), Owen (1881) named the genus *Tritaxeopus* for specimens with three sucker rows. Owen, who suggested that sucker arrangement was continuous among the Octopodidae, stated that because *Tritaxeopus* differed as much from *Octopus* in sucker row number as did *Eledone*, it merited equal taxonomic recognition. Owen's (1881) report that 286 suckers occupy the 584 mm-long third arm of his now missing type specimen is comparable to specimens included here with shorter arms (Fig. 1) and two sucker rows.

The rarity of specimens with multiple sucker rows may be associated with sucker size differentiation. In specimens with a single sucker row, the suckers occupy a comparatively narrow size range. Especially in specimens of *Pareledone*, the terminal suckers are large compared to those on the tips of arms with two sucker rows. In shallow-water octopuses with two sucker rows, the suckers near the margin of the web are distinctly the largest; distally, sucker size declines dramatically but continuously. Because few suckers are large, the amount of crowding is reduced, as is the crowding associated with the many small suckers. By partitioning sucker size, two discrete sucker rows may be maintained despite the presence of hundreds of suckers. Why multiple sucker rows appear to be avoided by octopuses may relate to functional difficulties or that increased nervous and muscular control are required.

That increased sucker density is associated with double sucker rows is consistent with data available for specimens of the deep-water genus *Benthoctopus* (Voight, unpubl.). Available specimens and data (Russell, 1922) for *Bathypolypus arcticus* and *B. faeroensis* show that despite their suckers being few in number and small in size (Voight, in press) they also form double rows. If the mechanism forming double rows can be shown to differ between *Bathypolypus* and the octopuses considered here, double sucker rows would be shown to be convergent in the Octopodidae, as predicted by Robson's (1932) classification of the family and my preliminary cladogram (Voight, 1990).

If the number of sucker rows is unreliable for phylogenetic reconstruction, could the underlying character suite of sucker number and arm length indicate close evolutionary relationships, e.g. between *Octopus* and *Eledone*? Higher order names have been assigned, not to reflect relationships, but to group outwardly similar taxa by readily apparent characters (e.g. Joubin, 1918). Anatomists who perhaps believed that the generic names indicated distinctly different taxa have compared these genera but have rarely found significant differences (Girod, 1882; Guérin, 1908; Kier & Smith, 1990).

Without an independent means of postulating relationships, and aware that a similarity in the relationship between sucker number and arm length can be produced by changes in either character, conclusions are premature. The number of suckers in *Octopus bimaculatus* and *O. bimaculoides*, very similar species thought to have diverged only recently (Pickford & McConnaughey, 1949), differ more than among species of *Octopus* and *Eledone* (Fig. 1), suggesting that this character does not necessarily reflect evolutionary history.

Eliminating the number of suckers rows as a taxonomic character does not affect most currently recognized genera. The genus *Pareledone* should be defined to reference its few suckers on each arm rather than one sucker row; its definition, however, may still be based solely on plesiomorphic, or ancestral, characters (Voight, 1993). *Eledone* remains as a distinct taxon; its members share the apparent synapomorphies of male heteromorphic arm tips formed by the lateral extension of sucker buds, the reduction or absence of a calamus, the anterior fusion of the branchial retractors and, pending more data, *in utero* fertilization (Perez et al., 1990).

Whether *E. palari* Lu & Stranks, 1991, shares homologous characters is uncertain.

Eledone, however, may not be monophyletic; it appears to share with *Aphrodoctopus* several characters that suggest common ancestry. A single male specimen was designated as type of the genus *Aphrodoctopus* by virtue of its apparent double sucker rows and characters unique in *Octopus* but shared with species in the genus *Eledone*. The type specimen, despite the appearance of having two sucker rows, plots with specimens having one row (Fig. 1), possibly due to its very large suckers, as discussed above.

Characters supporting the relationship between *A. schultzei* and species in *Eledone* include the heteromorphic arm tips of males and the structure of the ligula. Although Roper & Mangold (1991) stress the unusual ligula, the ligulae of males of *E. caparti* appear to be very similar (Adam, 1952: fig. 52), as, to a lesser degree, do those described for *E. thysanophora* by Voss (1962), *E. massyae* by Voss (1964), and for *Pareledone carlgreni* by Thore (1945).

Because the characters cited here as synapomorphies with *Eledone* were the basis for the new genus, and the number of sucker rows is an artifact of sucker size and density, I suggest that *A. schultzei* be placed in *Eledone*. Features distinguishing it from *E. thysanophora* are yet to be determined. The species are likely to be closely related to *E. caparti*; they share the structure of the ligula, sucker size differences, and arm formulae and may have adjacent geographic distributions. The species can be distinguished by the spermatophores; crochets are present in *E. schultzei* and *E. thysanophora* but absent in *E. caparti*.

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OVER-REPRESENTATION OF RARE ALLELES IN JUVENILES AND LACK OF PATTERN IN GEOGRAPHIC DISTRIBUTIONS OF ALLELES IN A LAND SNAIL

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ABSTRACT

Eight populations of *Mesodon zaletus* (Binney) (Gastropoda: Stylommatophora: Polygyridae), ranging from West Virginia to Alabama to Missouri and Arkansas, were examined at 16 allozymic loci, nine of which were variable. Available population samples were generally small (2–17), but a large sample (140) was taken from Monte Sano, Alabama. Chi-square tests using PGM-1 in this population showed a fit to Hardy-Weinberg equilibrium, and an over-representation of rare alleles in juveniles. Among the eight populations, *M. zaletus* showed substantial geographic differentiation in allelic frequencies, with no consistent pattern of geographical variation among loci. These results put important caveats on allozyme systematics of land snails.

Key words: allozymes, Gastropoda, Pulmonata, Polygyridae, *Mesodon zaletus*.

INTRODUCTION

Mesodon zaletus (Binney, 1837) is a large (shell diameter 24–31 mm) polygyrid land snail inhabiting deciduous forests up to an elevation of about 1,500 m. This species ranges from New York to Illinois, south to central Alabama, and west through a southern-Illinoisian constriction to Missouri and Arkansas (Fig. 1). In the course of phylogenetic studies on the tribes Triodopsini and Mesodontini (Emberton, 1988, 1991a), allozymic data (16 loci) were accumulated for eight populations of *M. zaletus* (Fig. 1), including one large sample (n = 140) with both adults and juveniles. Here I report unusual results encountered in the analysis of these data for patterns of allelic variation within and among populations.

MATERIALS AND METHODS

Collection data on the eight populations (Fig. 1) are as follows; voucher materials are all in the Field Museum of Natural History, Chicago (FMNH); field station numbers are in the author's "GS" series.

TN BLOUNT. Tennessee: Blount County: Great Smoky Mountains National Park: White Oak Sink: limestone bluffs at the north and west edges of the sink. Adults (17 collected and electrophoresed) were on or under leaf litter, juveniles (an unrecorded number collected, and none electrophoresed) were on the rock surfaces of the bluffs. 19 June 1981, 11 a.m.-6 p.m., Ken & Ellen Emberton collectors. Vouchers FMNH 214771 (GS-9; one dissected).

AL MADISON-1. Alabama: Madison County: Huntsville (east of): Monte Sano State Park: base of limestone bluffs below scenic outlook at main picnic area. The bluffs border a small permanent waterfall and stream. Adults (31 collected, 26 electrophoresed [all but numbers 7, 10, 16, 20, and 24]) were most prevalent on the peripheries of outcrops, on deep leaf litter. Several mating pairs were seen. An unrecorded number of juveniles were also collected, but none were electrophoresed. 16 July 1981, 8 p.m.-10:30 p.m.; 17 July 1981, 6:15 a.m.-9:30 a.m.; Ken Emberton collector. Vouchers FMNH 214772 (GS-20; none dissected).

AL MADISON-2. Same site as AL MADISON-1. On litter surface and in talus in the main cove, the day after a rain. Adults (95 collected, all but one [#78] electrophoresed) more commonly on the litter surface than the juveniles (an unrecorded number collected, 20 electrophoresed), some of which were on the cliff face. 30 April 1982, 9 a.m.-10:30 a.m., 1:15 p.m.-2:45 p.m., Ken Emberton collector. Vouchers FMNH 214773 (GS-101; three dissected).

AR CRAWFORD. Arkansas: Crawford County: Devils Den State Park: Self-Guided Nature Trail. *M. zaletus* was most common on talus and deep leaf litter in the lowlands along the creek at the head of the trail. Conditions

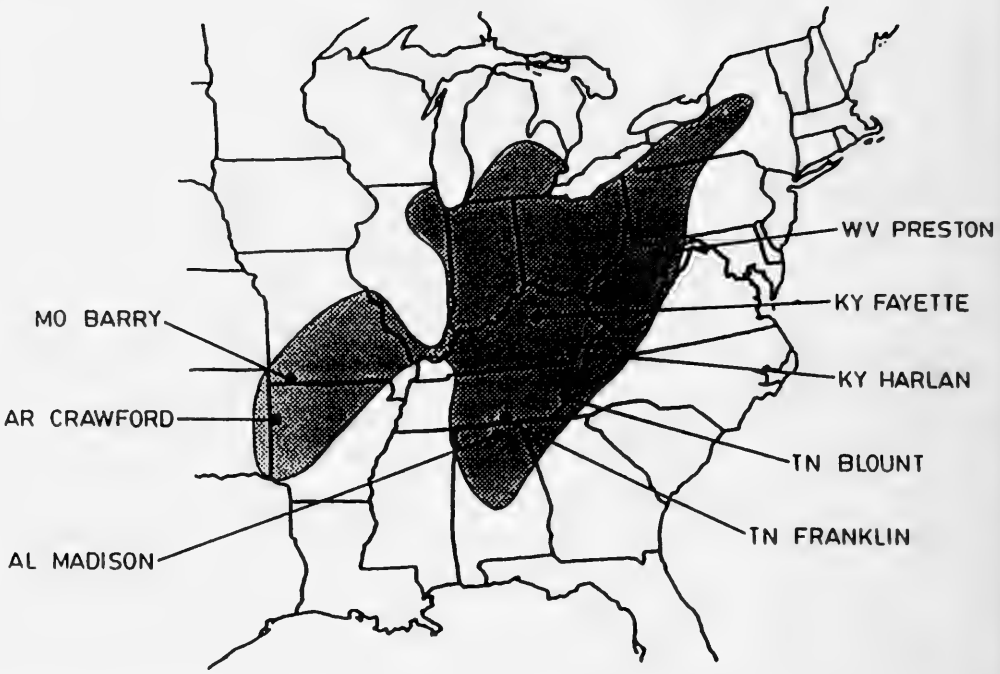


FIG. 1. The eight sampled populations of *Mesodon zaletus* within the species's geographic range in the eastern United States.

were very wet, due to a recent rain. Collected eight adults (all electrophoresed) and an unrecorded number of juveniles (one electrophoresed). 25 April 1982, 7 a.m.-10 a.m.; 25 April 1982, 4 a.m.-7:40 a.m.; Ken Emberton collector. Vouchers FMNH 214787 (GS-90; one dissected).

MO BARRY. Missouri: Barry County: Roaring River State Park: 1.1 miles west of junction with Road F on Missouri Route 112: wooded ravine at top of bluff overlooking the park, at the edge of the National Forest. Under logs and litter on scree slopes of chert-like rock with scattered leaf litter; all logs were charred by fire (this was the most productive site, nonetheless, for land snails found within the park). Two adults collected and electrophoresed; number of juveniles unrecorded, and none electrophoresed. 28 April 1982, 7:30 a.m.-11:00 a.m.; Ken Emberton collector. Vouchers FMNH 214788 (GS-96; two dissected).

TN FRANKLIN. Tennessee: Franklin County: 1.5 miles north of Sherwood Post Office, then a short distance east (along a small road) from the south side of bridge: wooded hillside above creek with limestone outcroppings. The area was partially cleared, with a large trash pile. Six adults collected and electrophoresed; no juveniles (number unrecorded) electrophoresed. 1 May 1982, 1:30 p.m.-3:30 p.m., Ken & Ellen Emberton collectors. Vouchers FMNH 214774 (GS-104; five dissected—Emberton, 1991a: figs. 3a-e, 4a-e).

KY FAYETTE. Kentucky: Fayette County: Grimes Mill Road at Boone Creek: upper edge of floodplain downstream from parking lot at crossing. Under logs and leaf litter in oak forest with limestone outcrops. Collected: four adults (all electrophoresed) and an unrecorded number of juveniles (six electrophoresed). 7 May 1982; 10 a.m.-2:30 p.m., Ken Emberton, John Petranka, and B. Kirkpatrick collectors; 3:15 p.m.-5:45 p.m., Ken Emberton and John Kirkpatrick collectors. Vouchers FMNH 214775 (GS-112; none dissected).

KY HARLAN. Kentucky: Harlan County: United States Route 421, 0.1–0.2 miles south of junction with Kentucky Route 221: oak-forested hillside with sandstone talus overlying limestone. Of eight adults, seven were electrophoresed; no juveniles (number unre-

corded) were electrophoresed. 9 May 1982, 2 ½—3 hours in the morning, Ken Emberton and John Petranka collectors. Vouchers FMNH 214777 (GS-119; one dissected).

WV PRESTON. West Virginia: Preston County: Coopers Rock State Forest: along thin belt of friable limestone about ⅓ of the way down the west slope of New River Gorge, just east of main overlook. Under patches of accumulated leaf litter on very steep slope. Ten of the 15 collected adults (numbers 1–5, 8, 9, 12, 13, and 15) were electrophoresed. An unrecorded number of juveniles were collected, none of which were electrophoresed. 14 May 1982, 10 a.m.-1:30 p.m., Ken Emberton collector. Vouchers FMNH 214778 (GS-126; one dissected).

Thus single collections were made of seven populations, but AL MADISON was sampled both in summer of 1981 and in spring of 1982. The latter collection was the largest, comprising 114 snails, including both juveniles and adults. Other population samples consisted of two to 17 adults and various numbers of juveniles, and ranged from northeastern West Virginia to southwestern Missouri (Fig. 1).

Specimens of *Mesodon zaletus* were collected into muslin bags. Within one hour after collection, the bags were placed over ice in a cooler and held for one-half to five days. Upon removal, the snails were placed onto a double layer of dampened paper towels. As each snail extended from its shell and began to crawl, the posterior, free portion of its foot was cut off with an Exacto knife. Each excised piece of tissue ("snail tail") was placed into a screw-top plastic cryogenic vial, which was dropped into liquid nitrogen contained in a portable vacuum-walled freezer. Amputated snails were labelled on their shells using a Rapidograph; cryogenic vials were labelled using a black Sharpie.

The amputated snails were drowned overnight in tap water laced with chloryl hydrate (one medium-sized crystal per liter), fixed in 95% ethanol (method of A. Solem, personal communication), and later removed to 70% ethanol for storage and dissection. One to three adults were dissected per population. Adults were detected by their reflected shell lip (Pilsbry, 1940). Dissections consisted of removing the reproductive system, slitting open the uneverted penial tube, and pinning open the tube to view the functional surface of the penis (Emberton, 1988: fig. 1). The penial morphology of *M. zaletus* is distinctive, is relatively invariant among populations, and thus is reliable for identification (Emberton, 1991a).

Undissected adult *M. zaletus* were identified by their conchological features. The only species in the same geographic range (Fig. 1) that might be confused for *M. zaletus* are (1) *M. thyroidus* (Say), (2) *M. elevatus* (Say), and (3) species of both *M.* (*Akromesodon*) and the *Neohelix albolabris* (Say) and *N. alleni* (Sampson) groups. Adults of these three groups can be distinguished from adult *M. zaletus* by their half-open umbilicus, domed spire, and lack of parietal denticle, respectively (Burch, 1962; Pilsbry, 1940; Emberton, 1988, 1991a). Juveniles of all these taxa, on the other hand, are often difficult, and sometimes seemingly impossible, to distinguish by shells alone. Shells of *M. zaletus* neoadults with newly reflected aperatural lips and unformed parietal denticles are easily mistaken for shells of *N. albolabris* (personal observations). Field identification of juveniles from AL MADISON was verified, therefore, using allozymes.

In the laboratory, vials containing tissue samples were removed from the portable freezer and sorted in a cold room at 2°C, then transferred to a −20°C freezer, where they were stored up to seven weeks until removed for electrophoresis. One-fifth to all of a given tissue sample ("snail tail") was used for each "run" of four to six electrophoretic gels. Used samples were placed into alternating wells of a pre-chilled glazed ceramic depression plate that was kept on Blue Ice during grinding and wicking. Grinding of tissues was by one of two methods, both of which were effective against the problem of high concentrations of mucus: (1) coating a large sample with a thin layer of powdered glass and with an equal volume of grinding buffer, and grinding slowly (to prevent mucous frothing) with a soft-plastic test tube, the diameter of which was slightly less than that of the depression well (tissue and mucus clings to the roughened bottom of the test tube when withdrawn, leaving a clear fluid for wicking); and (2) covering a small tissue sample with an equal volume of ground glass and three to four times its volume of grinding buffer, and slowly pulverizing the entire tissue sample, using a small glass test tube with a frosted bottom. The gummy clots resulting from this second method were dragged with forceps to the edge of the of the well; if insufficient fluid remained in the well, one or two drops of grinding buffer were dropped onto the clot, then pressed out of it to

run down the side of the well. Wicks cut from Whatman #5 filter paper were placed in the tissue fluid remaining in each well and were daubed on a KimWipe tissue before being loaded onto the gels.

Electrophoretic methods were those of Selander et al. (1971) and Shaw & Prasad (1970), as adapted by Davis et al. (1981) and Emberton (1988). Sixteen loci were used that were genetically interpretable, that represented a wide variety of metabolic pathways, that included loci of proven heritability (McCracken, 1976; McCracken & Brussard, 1980), and that excluded loci of demonstrated environmental inductability (Oxford, 1973, 1978; Gill, 1978a, b) in land snails. The loci used were SDH-1, MDH-1, MDH-2, ME, ICD, PGD, GD-1, GD-2, SOD-1, SOD-2, GOT-1, GOT-2, PGM-1, LAP-1, MPI, and GPI. All presumed alleles were tested in side-by-side comparisons on the same gel. A common allele of each locus was scored as 100, and the mobilities of other alleles in mm were scored relative to 100 mm. Details of electrophoretic procedures are given in Emberton (1988: appendix A).

Because of generally small sample sizes, only one enzyme locus in one population (PGM-1 in AL MADISON) provided reasonable tests for Hardy-Weinberg equilibrium and for homogeneity between adults and juveniles. Chi-square tests were used for both, collapsing the chi-square tables to get rid of small expectations (Sokal & Rohlf, 1969; Elston & Forthofer, 1977).

Geographic variation in allozymes was examined by the use of pie diagrams of allelic frequencies, and by two phenetic analyses (UPGMA and distance-Wagner), each based on two different indices of genetic distance (Nei's and Rogers). BIOSYS computer programs (Swofford & Selander, 1981) were used for all calculations.

RESULTS

In total, 35 allozymic alleles were detected, of which seven were from monomorphic and 28 from variable loci. Among the eight populations, the mean number of alleles per locus was 1.1 to 1.5, the percentage of loci polymorphic was 12%-25%, and mean heterozygosity ranged from 0.04 to 0.08. Allelic frequencies for the nine variable loci are presented in Table 1.

Hardy-Weinberg equilibrium was strongly supported for PGM-1 in the AL MADISON population (chi square = 0.000, p = 1.00):

Allelic Class	Observed	Expected
100/100	22	22.0
100/other	67	67.0
other/other	51	51.0

Comparison between 120 adults and 20 juveniles of the AL MADISON population gave the following allelic frequencies for PGM-1:

Allele	Adults	Juveniles
103	0.017	0.050
100	0.412	0.300
98	0.154	0.300
95	0.400	0.325
91	0.017	0.025

Collapsing this table for chi-square analysis and giving allelic counts rather than frequencies yields:

Allele(s)	Adults	Juveniles	Total
100	99	12	112
95	96	13	109
rare	45	15	60
	240	40	280

From this table, chi-square = 7.22, $p < 0.05$. This result indicates that rare alleles are significantly over-represented among the young.

Allelic geographical distributions are mapped in Figure 2. The distribution of the 35 alleles of all 16 loci among populations (Table 1, Fig. 2) was bimodal:

# of Populations	# of Alleles	% of Alleles
1	9	26%
2	6	17%
3	2	6%
4	2	6%
5	0	0%
6	1	3%
7	1	3%
8	14	40%

Thus, alleles predominantly were either localized or widespread geographically among the sampled populations: 43% occurred in only one or two populations, and 40% occurred in all eight populations. This bimodal pattern

TABLE 1. Allelic frequencies of the nine variable loci for the eight populations of *Mesodon zaletus*. Untabulated monomorphic alleles were: MDH-1, MDH-2, ICD, PGD, GD-1, GD-2, and GOT-2.

		Population							
Locus	Allele	Tn Blount (n = 17)	AR Crawford (n = 9)	MO Barry (n = 2)	AL Madison (n = 140)	TN Franklin (n = 5)	KY Fayette (n = 10)	KY Harlan (n = 7)	WV Preston (n = 10)
SDH-1	106	0.0	0.0	1.000	0.0	0.0	0.0	0.0	0.0
	100	1.000	1.000	0.0	1.000	1.000	1.000	1.000	1.000
ME	100	1.000	1.000	1.000	1.000	1.000	1.000	0.643	1.000
	98	0.0	0.0	0.0	0.0	0.0	0.0	0.357	0.0
SOD-1	110	0.0	0.0	0.0	0.0	0.900	0.0	0.0	0.0
	100	1.000	1.000	1.000	1.000	0.100	1.000	1.000	1.000
SOD-2	104	0.0	0.222	0.0	0.0	0.0	0.0	0.0	0.0
	100	1.000	0.778	1.000	1.000	1.000	1.000	1.000	1.000
GOT-1	103	0.0	0.222	0.0	0.018	0.0	0.0	0.0	0.0
	100	0.794	0.778	1.000	0.982	1.000	1.000	1.000	1.000
	97	0.206	0.0	0.0	0.0	0.0	0.0	0.0	0.850
PGM-1	103	0.0	0.0	0.0	0.021	0.0	0.400	0.857	0.0
	102	0.0	0.0	0.250	0.0	0.0	0.0	0.0	0.0
	100	0.882	1.000	0.0	0.396	0.100	0.300	0.0	1.000
	98	0.118	0.0	0.0	0.0	0.175	0.0	0.0	0.0
	97	0.0	0.0	0.0	0.0	0.100	0.300	0.0	0.0
	96.5	0.0	0.0	0.750	0.0	0.0	0.0	0.0	0.0
	95	0.0	0.0	0.0	0.389	0.800	0.0	0.143	0.0
	91	0.0	0.0	0.0	0.018	0.0	0.0	0.0	0.0
LAP-1	104	0.0	0.0	0.0	0.0	0.0	0.200	0.0	0.0
	100	0.912	1.000	0.250	0.986	0.500	0.800	1.000	1.000
	98	0.088	0.0	0.750	0.007	0.0	0.0	0.0	0.0
	96	0.0	0.0	0.0	0.007	0.0	0.0	0.0	0.0
MPI	102	0.0	0.556	0.0	0.0	0.0	0.0	0.0	0.550
	100	1.000	0.444	1.000	1.000	1.000	1.000	1.000	0.450
GPI	103	0.0	0.111	0.0	0.0	0.900	0.0	0.714	0.300
	100	0.824	0.889	1.000	0.993	0.100	1.000	0.286	0.700
	95	0.176	0.0	0.0	0.007	0.0	0.0	0.0	0.0

persisted even after the removal of rare alleles with sample frequencies less than 0.02.

Examination of Figure 2 reveals that each allele, regardless of whether it was localized or widespread, had a unique distribution among the eight populations; there was no obvious geographical correlation among loci.

This generally mosaic geographic distribution of alleles was further attested by phenetic analyses. Clustering results (not illustrated) differed, depending on which genetic similarity or distance measure was used (Nei vs. Rogers), and which clustering algorithm was used (UPGMA vs. Distance Wagner). For example, MO BARRY was at the base of the Nei UPGMA tree, interior to TN FRANKLIN in the Rogers UPGMA tree, and in the center (paired with KY FAYETTE) in the Rogers distance-Wagner tree. Furthermore, patterns of genetic similarity as revealed by the phenograms showed no consistent correlation with geographic proximities among populations. For example, the distance Wagner tree's tightest cluster consisted of AR CRAWFORD, TN BLOUNT, and WV PRESTON, which spanned the entire geographic range of sampling (Fig. 1).

DISCUSSION

The important implications of this study are that in *Mesodon zaletus*, populations are panmictic, rare alleles are over-represented in juveniles, and geographic differentiation in alleles is substantial and without consistent pattern.

Panmixy is not ubiquitous in polygyrid landsnail populations, however. Fairbanks & Miller (1983) found that 12 populations representing two species of *Ashmunella* in the Huachuca Mountains, Arizona, had significant heterozygote deficiencies. This discrepancy is probably due to differences in vagility

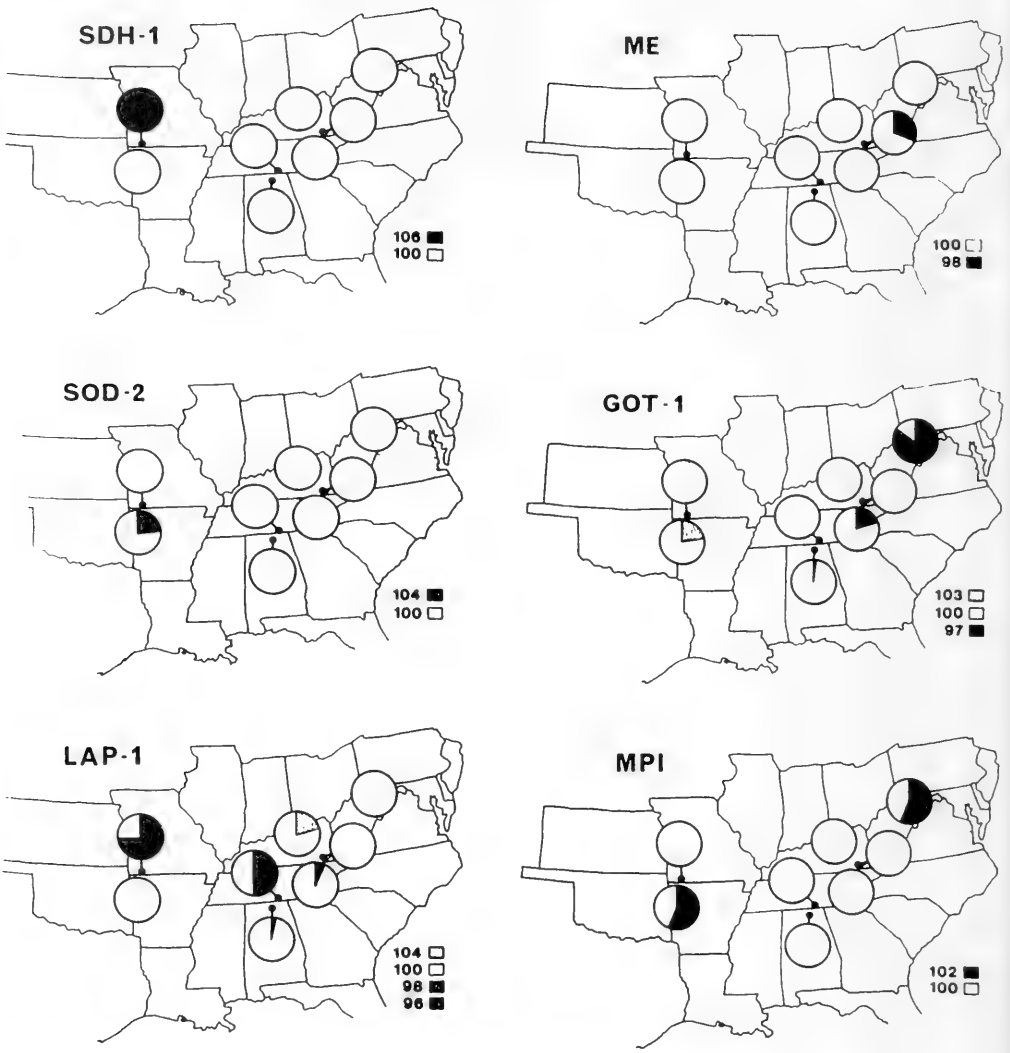
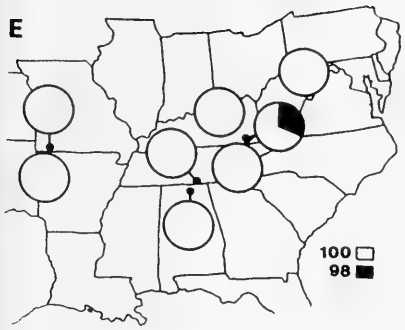
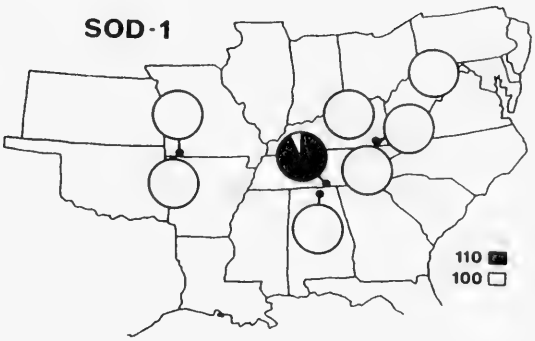


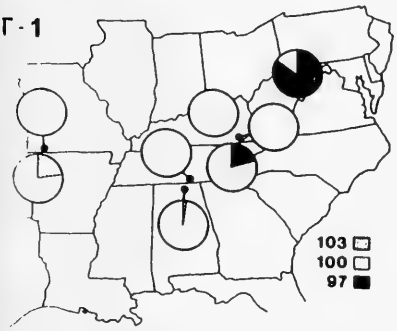
FIG. 2. Geographic variation in allelic frequencies of the nine variable loci. Each population (see Fig. 1) is represented by a pie diagram, the sections of which indicate the frequencies of alleles. A key to alleles is on the lower right of each map.

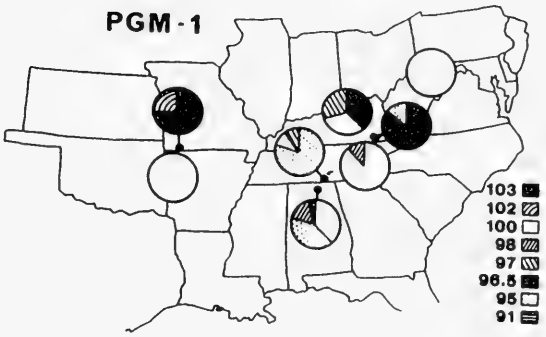
between the two genera; *Ashmunella* are smaller snails than *Mesodon* and are restricted to patchily distributed moist microhabitats in regions more arid than those inhabited by *Mesodon* (Pilsbry, 1940: *M. [Mesodon s.s.*.]). This view is supported by the allozymic evidence from other polygyrids. Combining the present results with those of McCracken & Brussard (1980) as taxonomically reinterpreted by Emberton & McCracken (unpublished), the following numbers of natural populations of polygyrids conform to Hardy-Weinberg expected levels of heterozygosity:

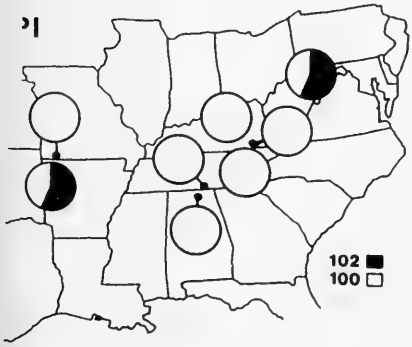
Species	# of Populations
Neohelix albolabris (Say)	6
Neohelix alleni (Sampson)	1
Neohelix major (Binney)	1
Neohelix solemi Emberton	2
Mesodon normalis (Pilsbry)	7
Mesodon zaletus	1

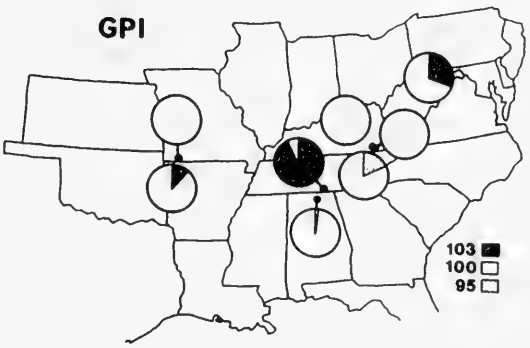












Unlike *Ashmunella*, all of these species are large, nocturnal and wet-weather foragers on the leaf-litter or ground surface (Pilsbry, 1940; McCracken, 1976; Emberton, 1981, 1986, 1991b; Hubricht, 1985; Asami, 1988a, b). Thus, the ecology of these species correlates with panmixis. Further tests of the relationship between ecology and panmixis might be possible using existing allozyme data on polygyrids (Emberton, 1988, 1991a) but are beyond the scope of this paper.

The preponderance of rare alleles in juvenile *Mesodon zaletus* is intriguing. Possible explanations include natural selection against rare alleles and ontogenetic shifts in genetic expression of alleles. The latter view may be supported by the mesodontin *Patera clarki* (Lea), in which juveniles seem to differ in alleles from adults in the MDH-1, GOT-1, and GOT-2 loci (Emberton, unpublished).

The mosaic, uncorrelated, non-clinal geographic distributions of alleles among popula-

tions of *Mesodon zaletus* may find at least partial explanation in the population biology of this snail, if it is similar to the population biology of the conchologically and ecologically similar *Neohelix albolabris*. Populations of *N. albolabris* are small (estimated at 100 or fewer individuals), fluctuating in size, genetically isolated, and probably ephemeral and are founded by only one or a few individuals (McCracken, 1976). Thus, geographically random founder effects could strongly influence the distributions and frequencies of alleles. On the other hand, or in conjunction with this, allelic distributions in *Mesodon zaletus* may provide hidden clues on glacial refugia for this species. Certainly the lack of clinal variation strongly indicates against post-glacial spread from a single refugium.

The implications of these findings for systematics are rather important. Allozyme systematics for *Mesodon*, and possibly for many other genera of land snails, ideally should include both ontogenetic and geographic assessments of variation for as many species as possible.

ACKNOWLEDGEMENTS

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MORPHOLOGICAL AND ALLOZYMIC POLYMORPHISM AND DIFFERENCES AMONG LOCAL POPULATIONS IN *BRADYBAENA FRUTICUM* (O. F. MÜLLER, 1777) (GASTROPODA: STYLOMMATOPHORA: HELICOIDEA)

Andrzej Falniowski[1], Andrzej Kozik[2], Magdalena Szarowska[1], Maria Rąpała-Kozik[2] & Izabela Turyna[2]

ABSTRACT

Morphological variation (shell colour and banding, mantle pigmentation, colour and pigmentation of reproductive organs, external form of the mucous gland) and allozymic polymorphism at 13 loci (by means of vertical slab polyacrylamide gel electrophoresis) were studied in *Bradybaena fruticum* (O. F. Müller, 1777) from 11 localities in southern Poland and Slovakia. Descriptions and illustrations of variation in all the morphological characters, and frequencies at every locality are given. Of the 13 loci studied, six were polymorphic. The proportion of polymorphic loci (15.5–46.1%, mean 36%) was relatively low for a morphologically polymorphic species. Heterozygote frequencies were as expected from Hardy-Weinberg equilibrium, with the exception of the CAP_1 locus, at which a significant heterozygote excess was found. The values of Nei's distances between populations (0.017–0.282) were relatively high for geographically close conspecific populations, and often a higher value of genetic distance did not correspond with a greater geographic distance. For morphological characters and for allozyme frequencies (directly and after computing Cavalli-Sforza & Edwards's arc distances) similarity trees were computed for all populations by means of the maximum likelihood and additive tree techniques.

Key words: polymorphism, *Bradybaena*, land snails, allozymes.

INTRODUCTION

Bradybaena fruticum (O. F. Müller, 1777) is one of the most widely distributed land snail species in Poland (Riedel, 1988), inhabiting all regions except the higher mountains. The species is distributed in Europe from the Urals and Caucasus to the Balkan Peninsula, southern Scandinavia, Germany, western France, and northern Italy (Shileiko, 1978; Kerney et al. 1983; Riedel, 1988). However, the populations it forms are not as dense as those of, for example, *Cepaea nemoralis* (Linnaeus, 1758). It inhabits bushes and sunny woodlands, sometimes also grasslands, parks and gardens, preferring herbs and nettles.

There are a few studies on the biology and life cycle of *B. fruticum*, (Zeifert & Shutov, 1979; Baba, 1985; Zeifert, 1987; Staikou et al., 1990), and its population genetics (e.g. Khokhutkin & Lazareva, 1975, 1983, 1987; Khokhutkin, 1979, 1984; Makeeva, 1987; Makeeva & Matiokin, 1987), although the only genetic characters considered have been shell colour and banding together with esterase pattern. The latter is widely known as difficult to score or interpret (Richardson et al., 1986), and in helicoids may vary with feeding status (Oxford, 1973a-c). Makeeva (1987) stressed the importance of physical barriers and the founder effect in determining differences among local populations. Also, Khoukhutkin (1979, 1984) and Khokhutkin & Lazareva (1975, 1983, 1987) pointed out the importance of semi-isolation of panmictic units together with a geographic pattern of variability including a slight cline from the west to the east. They have shown that every population is genetically distinct, more evidently in biochemical characters, and that differences among nearby populations are smaller than those among more distant populations.

The aims of the present paper are to describe both morphological and allozymic variation in the snail, very poorly known so far, especially as concerns the soft parts and non-esterase enzyme systems, and to assess whether more distant populations differ among one another more than less distant ones.

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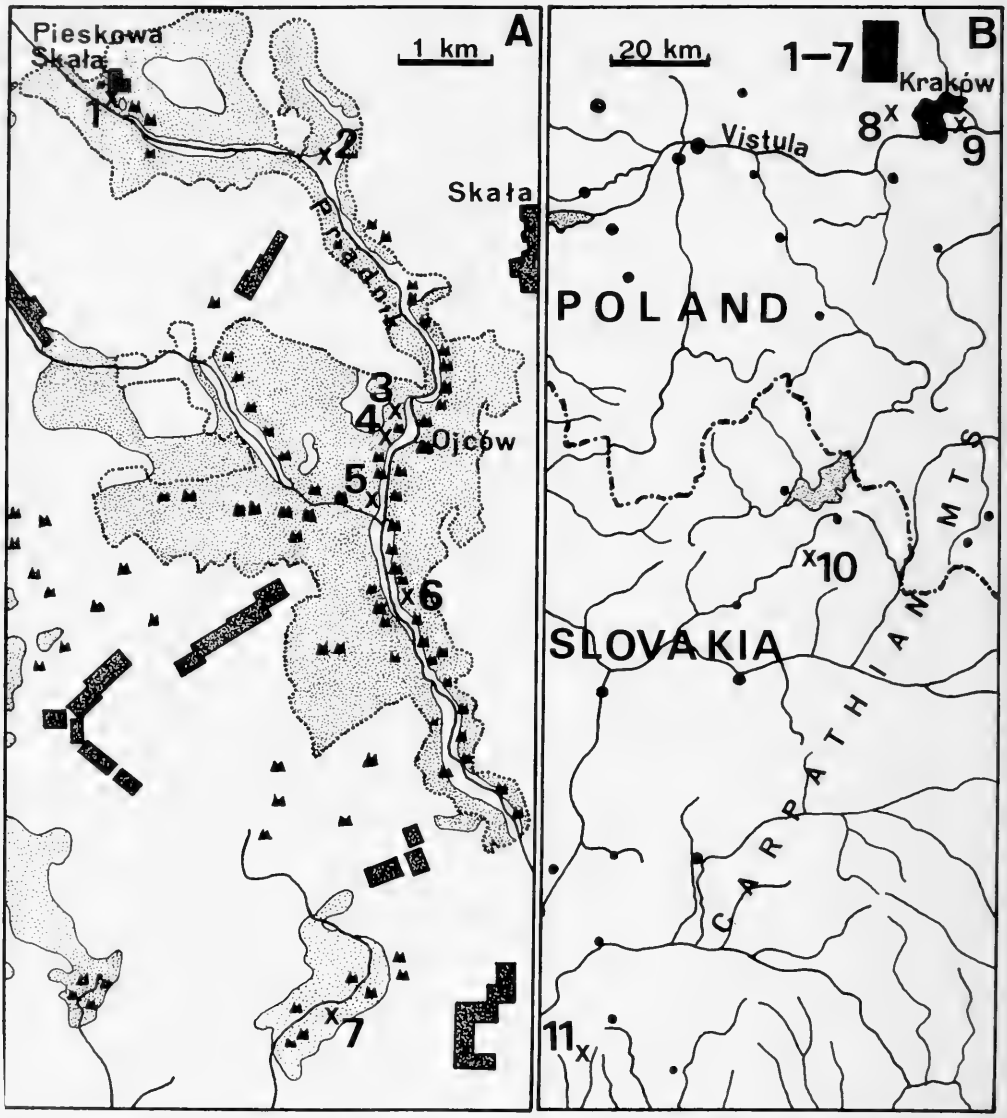


FIG. 1. Map of the sampling area. A. Localities 1–7: Shown are rivers, border of the Ojców National Park (dotted line), main groups of rocks, villages (dark shaded), and forest areas (light shaded). B. All localities: black rectangle = area of A. Shown are rivers, big man-made lakes (shaded), border between Poland and Slovakia, towns and villages.

MATERIAL AND METHODS

Description of Localities

The material was collected from 11 localities (Fig. 1). Nine of them are in South Poland: six (1–6) close to each other and generally similar in character, lying within the area of the Ojców National Park, which comprises a complex of valleys of various sizes, all connected with the Prądnik River Valley which is the largest. The predominant exposed formation is Upper Jurassic rocky limestone, which forms the slopes of the Prądnik River Valley

1. Pieskowa Skała, near a pond.
2. Dolina Zachwytu, a small branch of the Prądnik River Valley.

3. St. John's Spring, the bottom of the Prądnik River Valley.
4. Ruins of the mediaeval castle of Ojców.
5. At half the distance from Ojców to Brama Krakowska, by the road.
6. Brama Krakowska rocks, on the bottom of the Prądnik River Valley.
7. Dolina Kluczwody, the limestone valley of the Kluczwoda stream.
8. Skała Kmity, a nature reserve in the Jurassic limestone rocks of the Tenczyn Hump.
9. Lasek Mogilski, a nature reserve of a forest of old trees; situated close to a large steel mill and heavily polluted.
10. Slovakia, near Nizna, the valley of the Orawa River in the Skorusina Mountains, a forest.
11. Slovakia, near Uhliska, SW of Banska Stiavnica, the Stiavnicke Vrhy Mountains, banks of the Sikenica stream, a forest.

Collection and Morphological Techniques

The material was collected in July-August 1990, replicate sampling was done in August-September 1991, and June-July 1992. At each locality, at least 50 specimens were collected. Only adult snails having a fully developed lip (Staikou et al., 1990) were taken. The snails were collected from an area of a few square metres at each locality. All the specimens not frozen for allozyme study were fixed and stored in 70% ethanol.

All specimens were classified according to their shell colour, presence/absence of an equatorial band on the body whorl, presence/absence of a lip-adjacent band, presence/absence of yellow pigment on the mantle, the pattern and intensity of black pigment on the mantle. Then the specimens were dissected, and examined under a stereoscopic microscope, to describe the character states of the reproductive organ polymorphisms. All measurements of the reproductive organs were abandoned because of the observed wide variability being evidently physiological/artifactual in character. Emberton (1989) pointed out similar problems in camaenid land snails.

Electrophoretic Techniques

Acrylamide, bis-acrylamide, TEMED and Tris were obtained from Serva (Heidelberg, Germany), all other chemicals used for electrophoresis were purchased from Sigma (St. Louis, USA).

Snails were killed by freezing in liquid nitrogen and stored in a deep freeze (−70°C) until used. To make a suitable homogenate for electrophoresis, each individual animal was briefly thawed, put on ice and then the hepatopancreas was dissected out for electrophoresis, taking care to take as little ovotestis tissue as possible. The shell and all the remaining soft parts were then fixed in 70% ethanol for further morphological examination. The homogenization medium was partly as suggested by Wurzinger (1979) and contained 20 mM Tri-HCl buffer pH 8.0, 1 mM NAD+, 1 mM NADP+ and 15 mM mercaptoethanol in water; 0.3 ml of this solution was added to each sample in a teflo-glass homogenizer. The homogenates were stored frozen and electrophoresed within several days.

The electrophoretic procedures, buffers and solutions are detailed in Table 1. Snails from different populations were run on each gel to facilitate comparisons. Every population was run a minimum of five times, every time a different group of seven specimens of the population with a group of seven specimens of another population (each time a different one) being picked, which enabled direct comparisons among six populations to be made. In any dubious case, additional line-up gels were run, to enable side-by-side comparisons to be made. The line-up gels were provided to surround unknown mobility states by known control states. This strategy allowed exact comparisons of the alleles in all the populations studied to be made.

Scoring diagrams and photographs of gels at various stages of staining were taken, to record the relative mobilities and intensities of all alleles in the adjacent slots, and the absolute position of each band within each sample. Loci were numbered and alleles at given locus were assigned letters a, b, c, in order of decreasing anodal mobility. The mobilities of all alleles were determined by measurement of their distance from the origin. In Table 2, enzymes assayed, with their E.C. numbers and staining technique references, are listed. Zymograms were interpreted following generally accepted principles (Richardson et al., 1986) especially the principle of conservativity, that is, to assume a minimal genetic contribution to overall variation.

Numerical Methods Applied

All the allele frequencies obtained were tested for homogeneity by means of a chi-squared test of homogeneity (Richardson et

TABLE 1. Polyacrylamide gel electrophoresis technique applied

Electrophoresis: in slabs (180 × 130 × 0.7 mm) of 7.5% polyacrylamide gel in a discontinuous high-pH buffer system of B. J. Davis (1964).

Reservoir buffer: Tris-glycine (pH 8.3); 3 g Tris and 14.4 glycine per 1 l water.

Stacking gel buffer: Tris-HCl (pH 6.8); 6 g Tris titrated to pH 6.8 with 1M HCl in 100 ml final volume.

Resolving buffer: Tris-HCl (pH 8.8); 36.3 g Tris and 48 ml 1M HCl mixed and diluted to 100 ml final volume.

Acrylamide-bisacrylamide solution: 30 g acrylamide and 0.8 g bisacrylamide diluted to 100 ml final volume and filtered.

Stacking gel: 2.5 ml acrylamide-bisacrylamide solution, 5 ml stacking gel buffer, 2.5 ml 0.004% riboflavin, 10 ml water and 0.015 TEMED mixed and photopolymerized.

Resolving gel (7.5%): 15 ml acrylamide-bisacrylamide solution, 7.5 ml resolving gel buffer, 39.5 ml water and 0.03 ml TEMED polymerized with 3 ml 1.5% ammonium persulfate as the catalyst.

Runs: Fourteen samples, 20 μl each, applied for a slab; typically, a current 20–30 mA for about 4 hrs until a marker dye (bromophenol blue) passed all the slab.

TABLE 2. Enzymes assayed by polyacrylamide gel electrophoresis

Symbol	Enzyme name	Enzyme number	Staining after
ACP	Acid phosphatase	EC 3.1.3.2	Wurzinger (1979)
ALP	Alkaline phosphatase	EC 3.1.3.1	Wurzinger (1979)
AAT	Aspartate aminotransferase	EC 2.6.1.1	Wurzinger (1979)
"*CAP*"	Cytosol aminopeptidase	EC 3.4.11.1	Rudolph & Burch (1987)
G3PDH	Glycerol-3-phosphate dehydrogenase	EC 1.1.1.8	Wurzinger (1979)
HBDH	3-Hydroxybutyrate dehydrogenase	EC 1.1.1.30	Wurzinger (1979)
MDH	Malate dehydrogenase	EC 1.1.1.37	Wurzinger (1979)
PGDH	Phosphogluconate dehydrogenase	EC 1.1.1.44	Wurzinger (1979)
XO	Xanthine oxidase	EC 1.2.3.2	Wurzinger (1979)

Enzyme nomenclature and numbers after: Murphy et al. (1990), *XO* after Richardson et al. (1986)

al., 1986). Smith's H statistic was calculated for each case in which the lowest allele frequency exceeded 0.2, to test whether a single panmictic subpopulation was involved (Richardson et al., 1986). Then, each locus was tested for independence, using an m × n chi-squared test.

Data processing was done using the PHYLIP package (Felsenstein, 1990). In numerous studies of this kind, different populations are compared by computing Nei's distances (Nei, 1972, 1978), and then the clustering UPGMA technique is applied. This is, however, not necessarily the most appropriate approach. Nei's distances are seriously influenced by numerous assumptions that are commonly violated (Wright, 1978). Nei's distance was originally intended to measure the number of codon substitutions per locus that had occurred after divergence between a pair of populations. However, a rate of gene substitutions per locus has to be uniform at the locus in all the populations. Moreover, Nei's distance is based on Kimura's infinite isoalleles model of mutation (e.g. Cook, 1991) being selectively neutral, with each mutant to a completely new allele (a very unusual phenomenon), a constant rate of mutation for all loci, and with genetic variability which initially in a population is at equilibrium between mutation and genetic drift. Nei's distance is also heavily influenced by within-population heterozygosity (Felsenstein, 1985, 1990; Swofford & Olsen, 1990). Therefore, the application of Nei's distance, even if we accept its usefulness in general, is dubious in most cases; in fact, it can hardly be applied in any comparisons among conspecific populations, especially if our knowledge of the species' biology, genetics, mutation rate, mutations' selective values, etc., is poor.

Therefore, although we have computed Nei's distances to facilitate comparisons with other studies, we have not used these values for any further comparisons. Instead, we have calculated the values of Cavalli-Sforza and

Edwards's arc distance (Cavalli-Sforza & Edwards, 1967), an index that is not affected by within-population heterozygosity and that assumes genetic drift as the only source of variability (Wright, 1978). Then, the values of Cavalli-Sforza and Edwards's arc distance were used to compute a tree of relationships between the populations, by means of FITCH of PHYLIP (Felsenstein, 1990), assuming the error absolute value to be nearly constant. It is based on the Fitch-Margoliash's algorithm (Fitch & Margoliash, 1967), under the "additive tree model" (Felsenstein, 1984, 1990), without the dubious assumption of ultrametricity, which is necessary when using UPGMA. The second method applied was KITSCH from the same package, based also on the additive tree model, but with an assumption of a molecular clock, and therefore with an assumption of ultrametricity of the data. We used it working with the option of the Cavalli-Sforza & Edwards least squares method (Edwards & Cavalli-Sforza, 1964), so the technique was very similar in spirit to the UPGMA (Felsenstein, 1990). KITSCH can be considered as a phenetic clustering of the tip species (Felsenstein, 1990); it is similar to UPGMA but much better (Felsenstein, 1990; Weir, 1990).

Gene frequencies have also been used directly to compute "phylogenetic" (in our case: phenetic similarity) trees by means of the CONTML program of the PHYLIP package (Felsenstein, 1990). This program applies the restricted maximum likelihood method based on the Brownian motion model, and Cavalli-Sforza & Edwards's model of evolution (Felsenstein, 1981, 1990; Weir, 1990). The method assumes neither a molecular evolutionary clock nor a new mutation. The CONTML method has also been applied to compute phenetic similarity trees based on morphological character frequencies. In total, 16,965 trees have been analyzed.

RESULTS

Morphological Polymorphism

Frequencies of all morphological polymorphisms at all localities together with sample sizes are given in Table 3. In *Bradybaena fruticum*, a shell colour-banding pattern polymorphism is observed, but simpler and less clear-cut than that of the well-known *Cepaea nemoralis*. In contrast to *Cepaea*, the shell wall of *B. fruticum* is much thinner and translucent: the soft part pigment, therefore, is visible through it, which makes the pattern variability observable in a living snail more complicated than in *Cepaea*.

The shell (Figs. 2–14) is either light (from ivory to moderately yellowish) or dark (from pale brown to brown, with a reddish shade). The two types always could easily be distinguished in shells from one locality, there being no intermediates, but in some cases a dark morph from one locality might resemble a light morph from another one, though in no instance the two morphs could be confused. In a single specimen from locality 7, we observed a sharp ontogenetic change in the shell colour: from reddish brown to dark yellow; the border between the two colours was situated at the body whorl, about 120° from the lip.

In addition to the shell colour polymorphism, there is a banding-pattern polymorphism (Figs. 5–9), although this is much simpler than in *Cepaea*. In *B. fruticum*, usually only one dark equatorial band occurs along the body whorl (pattern 00300: Figs. 5, 6), and/or a pale chestnut band along the lip (e.g. Fig. 2). The latter does not cover the edge of the lip (Fig. 3). The dark equatorial band is not common (Table 3). The dark-lipped shells occurred at each locality in higher proportions than the banded shells did.

It must be added, however, that exceptionally the banding pattern may be more complicated. In our material of about 700 specimens, we found two shells with a different banding pattern: 02300 (Figs. 8–9). One of them was collected at locality 9, and had on its dark shell the upper, "accessory" band broader than the "normal" one, diluted on its margins and somewhat fused with the other (Fig. 9). The other specimen had a light shell and was collected at locality 4: the upper, "accessory" band was very wide and strongly marked, with a much weaker and narrower band in the usual position, fused with the accessory one (Fig. 8).

Along with the shell colour/banding polymorphism, a polymorphism of the soft parts (especially the mantle) pigmentation was observed (Table 3, Fig. 15). The pattern of the mantle pigmentation was rather complicated: composed of yellow and black pigment, more or less intensive and forming spots of various kind. The yellow pigment usually accompanied the black one. The black pigment occurred in practically all the specimens, but showing two different patterns of distribution:

TABLE 3. Frequencies of all morphological polymorphisms

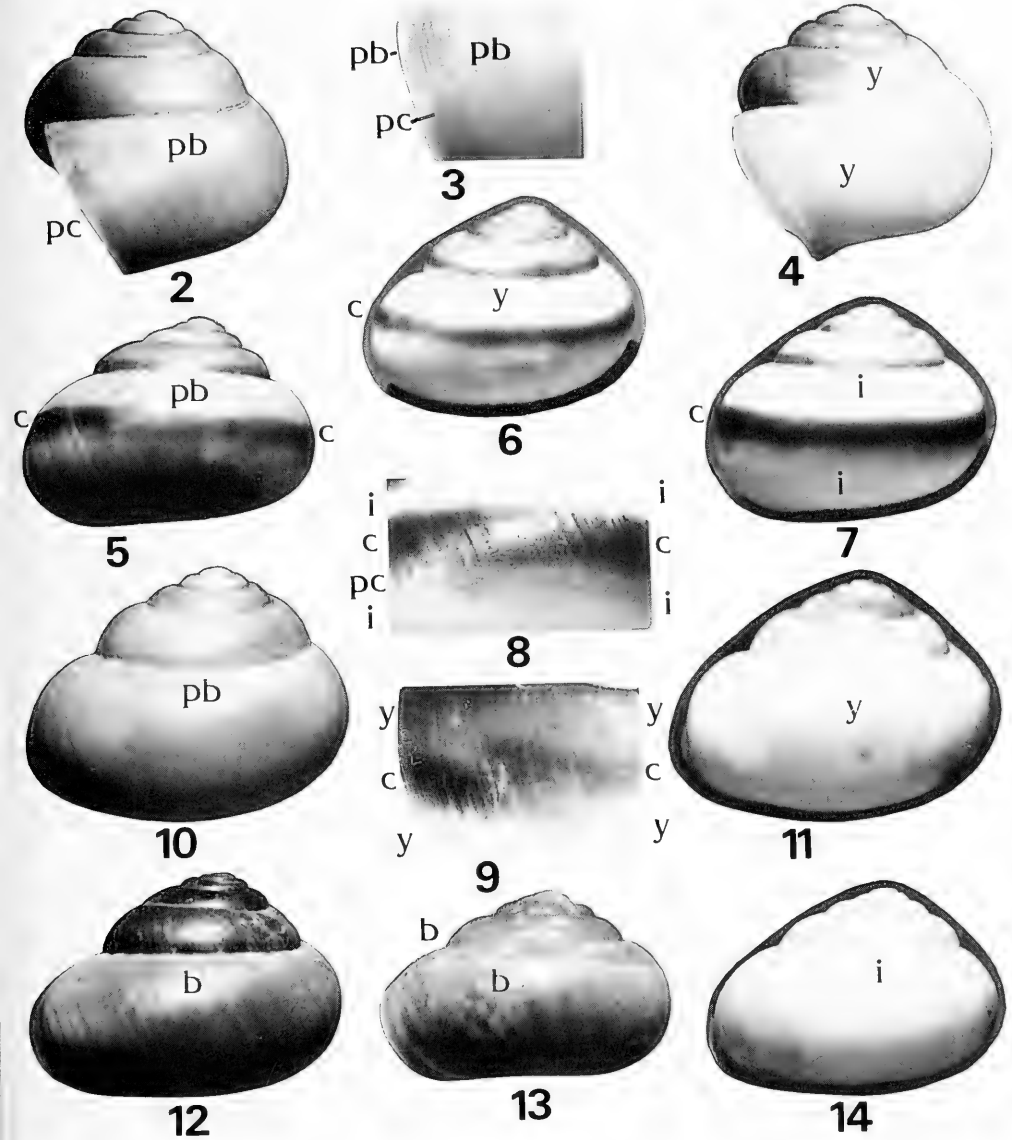
	locality										
	1	2	3	4	5	6	7	8	9	10	11
shell colour											
dark	0.800	0.714	0.629	0.429	0.758	0.586	0.571	0.486	1.000	0.850	0.800
light	0.200	0.286	0.371	0.571	0.242	0.414	0.429	0.514	0.000	0.150	0.200
equatorial band											
present	0.000	0.000	0.000	0.457	0.257	0.143	0.000	0.014	0.586	0.600	0.050
absent	1.000	1.000	1.000	0.543	0.743	0.857	1.000	0.986	0.414	0.400	0.950
lip band											
present	0.857	0.329	0.600	0.671	0.757	0.571	0.714	0.500	0.843	1.000	0.675
absent	0.143	0.671	0.400	0.329	0.243	0.429	0.286	0.500	0.157	0.000	0.325
yellow pigment											
present	0.771	0.148	0.829	0.300	0.500	0.286	0.429	0.186	0.029	0.425	0.000
absent	0.229	0.852	0.171	0.700	0.500	0.714	0.571	0.814	0.971	0.575	1.000
black pigmentation											
hachured	0.814	0.729	0.414	0.572	0.886	0.586	0.129	0.471	0.957	0.725	0.775
dotted	0.186	0.271	0.586	0.428	0.114	0.414	0.871	0.529	0.043	0.275	0.225
black pigmentation											
strong	0.000	0.286	0.000	0.571	0.257	0.300	0.286	0.157	0.571	0.500	0.000
weak	1.000	0.714	1.000	0.429	0.743	0.700	0.714	0.843	0.429	0.500	1.000
reproductive organs											
pinkish	0.000	0.171	0.000	0.171	0.129	0.129	0.586	0.209	0.300	0.600	0.025
whitish	1.000	0.829	1.000	0.829	0.871	0.871	0.414	0.971	0.700	0.400	0.975
reproductive organs											
pigmented	0.257	0.200	0.400	0.171	0.357	0.271	0.314	0.000	0.157	0.025	0.000
unpigmented	0.743	0.800	0.600	0.829	0.643	0.729	0.686	1.000	0.843	0.975	1.000
mucous gland											
lobate	0.986	0.829	0.500	0.414	0.571	0.572	0.529	0.271	0.314	1.000	1.000
unlobate	0.014	0.171	0.500	0.586	0.429	0.428	0.471	0.729	0.686	0.000	0.000
mucous gland outlet											
multiple	1.000	0.971	0.771	0.400	0.871	0.557	0.986	0.514	0.671	0.975	1.000
single	0.000	0.029	0.229	0.600	0.129	0.443	0.014	0.486	0.329	0.025	0.000
sample size	70	70	70	70	70	70	70	70	70	40	40

"dotted" (Fig. 15A-F) and "shaded" (Fig. 15G-J). The two patterns never occurred in one specimen, but both were found at almost all the localities. Within the two patterns, wide ranges of continuous variability were observed (Fig. 15). The "shaded" pattern covered a larger or smaller part of the mantle, forming irregular, pigmented patches of various size or covering almost all the surface. The "shaded" pigmentation was often intensive or very intensive, covering the major part of the mantle. Also the "dotted" pattern showed a wide variability: from minute dots to big, black spots, which usually were approximately circular or oval.

In addition to external morphological polymorphisms, we have also found polymorphic characters in the reproductive organs (Fig. 16; Table 3), which have been described and figured by Shileiko (1978: figs. 52–53, p. 126), although his drawing is not adequately detailed. The colour of the penis, atrium, dart sac and oviduct may be whitish or pinkish (Fig. 16). This colour variation is observed in mature snails and specimens fixed in ethanol, frozen in liquid nitrogen, and fresh, indicating that it is not an artifact of preservation. There was also a black pigment on the reproductive organs (Fig. 16); it occurred in grains, more or less dense and covering a variable part of the penis and atrium.

The mucous gland of the reproductive organs (Figs. 16, 17) is divided externally into lobes (Fig. 17B-D, H-K) or not (Fig. 17A, E-G). Also, the outlet of the gland was variable, consisting of either externally distinguishable, separate ducts (Fig. 17E-K), or a single, fused outlet (Fig. 17A-D).

The frequency distributions of all polymorphic characters in the studied populations were tested for normality. For each pair of polymorphic characters, Pearson's product-moment correlation coefficients (Sokal & Rohlf, 1987) were calculated between the fre-



FIGS. 2–14. Shell colour polymorphism in *Bradybaena fruticum*: 2, 5, 10, 12, 13—dark morph; 4, 6, 7, 11, 14—light morph; 3—band adjacent to lip; 8, 9—atypical double equatorial band; (b—brown, c—chestnut, i—ivory, pb—pale brown, pc—pale chestnut, y—yellowish); 12, 13—soft parts visible through shell wall.

quencies in all populations. Significant correlations were found only between the equatorial band on the shell and the band adjacent to the lip ($r = 0.6149$, $p < 0.05$); the dark shell and the band adjacent to the lip ($r = 0.5364$, $p < 0.10$); the dark shell and the shaded pigmentation of the mantle ($r = 0.7296$, $p < 0.01$); the yellow pigment on the mantle and the black pigment on the reproductive organs ($r = 0.6589$, $p = 0.02$); the lobate mucous gland and the multiple outlets of the gland ($r = 0.7687$, $p < 0.005$).

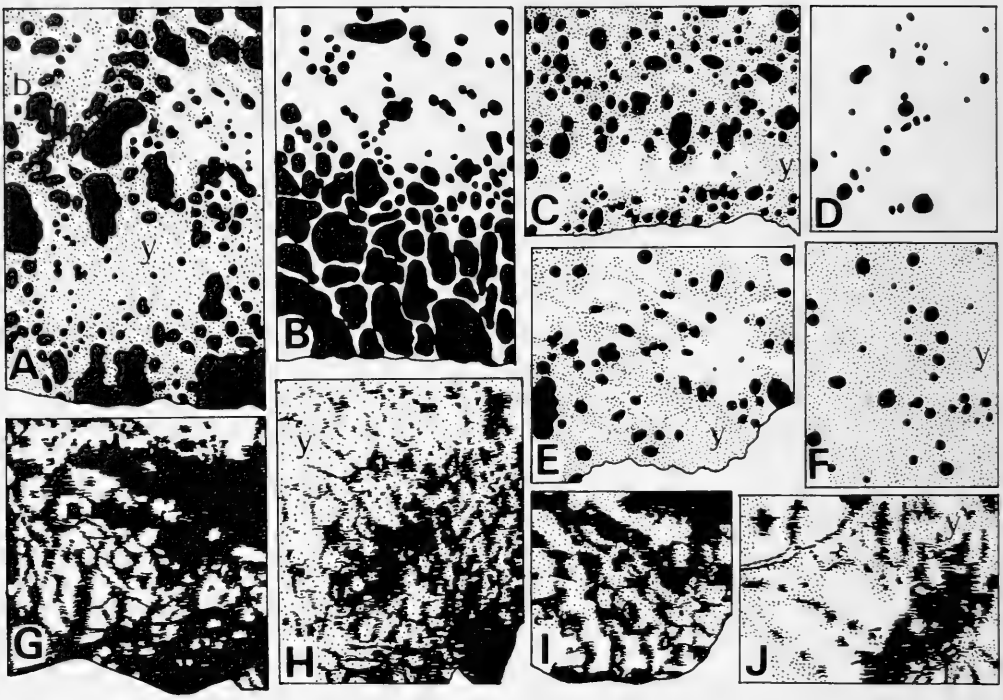


FIG. 15. Mantle pigmentation polymorphism: A–F—dotted black, G–J—shaded black. Black pigment (b) represented by black, yellow pigment (y) represented by shadings (minute dots).

Enzymatic Polymorphism

For all the individuals studied, the enzyme ACP separated into three diffuse but well-resolved bands. Such a pattern is characteristic of a dimeric enzyme having two monomorphic loci, with hybrids as the middle band. This interpretation is consistent with general comments of Richardson et al. (1986). Similar conclusions concern ALP. AAT appeared as a single diffuse band in all individuals screened for this enzyme. The G3PDH activity appeared on gels as multiple, sharp bands concentrated in a relatively narrow zone (= presumptive locus), showing no detectable variation among individuals, so the locus was regarded as monomorphic. Similar remarks concern HBDH. For both enzymes, there was some indication of a second locus but a very low activity.

For "*Cap*," staining with L-leucine-β-naphthylamide, two of probably many peptidase loci were observed. The loci detected are perhaps related to the human E and S peptidases (Harris & Hopkinson 1976). According to Richardson et al. (1986), the PEP-E of vertebrates is identical with CAP. For both loci, a monomeric structure of *CAP* is evident, as in other snails (Johnson et al., 1977; Rudolph & Burch, 1987, 1989) in which one locus (Rudolph & Burch 1987; Emberton, 1988; Woodruff et al., 1988), two loci (Ayala et al., 1973; Selander & Kaufmann, 1975; Johnson et al., 1977; Kitikoon, 1982; Hoagland, 1984; Brown & Richardson, 1988) or three loci (G. M. Davis et al., 1988) have been detected.

MDH separated into two rather diffuse zones (= presumptive loci) consistent with a dimeric structure and two loci (Harris & Hopkinson, 1976; Wurzinger, 1979; Hoagland, 1984; Richardson et al., 1986; Rudolph & Burch, 1987; Emberton, 1988; G. M. Davis et al., 1988; Mulvey et al., 1988; Mimpfoundi & Greer, 1990a). Weak bands of PGDH activity were observed but gels were still scorable and interpretable, showing a single polymorphic locus. A dimeric structure of PGDH has been proposed from studies on vertebrates (Richardson et al., 1986; Harris & Hopkinson, 1976) and on *Stagnicola* (Rudolph & Burch, 1987). A single, polymorphic locus of dimeric XO was found, though the overall activity was low.

Allele frequencies, sample sizes, mean

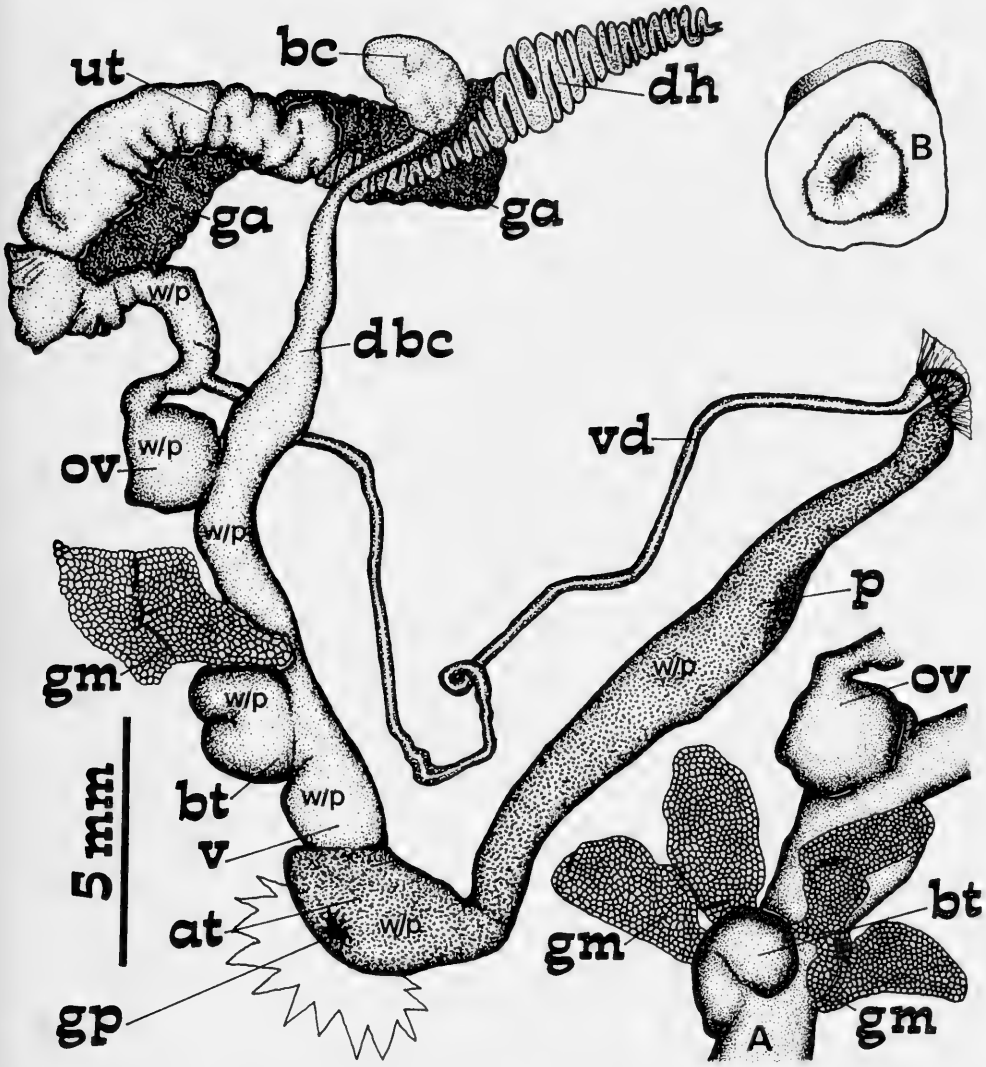


FIG. 16. Reproductive organs of *Bradybaena fruticum* (A. A fragment with plural outlets of mucous glands, divided into four separate lobes; B. Cross section of the penis); at—atrium, bc—bursa copulatrix, bt—dart sac, dbc—duct of bursa copulatrix, dh—ductus haermaphroditicus, ga—albuminoid gland, gm—mucous gland (glands), gp—gonoporus, ov—oviduct, p—penis, ut—uterus, v—vagina, vd—vas deferens. Pigmentation of penis and atrium represented by coarse dotting; colour polymorphism represented by w/p (white or pink)

numbers of alleles per locus, proportions of polymorphic loci, and proportions of heterozygosities both observed and estimated for all the studied populations are given in Table 4. The proportion of polymorphic loci was relatively low (Pmean = 36.4%) for a polymorphic helicoid species, and widely variable among the populations. In several cases, a population was fixed for one allele at a given locality, while polymorphic at the same locus at another locality. In all but one observed cases, chi-squared tests of genotype frequencies provided no evidence for a significant departure from random mating expectations ($p \geq 0.10$). A significant excess of heterozygotes was found in the CAP_1 locus (Table 4).

No relation of enzyme polymorphism to any morphological polymorphism was found.

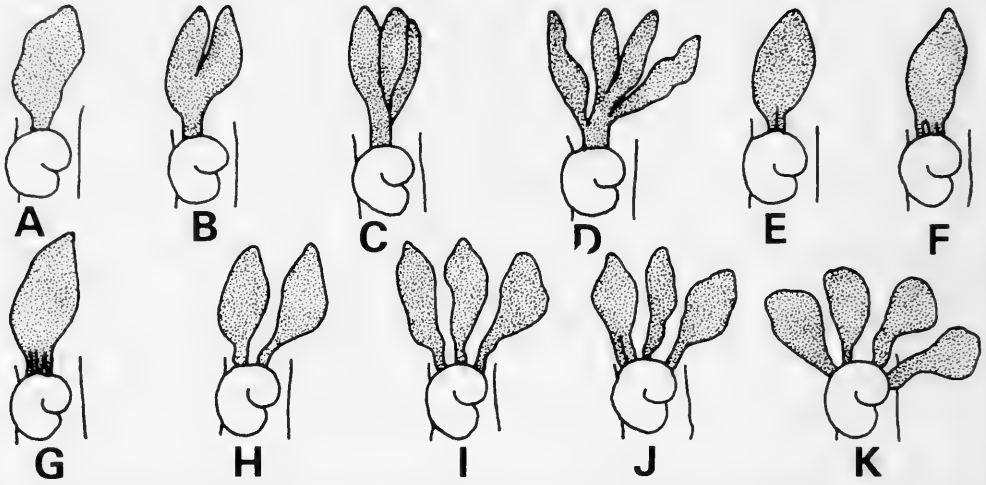


FIG. 17. Schematic representation of mucous gland polymorphism: A. Gland not lobate, outlet fused; B–D. Gland lobate, outlet fused; E–G. Gland not lobate, outlet divided; H–K. Gland lobate, outlet divided.

Differences Between Local Populations

To illustrate distances between studied populations based on morphological polymorphism frequencies, the CONTML technique has been used (Fig. 18). The resulting tree shows numerous relatively long distances between closely situated populations. The same technique has been used for enzyme allele frequencies (Fig. 19). The resulting grouping is different, especially in linking populations 10 and 11, but also in this case the distance between, e.g., populations 1 and 6 (within the Ojców National Park) is not much longer than the distances between 1 and 10 or 1 and 11.

For each pair of populations, Nei's distances and Cavalli-Sforza & Edwards's arc distances were calculated (Table 5). The high Nei's distance values between populations 10 and 11 and the majority of the others on the one hand, and the very low value of the distance between the geographically distant populations 10 and 11 on the other, are noteworthy. Cavalli-Sforza & Edwards's arc distances were used to compute a Fitch-Margoliash additive tree (Fig. 20) showing a pattern similar to Nei's distances; the distance between populations 1 and 6, as well as the ones between all the Polish populations, were longer than the distance between populations 10 or 11 and population 7. Finally, a Cavalli-Sforza & Edwards least square tree with contemporary tips (Fig. 21) was computed. It shows even better the same pattern: populations 10 and 11 are equally distant from all the others, while within the Polish group of populations there is practically no geographic pattern.

For each pair of populations, Spearman's rank correlation coefficients between genetic distances and geographic distances (in km) were calculated. For Nei's distance the correlation was not significant, while for Cavalli-Sforza & Edwards's arc distance the correlation was significant ($r = -0.7060$, $p < 0.001$), but when the most distant populations 10 and 11 were excluded, it was not significant.

DISCUSSION

In *Bradybaena fruticum* all the three types of external colouration polymorphism described by Clarke et al. (1978) (mantle and body, shell colour, shell banding) can be distinguished. In another bradybaenid, *B. similaris* (Férussac, 1821), brown shell colour is dominant to yellow, a single banded pattern is dominant to unbanded, and the two loci are linked (Komai & Emura, 1955: cited in Clarke et al., 1978). The dominance of a dark shell and a banded shell seems common in polymorphic terrestrial pulmonates (e.g. Clarke et al., 1978; Cain, 1983: the references therein). Khokhutkin (1979, 1984) and Khokhutkin & Lazareva (1975, 1983, 1987) considered the single

TABLE 4. Allele frequencies in all polymorphic loci studied

locus/ allele		locality 1	2	3	4	5	6	7	8	9	10	11
CAP_1	a	0.647	0.343	0.437	0.732	0.036	0.457	0.176	0.167	0.109	0.000	0.000
	b	0.353	0.657	0.563	0.268	0.964	0.543	0.824	0.833	0.891	1.000	1.000
CAP_2	a	0.000	0.157	0.125	0.027	0.196	0.300	0.191	0.183	0.094	0.138	0.129
	b	0.779	0.629	0.719	0.491	0.340	0.557	0.588	0.567	0.609	0.500	0.532
	c	0.221	0.214	0.156	0.482	0.464	0.143	0.221	0.250	0.297	0.362	0.339
MDH_1	a	0.029	0.929	0.047	0.848	0.268	0.157	0.015	0.517	0.594	1.000	0.661
	b	0.000	0.000	0.000	0.000	0.000	0.114	0.000	0.000	0.172	0.000	0.000
	c	0.971	0.071	0.953	0.152	0.732	0.729	0.985	0.483	0.234	0.000	0.339
MDH_2	a	0.000	0.000	0.000	0.009	0.018	0.957	0.000	0.000	0.516	0.000	0.000
	b	0.985	0.443	1.000	0.911	0.982	0.043	0.029	0.783	0.484	0.000	0.000
	c	0.015	0.557	0.000	0.080	0.000	0.000	0.971	0.217	0.000	1.000	0.726
	d	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.274
PGDH	a	0.000	0.000	0.000	0.000	0.000	0.186	0.000	0.150	0.063	0.000	0.000
	b	1.000	1.000	1.000	1.000	1.000	0.814	1.000	0.850	0.937	1.000	1.000
XO	a	0.235	0.486	0.031	0.304	0.500	0.243	0.300	0.367	0.406	0.000	0.000
	b	0.765	0.228	0.531	0.339	0.286	0.757	0.286	0.283	0.187	0.172	0.000
	c	0.000	0.286	0.438	0.357	0.214	0.000	0.414	0.350	0.407	0.828	1.000
n_{min}		34	35	32	56	28	35	34	30	32	29	31
A_{mean}		1.38	1.54	1.46	1.61	1.54	1.61	1.54	1.61	1.69	1.23	1.31
P%		38.5	38.5	30.8	38.5	38.5	46.1	38.5	46.1	46.1	15.4	23.1
$H_{mean(e)}$		0.096	0.172	0.119	0.149	0.134	0.174	0.119	0.201	0.195	0.068	0.110
SE		0.045	0.067	0.056	0.060	0.065	0.060	0.062	0.067	0.069	0.047	0.057
$H_{mean(o)}$		0.103	0.182	0.134	0.159	0.134	0.166	0.119	0.205	0.197	0.069	0.111
SE		0.050	0.070	0.065	0.064	0.065	0.057	0.062	0.068	0.069	0.048	0.057
$H_{CAP_1(e)}$		0.457	0.451	0.492	0.392	0.069	0.496	0.290	0.278	0.194	0.000	0.000
$H_{CAP_1(o)}$		0.559	0.571	0.687	0.518	0.071	0.400	0.294	0.333	0.219	0.000	0.000

n_{min}—minimum number of specimens screened at given locality; A_{mean}—mean number of alleles per locus (including monomorphic loci); $P_{\%}$—proportion of polymorphic loci; H_{mean}—mean individual heterozygosity (including monomorphic loci: $H_{mean(e)}$—expected from Hardy & Weinberg equilibrium, $H_{mean(o)}$—observed; H_{CAP_1}—heterozygosity in CAP_1 locus: $H_{CAP_1(e)}$—expected, $H_{CAP_1(o)}$—observed; SE—standard error; monomorphic loci: ACP_1, ACP_2, ALP_1, ALP_2, *AAT*, $G3PDH_1$ and $G3PDH_2$.

banded pattern to be recessive to unbanded one. On the other hand, the existence of atypically banded specimens, as well as the observed change in shell colour from reddish brown to yellow in one specimen, and wide ranges of continuous colour variability within the two morphs distinguished seem to suggest that the inheritance mechanism of these polymorphic characters may be more complicated, with numerous loci being involved; similar remarks concerning *Theba pisana* (O. F. Müller, 1774) were given by Cowie (1984). Also environmental effects on the expression of the shell colour genes cannot be excluded.

In our populations of *B. fruticum*, the proportion of polymorphic enzyme loci was 15.4%–46.1%, mean 36.4%. In the majority of marine molluscs, the proportion is between 30 and 50% (Berger, 1983); in the freshwater *Anodonta*, 11–36%, depending on species (Kat, 1983); in the brackish water *Hydrobia*, 13–23% (G. M. Davis et al., 1988); in freshwater gastropods, 14–62% (Brown & Richardson, 1988; Woodruff et al., 1988). In land snails, it varies form 0 to 100% (Nevo, 1978). For example, in Australian camaenids it ranges from 19 to 71% (Woodruff & Solem, 1990), from 65 to 80% in *Partula* (Johnson et al., 1977), but reaches only about 4% in *Liguus* (Hillis et al., 1987). In *Cepaea,* it is about 60% (Clarke et al., 1978). Therefore, the value found in *B. fruticum* is rather low for a polymorphic species.

Heterozygosity in *B. fruticum* in this study varied from 0.069 to 0.205, mean 0.144. The values are similar to the ones given by Nevo (1978) for *Theba* (0.054–0.165), Brown & Richardson (1988) for *Cepaea nemoralis* (0.134), and by Woodruff & Solem (1990) for camaenids (0.08–0.24). On the other hand, in *Bradybaena similaris* it is lower (0.083: Brown & Richardson (1988). In land slugs, average heterozygosity varies among species (0–0.19: Foltz et al., 1984), but also

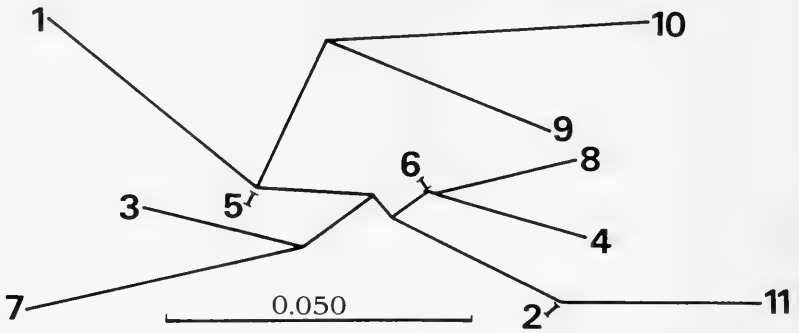


FIG. 18. Distances between populations, based on morphological character states frequencies, generated by maximum likelihood method for continuous characters (CONTML). Distances drawn proportionally. Ln Likelihood = 109.47078; examined 4,770 trees; 1–11, locality numbers, as in text.

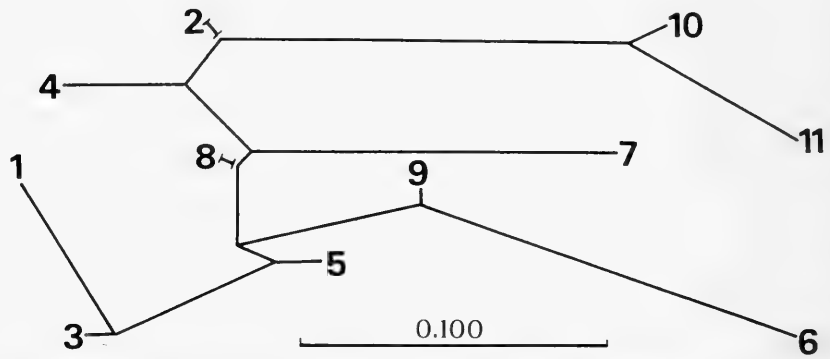


FIG. 19. Distances between populations, based on allele frequencies, generated by maximum likelihood method for continuous characters (CONTML). Distances drawn proportionally. Ln Likelihood = 83.33746; examined 3,724 trees; 1–11, as in Fig. 18.

among conspecific populations from various parts of the range (0.006–0.19, *Milax*: Foltz et al., 1984; means: 0.04–0.19, *Oncomelania*: Woodruff et al., 1988). In *Partula,* it ranges from 0.13 to 0.17 (Johnson et al., 1977), whereas in the closely related *Samoana,* it does not exceed 0.002 (Johnson et al., 1986).

The heterozygote proportion did not depart significantly from Hardy-Weinberg equilibrium, with the exception of the CAP_1 locus at localities 1–4, 6, 8, and 9. At locality 6, there was a heterozygote deficiency, while at all the other listed localities, a heterozygote excess (Table 5). Heterozygote deficiency is commonly observed in molluscan populations, especially in bivalves (Berger, 1983; Zouros & Foltz, 1984; Hillis et al., 1987; Brown & Richardson, 1988; Hillis, 1989; Mimpfoundi & Greer, 1990b, c). Heterozygote excess is much less common, but has been observed [Selander & Kaufman, 1975, in introduced *Helix aspersa* (O. F. Müller, 1774) populations; Berger, 1983, in marine molluscs]. Possible explanations of the observed excess are assortive mating or heterozygote advantage, or Wahlund effect. The heterozygosity data seem to indicate that there is neither self-fertilization nor inbreeding in *B. fruticum.*

The theoretical background to the discrodance between the patterns of morphological variation and enzymatic polymorphism is clear (Lewontin, 1984; Cheverud, 1988). Such inconsistency between molecular and morphological data sets seems common (e.g. Johnson et al. 1977, 1986; Hillis et al., 1987; Woodruff & Solem, 1990; Murray et al., 1991). This is confirmed when comparing the trees based on morphological (Fig. 18) and enzymatic (Figs. 19–21) characters. For example, Slovakian populations 10 and 11 are close to

TABLE 5. Genetic distances between studied populations (below diagonal: Nei distances, above diagonal: Cavalli-Sforza & Edwards arc distances)

	locality										
	1	2	3	4	5	6	7	8	9	10	11
1	***	0.467	0.142	0.294	0.265	0.476	0.482	0.302	0.489	1.192	1.139
2	0.136	***	0.411	0.118	0.289	0.661	0.323	0.108	0.296	0.307	0.423
3	0.017	0.120	***	0.256	0.171	0.519	0.409	0.197	0.357	0.923	0.780
4	0.083	0.043	0.081	***	0.238	0.593	0.514	0.150	0.253	0.611	0.688
5	0.067	0.086	0.045	0.083	***	0.483	0.425	0.113	0.189	0.790	0.708
6	0.101	0.149	0.110	0.159	0.131	***	0.625	0.510	0.281	1.109	1.116
7	0.126	0.101	0.100	0.180	0.103	0.125	***	0.266	0.571	0.498	0.360
8	0.069	0.034	0.043	0.049	0.019	0.114	0.080	***	0.201	0.477	0.473
9	0.121	0.043	0.089	0.068	0.050	0.083	0.115	0.027	***	0.661	0.657
10	0.282	0.053	0.215	0.146	0.173	0.235	0.103	0.099	0.097	***	0.158
11	0.237	0.069	0.160	0.148	0.135	0.204	0.071	0.081	0.081	0.019	***

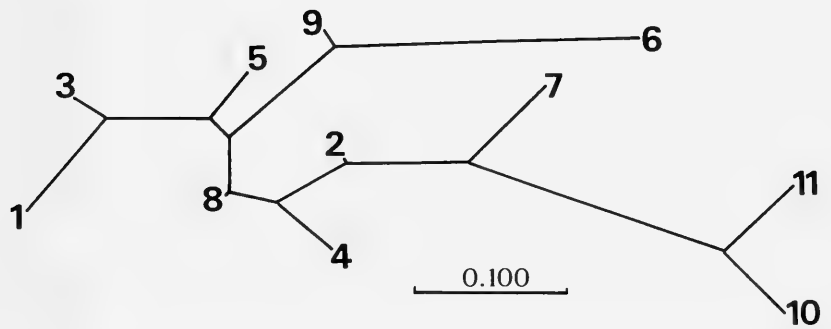


FIG. 20. Distances between populations, based on Cavalli-Sforza and Edwards' arc distances, generated by Fitch-Margoliash's method (FITCH). Distances drawn proportionally. Sum of squares = 3.40454; average percent standard deviation = 17.75488; 3,242 trees examined; 1–11, as in Fig. 18.

each other and distant from the Polish populations in all the trees based on molecular data (Figs. 19–21), but not in the tree based on morphological characters (Fig. 18).

Nei's distance among populations in *B. fruticum* ranged form 0.017 to 0.282. The latter value exceeds the one characteristic of the subspecies level in the *Drosophila willistoni* group (Ayala, 1975). The value of 0.019 between populations 10 and 11 (150 km away form each other), compared with values over 0.1 within a few km distance, is noteworthy. From among the reasons for the observed relatively high values of Nei's distances, the fixation on one allele at some loci in some populations has to be mentioned. Cavalli-Sforza & Edwards's arc distance shows a similar picture.

Woodruff et al. (1988) list Nei's distances for various molluscan species. They point out that typically within molluscan species the value does not exceed 0.1 between local populations, whereas interspecific differences for congeners are within the range 0.2–0.6 (e.g. for *Cerion, Triodopsis*). In their study on *Oncomelania*, the distances between rather close populations were within the range 0.002–0.104, but between the Philippines and the Chinese populations reached 0.648, within the same species. In *Biomphalaria*, with growing geographic distance, conspecific populations differed by distance values of 0.00–0.18. In *Hydrobia,* distances within a species were not higher than 0.013 (G. M. Davis et al., 1988). The highest value of interpopulation Nei's distance within a species of snail is 0.701 noted in *Melanoides tuberculata* by Livshits et al. (1984), but between par-

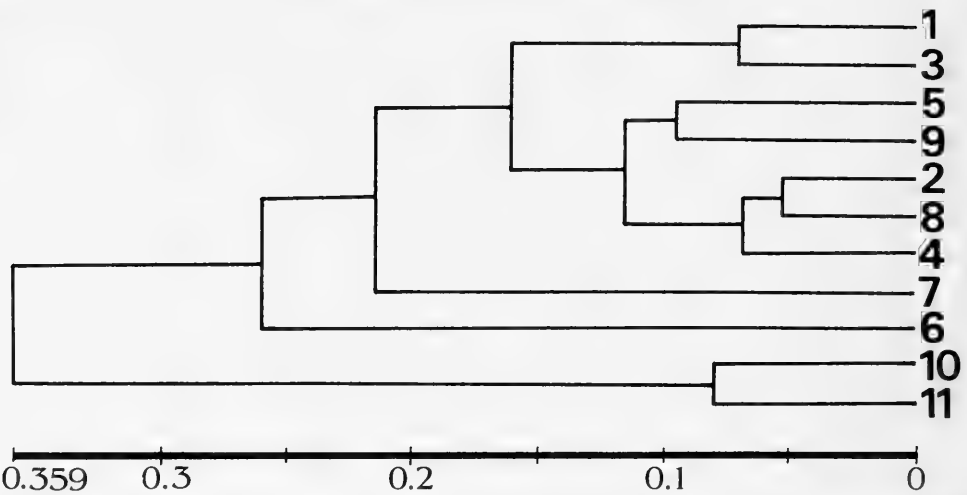


FIG. 21. Distances between populations, based on Cavalli-Sforza and Edwards's arc distances, generated by Fitch-Margoliash's method with contemporary tips (KITSCH). Distances drawn proportionally. Sum of squares = 3.256; 5,229 trees examined; 1–11, as in Fig. 18.

thenogenetically reproducing populations. The highest intraspecific value reported for sexually reproducing gastropods (0.63) is the one between Italian and British populations of *Cepaea nemoralis* (Johnson et al., 1984). On the other hand, the distance found between two *Partula* species, about 8,000 km distant from each other, is 0.125 (Johnson et al., 1977). In *Samoana,* Nei's distances between species varied from 0.004 to 0.602 (Johnson et al., 1986) and between *Cristilabrum* species (Woodruff & Solem, 1990) from 0.00 (!) to 0.199, but the average distance for five species was only 0.081; within camaenids the intergeneric distances were 0.27–0.50 (Woodruff & Solem, 1990). The above data clearly indicate that there is no general rule concerning genetic distances in snails. The values of Nei's distances in *B. fruticum* are relatively high for local populations, and in numerous cases relatively high values of genetic distance observed correspond with rather low values of geographic distance.

The allozyme polymorphism shows more geographic pattern (Figs. 19–21) than the morphological variation (Fig. 18), which is in agreement with Makeeva (1987). However, Makeeva (1987), Makeeva & Matiokin (1987), Khokhutkin & Lazareva (1975, 1983, 1987) and Khokhutkin (1984) report a hierarchical pattern of population structure in *B. fruticum.* They describe the species as composed of semi-isolated, small panmictic colonies (the latter confirmed by our study). There are some differences among local panmictic units, but always less pronounced within a region than among regions; the main component of interpopulation differences is a macrogeographic clinal one. In our study, we have not observed such a hierarchical structure. Although localities 10 and 11 are both genetically and geographically distant from the other localities, they are genetically much similar to each other, but the geographic distance between localities 10 and 11 is greater than the ones between 10 and each of localities 1–9. At the same time, the genetic distance between populations 1 and 6, which are situated very closely to each other, is not much shorter than the genetic distance between 1 and 10 or 1 and 11. The observed genetic similarity of the Slovakian populations 10 and 11 is difficult to explain, the more that *B. fruticum* is rather uncommon in Slovakia (Steffek, personal communication). On the other hand, the relatively high values of genetic distance between each of the two Slovakian populations and each of the Polish ones can easily be explained. The high Tatra Mountains at the border between Poland and Slovakia form an effective barrier for this lowland snail.

It seems that in *B. fruticum*, the "stepping stone" model of Wright (1965) rather than the "isolation by distance" model (Wright, 1965) can be applied to describe macrogeographic

differentiation. The gene and morphological differentiations we observed were in general significant among populations, but negligible among regions. A similar pattern has been observed in *Hydrobia* (G. M. Davis et al., 1988). On the other hand, in what we observed there still was more geographic pattern than was found in parthenogenetic populations of *Melanoides* (Livshits et al., 1984), in which there was no correlation between the genetic and geographic distances.

As stressed by Goodhart (1962, 1963) and Selander & Kaufman (1975) for populations of *Cepaea* and *Helix* respectively, the genetic structure of a population is a result of the interaction of deterministic and stochastic processes. Although in Poland *B. fruticum* is a common species in general, it becomes uncommon or rare in the mountainous regions of South Poland (Riedel, 1988). It is never found in the mountainous beech forest, which is a typical natural biotope of the Ojców National Park. The deforestation caused by man changed the environment to a one that is more suitable for the snail. On the other hand, pieces of arable land are barriers for *B. fruticum*. The successive deforestation and changes in agricultural activities have resulted in the observed pattern of small spots of biotopes inhabited by the species. This, along with the relatively low densities of the populations, have resulted in the existence of several demes which are almost completely isolated and consist of relatively few individuals. Such populations' genetic structure is the most dependent on stochastic processes and this can be an explanation of the observed high genetic distances between some of the closely situated Ojców populations.

Within the area of the Ojców National Park, there are some barriers to dispersal, such as streams or roads, or beech forest. For example, populations 2 and 4, which are situated not very closely to each other and are separated by a river and a road, are genetically similar, whereas the very closely situated populations 3 and 4, separated by a beech forest, are much different genetically. The comparison of several genetic distances within the Ojców National Park seems to indicate that for the snail a beech forest is a much more effective barrier than a river, a stream or a road. It is not clear in general how effective such barriers must be to prevent or strongly limit gene flow. Even a small river may be a true barrier for land snails (e.g. Hillis et al., 1987). On the other hand, Grant & Utter (1988) observed considerable genetic differences among 12 breeding colonies of the marine, intertidal whelk *Nucella*, distributed within a distance of 100 m of a shore, where no barrier of any kind was found. They acknowledged that random genetic drift among small subpopulations was a source of differentiation, and the distinctness of the colonies had a behavioural background. Especially juvenile site fidelity and homing behaviour limited gene flow among colonies. Little is known about the behaviour of *B. fruticum*, but observations of Zeifert & Shutov (1979) and Zeifert (1987) suggest both homing and juvenile site fidelity in the species. These authors also reported variation in mobility: snails inhabiting microhabitats of milder microclimatic conditions in winter stayed at the same place, whereas the ones inhabiting less suitable microhabitats migrated from their winter shelters to their feeding territories. Such migration may increase gene flow, resulting in a range of patterns of microgeographic differentiation. All the above factors, coupled with a spotty pattern of distribution and with barriers of various kind and efficiency may explain the observed pattern.

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THE GENETIC DIFFERENTIATION IN THREE SPECIES OF THE GENUS *HYDROBIA* AND SYSTEMATIC IMPLICATIONS (CAENOGASTROPODA, HYDROBIIDAE)

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ABSTRACT

In order to investigate whether the genus *Hydrobia* should be subdivided, three species representing the nominal genera involved (*Hydrobia, Ventrosia*, and *Peringia*) were compared on the basis of allozyme data. Based on genetic distances, anatomical and ecological data, as well as data on reproductive biology, it is argued that (1) there is no reason to split the genus *Hydrobia* into different genera, (2) *Hydrobia* can be subdivided into the subgenera *Hydrobia s. s.* and *Peringia*, and (3) *Ventrosia* has to be considered synonymous with *Hydrobia*.

The analysis of the genetic structure of the three populations investigated revealed heterozygote deficiencies in practically all polymorphic loci in one case, and low, respectively complete lack of variability in the remaining two populations. The deficiencies of heterozygotes are primarily attributed to selection, probably due to a high infection rate with parasites, whereas the reduced variability is explained by genetic drift following a bottleneck.

Key words: Allozymes, electrophoresis, genetics, systematics, Hydrobiidae, *Hydrobia, Peringia, Ventrosia*.

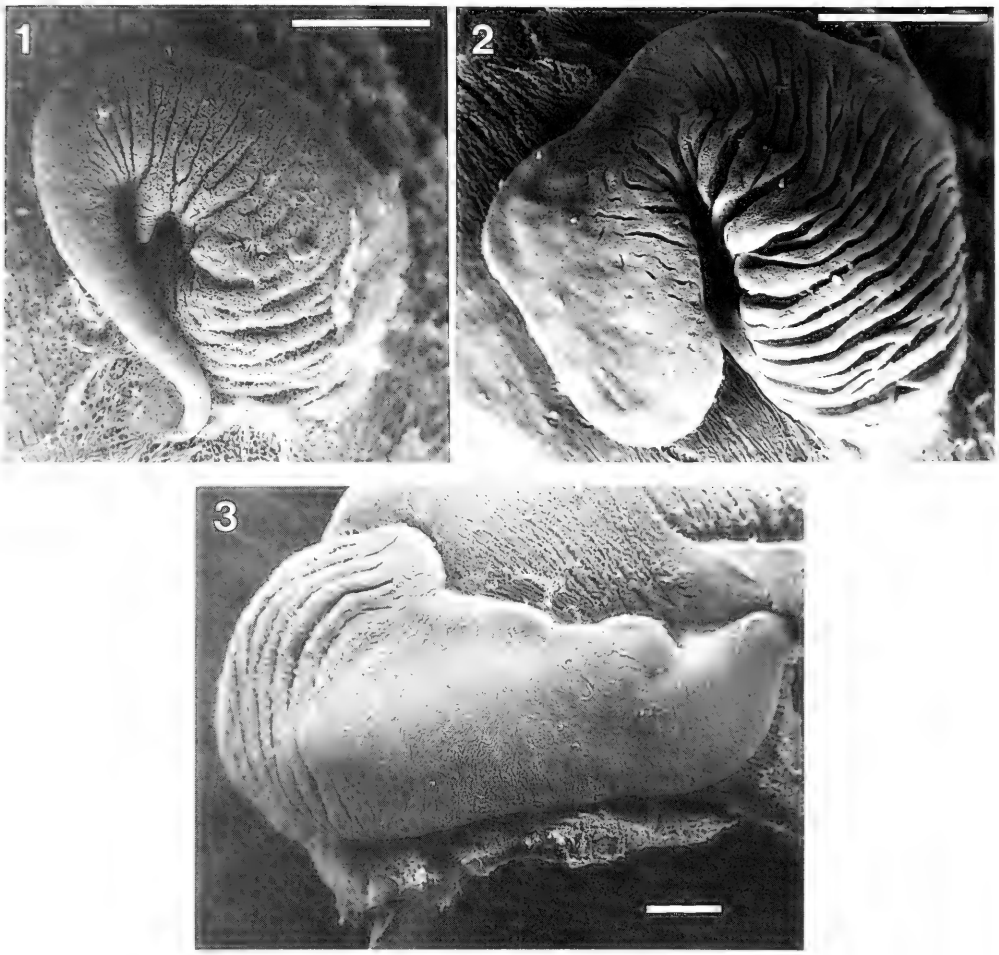
INTRODUCTION

The family Hydrobiidae is one of the largest among gastropods, and its systematics are one of the most confusing in malacology. A principal problem is the assessment of the systematic value of minor differences among these usually tiny snails, which are poor in characters and reveal a considerable degree of convergence. In many issues, there exist as many opinions as there are authors. Such a case is the debate whether the genus *Hydrobia* Hartmann, 1821, which defines the whole family, should be subdivided into subgenera or even split into several genera. In order to evaluate the status of the three nominal genera involved—*Hydrobia, Ventrosia* Radoman, 1977, and *Peringia* Paladilhe, 1874—their type species *H. acuta* (Draparnaud, 1805) (Fig. 2), *V. ventrosa* (Montagu, 1803) (Fig. 1), and *P. ulvae* (Pennant, 1777) (Fig. 3), respectively, were investigated genetically using standard methods of allozyme electrophoresis.

As to the specific (not generic) designation of the populations used in this study—topotypes were not available—I have followed Giusti & Pezzoli (1984) and their suggestion that within *Hydrobia* populations with identical anatomy belong to a single species despite slight, mainly conchological differences (in contrast to the views of Radoman, 1973, and Boeters, 1988). This assumption is corroborated by the morphological, anatomical and genetic studies of Davis et al. (1988, 1989), who compared six populations of *H. truncata* (Vanatta, 1924) from Massachusetts, New York and Maryland. But even if this assumption turned out to be unwarranted, the purpose of this paper would not be affected, because each population can unambiguously be attributed to one of these nominal genera. Until further notice, the genus *Hydrobia* is used for all three species for reasons of simplicity and clarity.

Nomenclatural History

The genus *Hydrobia* was introduced by Hartmann (1821), who included *Cyclostoma acutum* Draparnaud, 1805, which later was designated as type species by Gray (1847). Radoman (1977) was the first who anatomically described a *Hydrobia* from southern France, the presumptive origin of Draparnaud's specimens, with males possessing a distally lobed penis (Fig. 2). He ascribed this anatomy to *H. acuta* and restricted the type locality to Palavas, Etang du Prévost. Previously, Radoman (1974) had introduced the genus *Obrovia* Radoman, 1974, for two taxa with this type of penis from the Adriatic coast. So, after having identified *H. acuta, Obrovia*



FIGS. 1–3. Penis. 1. *Hydrobia ventrosa*; 2. *H. acuta*; 3. *H. ulvae* (scale bars = 100 μm).

became a synonym of *Hydrobia* (Radoman, 1977). In the same paper, Radoman described the new genus *Ventrosia* Radoman, 1977, for the species with a slender penis bearing a pointed lobe on the left side (Fig. 1). This type of verge has always been associated with the taxon *H. ventrosa* (Montagu, 1803) (Robson, 1922; Krull, 1935; Muus, 1963; Bank & Butot, 1984; Giusti & Pezzoli, 1984; Falniowski, 1987). [Radoman (1977) erroneously used the name *Ventrosia stagnorum* (Gmelin, 1791), which is a *Heleobia* Stimpson, 1865, and considered *Hydrobia ventrosa* a junior synonym (c.f. Bank & Butot, 1984).]

Boeters (1984) found species with both penial types at Radoman's restricted type locality of *H. acuta* and claimed that Draparnaud's original material of *H. acuta* also contained both species. This assumption is based on the comparison of two syntypes deposited at the Muséum d'Histoire Naturelle in Paris. One of these shells has significantly deeper sutures, like, according to Boeters (1984), the species with males possessing the pointed penis. In order to save the traditional view of *Hydrobia*, Boeters (1984) designated this shell as lectotype of *H. acuta* and attributed to it the anatomy of what all authors cited above thought was *H. ventrosa*. Thus, *Ventrosia* would have to be considered a junior synonym of *Hydrobia* and *H. acuta* a junior syn-

TABLE 1. Conditions for electrophoresis.

	Enzyme	Buffer System	Current/ Voltage	Run time (hrs)	Loci[1]
AAT	Aspartate Amino Transferase	TEB 9.1[2]/TEB 8 (gel/tray)	35 MA	2	2
ACPH	Acid Phosphatase	TC[3]7	35 MA	2	1
AK	Adenylate Kinase	TC 7	35 MA	2	1
AO	Aldehyde Oxidase	TEB 8	35 MA	3.5	1
APH	Alkaline Phosphatase	TEB 9.1	350 V	4.5	1
CK	Creatine Kinase	TEB 8	35 MA	3.5	1
EST	Carboxyl Esterase	TC 8 & TEB 9.1/TEB 8	40 MA/35 MA	3.25/2	0
GDH	Glutamate Dehydrogenase	TEB 8	35 MA	3.5	1
G6PD	Glucose-6-Phosphate Dehydrogenase	TEB 9.1	350 V	4.5	1
GPI	Glucose-6-Phosphate Isomerase	Poulik	350 V	2	1
ISDH	Isocitrate Dehydrogenase	TEB 8	35 MA	3.5	2
LAP	Leucine Aminopeptidase (= Cytosol Aminopeptidase)	TC 7	35 MA	2	0
LDH	Lactate Dehydrogenase	TEB 8	35 MA	3.5	1
MDH	Malate Dehydrogenase	TC 8	40 MA	3.25	1
ME	Malic Enzyme	TC 8	40 MA	3.25	0
MPI	Mannose-6-Phosphate Isomerase	Poulik	350 V	2	1
NADD	Nicotinamide Adenosine Dinucleotide Dehydrogenase	TEB 8	35 MA	3.5	1
OCT	Octopine Dehydrogenase	TEB 8	35 MA	3.5	1
6PGD	6-Phosphogluconic Dehydrogenase	TEB 8	35 MA	3.5	2
PGM	Phosphoglucomutase	Poulik & TEB 9.1/TEB 8	350 V/35 MA	2/2	2
SDH	Sorbitol Dehydrogenase	TEB 9.1	350 V	4.5	1
SOD	Superoxide Dismutase	see text			2
XDH	Xanthine Dehydrogenase	TEB 8	35 MA	3.5	1

[1]Number of loci included in the analysis
[2]Tris-EDTA-Borate, pH 9.1
[3]Tris-Citrate

onym of *H. ventrosa*. The latter synonymy is not mentioned by Boeters. He refrained from discussing any consequences, left the other species unnamed and did not state its generic allocation (Boeters, 1984).

Subsequent authors explicitly (Giusti & Pezzoli, 1984) or implicitly (Davis *et al.*, 1989) rejected Boeters' view. To avoid the consequences and further systematic confusion arising from Boeters' article, and because there is no biological reason for Boeters' purely taxonomic action, as is demonstrated in this paper, Boeters' type designation should be suppressed by the International Commission of Zoological Nomenclature, and I am preparing a petition to this effect.

Peringia Paladilhe, 1874, is occasionally used as a full genus (Kennard & Woodward, 1926; Wenz, 1938–1944; Nordsieck, 1982) or as a subgenus (Zilch & Jaeckel, 1956; Fretter & Graham, 1978; Boeters, 1988) for *Hydrobia ulvae* (Pennant, 1777) (Fig. 3), although most authors consider *Peringia* as a synonym of *Hydrobia* (Ehrmann, 1933; Giusti & Pezzoli, 1984; Falniowski, 1987).

MATERIALS AND METHODS

Hydrobia ventrosa and *H. ulvae* were collected on the German Baltic island Fehmarn in August 1991, *H. ventrosa* from the west bank of the Burger Binnensee, where it lives on mud, and *H. ulvae* from the sandy Südstrand. The salinity in both localities was 12‰. *Hydrobia acuta* was found in a muddy marsh (22‰) on Torcello, an island in the Gulf of Venice/Italy, in July 1991. The animals were taken alive to the University of Vienna. The specific identity of the samples was determined by investigating the male copulatory organ in living specimens under the stereo microscope. In each sample, only one type of penis was found, indicating the presence of only one species per sample. Most of the animals were deep frozen at −70°C in tissue buffer. The frozen material was carried in liquid nitrogen to the Academy of Natural Sciences in Philadelphia, where electrophoresis was done. Parts of the samples were fixed in 70% ethanol or BOUIN's fixative and deposited at the Museum of Natural Histcry

TABLE 2. Allele frequencies. N, number of specimens.

Locus	Alleles	*H. ventrosa*	*H. acuta*	*H. ulvae*
AAT 1	N	38	27	20
	A	0.684	1	0
	B	0.316	0	1
AAT 2	N	22	27	10
	A	1	0	0
	B	0	1	1
ACPH	N	43	27	30
	A	1	1	0
	B	0	0	1
AK	N	20	27	20
	A	0.600	0	0.700
	B	0.400	1	0
	C	0	0	0.300
AO	N	35	10	25
	A	1	1	0
	B	0	0	1
APH	N	20	26	10
	A	0.625	0.981	0
	B	0.100	0	0
	C	0.250	0	0
	D	0.025	0.019	0
	E	0	0	1
CK	N	25	40	10
	A	1	1	0
	B	0	0	1
GDH	N	35	30	15
	A	1	1	0
	B	0	0	1
G6PD	N	20	26	10
	A	1	1	0.700
	B	0	0	0.300
GPI	N	38	27	20
	A	0.987	1	0
	B	0.013	0	1
ISDH 1	N	40	44	25
	A	1	1	0
	B	0	0	1
ISDH 2	N	30	40	25
	A	1	1	0
	B	0	0	1
LDH	N	30	30	15
	A	1	1	0
	B	0	0	1
MDH	N	25	27	20
	A	0.780	1	0.500
	B	0.220	0	0.500
MPI	N	38	27	20
	A	0.605	1	0
	B	0.395	0	1
NADD	N	35	10	15
	A	1	1	0
	B	0	0	1
OCT	N	35	30	25
	A	1	1	0
	B	0	0	1

TABLE 2. (*Continued*)

Locus	Alleles	*H. ventrosa*	*H. acuta*	*H. ulvae*
6PGD 1	N	40	30	15
	A	1	1	1
6PGD 2	N	35	30	15
	A	1	1	1
PGM 1	N	39	27	20
	A	0.744	0	0
	B	0.256	1	0
	C	0	0	0.925
	D	0	0	0.075
PGM 2	N	28	27	10
	A	0.482	1	0
	B	0	0	1
	C	0.143	0	0
	D	0.286	0	0
	E	0.089	0	0
SDH	N	20	26	10
	A	1	1	0
	B	0	0	1
SOD 1	N	15	10	15
	A	1	1	0
	B	0	0	1
SOD 2	N	5	40	15
	A	1	1	0
	B	0	0	1
XDH	N	40	30	25
	A	1	1	0
	B	0	0	1

(NHMW) under the following collection numbers: *H. ventrosa* (NHMW 86801), *H. acuta* (NHMW 86802), *H. ulvae* (NHMW 86803).

Horizontal starch-gel electrophoresis was carried out following Davis *et al.* (1988). Instead of tris-citrate (TC) buffer with pH 6, TC pH 7, was used (Shaw & Prasad, 1970). Table 1 lists the 22 enzymes stained for and the conditions for electrophoresis. Superoxide dismutase was scored on gel slices stained for a dehydrogenase. The data were analyzed using the computer program BIOSYS-1 release 1.7 by Swofford & Selander (1981). Nei's standard genetic distance (Nei, 1972) and unbiased genetic distance (Nei, 1978) and Cavalli-Sforza & Edwards's arc and chord distances (Cavalli-Sforza & Edwards, 1967) were calculated, and cluster analysis based on Nei's unbiased distance and Cavalli-Sforza & Edwards's arc distance using UPGMA were performed.

RESULTS

The enzymes LAP and ME were hardly detectable. The esterases were extremely polymorphic and therefore not interpretable. Thus, these enzymes had to be excluded from the analysis. Allele frequencies for the remaining 25 loci with 57 alleles are given in Table 2. *Hydrobia ulvae* is characterized by 19 and *H. ventrosa* by seven unique alleles. *Hydrobia acuta* shares all alleles with at least one of the other two species. The genetic variability of the three populations is summarized in Table 3. In *H. ventrosa*, eight loci are polymorphic; seven of these are not in Hardy-Weinberg equilibrium (Table 4). *Hydrobia acuta* is remarkably uniform, with only one polymorphic locus (Table 5). The variability of *H. ulvae* lies between the other two species, but is still very low. Only four loci have more than one allele (Table 6). The MDH is 100% heterozygous. Tables 7 and 8 give the genetic distances between the three species. *Hydrobia ventrosa* and *H. acuta* are obviously very closely related. The remarkably and unexpectedly large distance of *H. ulvae* from the other two species is also depicted in the phenograms of Figures 4 and 5. The cophenetic correlation is 0.998 for the cluster analysis based on Nei's unbiased distance and 0.999

TABLE 3. Genetic variability. Standard errors in parentheses.

	Mean Sample Size Per Locus	Mean No of Alleles Per Locus	Percentage of Loci Polymorphic[1]	Mean Heterozygosity	
				Direct Count	HdyWbg Expected[2]
H. ventrosa	30.0	1.5	32.0	0.043	0.136
	(1.9)	(0.2)		(0.016)	(0.045)
H. acuta	27.8	1.0	4.0	0.002	0.002
	(1.7)	(0.0)		(0.002)	(0.002)
H. ulvae	17.2	1.2	16.0	0.070	0.062
	(1.2)	(0.1)		(0.043)	(0.031)

[1]A locus is considered polymorphic if more than one allele was detected.
[2]Unbiased estimate (see NEI, 1978).

TABLE 4. Chi-square test for deviations from Hardy-Weinberg equilibrium in *H. ventrosa*.

Locus	Genotype	Observed Frequency	Expected Frequency	χ^2	DF	P
AAT 1	A-A	25	17.680			
	A-B	2	16.640			
	B-B	11	3.680	30.471	1	0
AK	A-A	11	7.077			
	A-B	2	9.846			
	B-B	7	3.077	13.429	1	0
APH	A-A	12	7.692			
	A-B	0	2.564			
	A-C	0	6.410			
	A-D	1	0.641			
	B-B	0	0.154			
	B-C	4	1.026			
	B-D	0	0.103			
	C-C	3	1.154			
	C-D	0	0.256			
	D-D	0	0.000	23.680	6	0.001
GPI	A-A	37	37.000			
	A-B	1	1.000			
	B-B	0	0.000	0	1	1
MDH	A-A	18	15.122			
	A-B	3	8.755			
	B-B	4	1.122	11.708	1	0.001
MPI	A-A	18	13.800			
	A-B	10	18.400			
	B-B	10	5.800	8.154	1	0.004
PGM 1	A-A	26	21.468			
	A-B	6	15.065			
	B-B	7	2.468	14.737	1	0
PGM 2	A-A	13	6.382			
	A-B	0	3.927			
	A-C	0	7.855			
	A-D	1	2.455			
	B-B	3	0.509			
	B-C	0	2.327			
	B-D	2	0.727			
	C-C	8	2.182			
	C-D	0	1.455			
	D-D	1	0.182	56.901	6	0

TABLE 5. Chi-square test for deviation from Hardy-Weinberg equilibrium in *H. acuta*.

Locus	Geno-type	Observed Frequency	Expected Frequency	χ^2	DF	P
APH	A-A	25	25.000			
	A-D	1	1.000			
	D-D	0	0.000	0	1	1

for the analysis based on Cavalli-Sforza & Edwards's arc distance, respectively.

DISCUSSION

All but one polymorphic loci of *H. ventrosa* significantly lack heterozygotes. That one, GPI, is polymorphic due only to a rare allele. Under the frequently applied 95% criterion (a locus is considered polymorphic if the frequency of the most common allele does not exceed 95%), the GPI locus would be considered monomorphic. The theoretically possible reasons for heterozygote deficiencies are: (1) inbreeding, (2) the Wahlund effect, (3) biased sampling of homozygotes due to genetic patchiness caused by ecological or behavioural factors across a population's habitat, (4) scoring bias for homozygotes, (5) differential survival of homozygotes following collection, (6) location of the locus on a sex chromosome, (7) assortative mating, (8) presence of null alleles, and (9) selection against heterozygotes (Crouau-Roy, 1988; Staub et al., 1990).

Because practically all polymorphic loci are deficient in heterozygotes, it is tempting to assume a single explanation. Inbreeding or the Wahlund effect would affect the allele frequencies of all loci. Both hypotheses, however, are rejected for the following reasons. The population is very big and the habitat very uniform, so that there are no constraints for inbreeding. The Wahlund effect can be excluded, because the sample stems from a homogeneous area of less than ½ m^2, so it seems very unlikely that the sample contained members of two or more subpopulations. The remaining causes are more likely to affect a single locus rather than the whole genome. Thus, probably a combination of factors accounts for the heterozygote deficiencies. However, three more of the above-listed points can be excluded. The habitat of the population is too homogeneous to establish genetic patchiness, so that there is certainly no sampling bias. The staining patterns were easily and unambiguously interpretable. Thus, a scoring bias can be excluded, as can the differential survival of homozygotes following collection, because the sample was frozen less than one week after collection, and few snails had died during that time. It cannot be estimated to which degree location of polymorphic loci on a sex chromosome and assortative mating are involved, because nothing is known about the determination of sex and the choice of mates in *Hydrobia*. The presence of null alleles cannot be excluded. The most probable explanation is selection against heterozygotes. The population is highly infected with trematode sporocysts and rediae, which might cause a considerable selective pressure. Four alleles each were detected in APH and PGM 2. For these two loci, the small sample sizes (20 and 28, respec-

TABLE 6. Chi-square test for deviation from Hardy-Weinberg equilibrium in *H. ulvae*.

Locus	Genotype	Observed Frequency	Expected Frequency	χ^2	DF	P
AK	A-A	5	4.789			
	A-C	4	4.421			
	C-C	1	0.789	0.105	1	0.745
G6PD	A-A	6	4.789			
	A-B	2	4.421			
	B-B	2	0.789	3.488	1	0.062
MDH	A-A	0	4.872			
	A-B	20	10.256			
	B-B	0	4.872	19.000	1	0
PGM 1	C-C	17	17.077			
	C-D	3	2.846			
	D-D	0	0.077	0.086	1	0.770

TABLE 7. Matrix of Nei's genetic distances. Above the diagonal: Nei's (1972) standard distance; below: Nei's (1978) unbiased distance.

	H. ventrosa	*H. acuta*	*H. ulvae*
H. ventrosa	—	0.111	1.648
H. acuta	0.110	—	1.753
H. ulvae	1.645	1.751	—

TABLE 8. Matrix of Cavalli-Sforza & Edwards's (1967) distances. Above the diagonal: chord distance; below: arc distance.

	H. ventrosa	*H. acuta*	*H. ulvae*
H. ventrosa	—	0.306	0.790
H. acuta	0.323	—	0.814
H. ulvae	0.873	0.903	—

tively) alone might account for the deviations from Hardy-Weinberg equilibrium.

The 100% heterozygosity of the MDH in *H. ulvae* is probably due to selection against homozygotes, which means the remarkable loss of 50% of the offspring.

Lack of genetic variation as in *H. acuta*, which has no polymorphic locus under the 95% criterion (the polymorphism of the APH locus is again due to a rare allele), is usually explained by the assumption of genetic drift following a bottleneck in the population's past (Nei et al., 1975).

Nei's commonly used distances were chosen for reasons of comparability, although these measures are nonmetric (Wright, 1978) and the constant substitution of amino-acids, on which Nei based his model (Nei, 1972), is hardly, if ever, met (Hillis, 1984). Cavalli-Sforza & Edwards's arc distance is, according to Wright (1978), superior to all other distance coefficients due to its geometrical clarity. But the validity of Cavalli-Sforza & Edwards's distances is restricted in that only random genetic drift and selection are considered causes for divergence between populations (Cavalli-Sforza & Edwards, 1967). More comprehensive presentations of the strengths and limitations of the various distance measures can be found in Wright (1978), Davis et al. (1988), and Swofford & Olsen (1990). However, the cophenetic correlations (cc) of the phenograms of Figures 4 and 5 (cc = 0.998 and 0.999, respectively) indicate that in the present case both distance measures applied yield equivalent results.

Nei's (1972) genetic distance D between congeneric species of molluscs is typically in the range from 0.20–0.60 (Woodruff et al., 1988). In a survey on distance data, Thorpe (1983) found D values larger than 1.05 in only 15% of approximately 900 estimates of interspecific distances of congeners of various eukaryotes. This value was exceeded in 80% of about 160 comparisons between confamilial genera. Davis et al. (1989) compared six populations of the North American *H. truncata* (Vanatta, 1924). The highest distance value (Nei's unbiased distance, 1978) was 0.018. However, one has to be careful drawing taxonomic conclusions from distance data only. Certain ranges of genetic distance do not have simple correspondence to taxonomic levels (Hoagland & Davis, 1987). Based on the genetic distances in Tables 7 and 8, one could conclude that *H. ventrosa* and *H. acuta* were conspecific populations or very closely related species, whereas *H. ulvae* belonged to another genus. Taking anatomical (Krull, 1935; Giusti & Pezzoli, 1984; Falniowski, 1987; personal observations) and cytological (Butot & Kiauta, 1966) data into account, it becomes clear that *H. ventrosa* and *H. acuta* are distinct species and that there is no character that would separate *H. ulvae* from the other two species on a higher level. [The duct connecting the prostate with the mantle cavity described by Johansson (1948) for *H. ulvae* has also been found in *H. acuta* and *H. ventrosa* (personal observations).] However, the large distance values between *H. ulvae* and the other two species correspond with ecological differences and differences in reproductive biology. *Hydrobia ventrosa* and *H. acuta* prefer sheltered bays, whereas *H. ulvae* also tolerates higher water movement (Fretter & Graham, 1978; Falniowski, 1987; personal observations). *Hydrobia ulvae* has free swimming veligers (Fish & Fish, 1977), whereas in *H. ventrosa* the whole veliger stage is intracapsular (Thorson, 1946). For *H. acuta* there is only indirect evidence for the same mode of reproduction as in *H. ventrosa*. The animals reproduced in an aquarium equipped with pump and filter (personal observations). Planktonic larvae would not have survived these conditions.

In this study, only a single population of each species could be investigated, and the following systematic conclusions should be taken with some reservation. However, because the genetic distances correspond with ecological and developmental data, it can well be assumed that the results obtained from

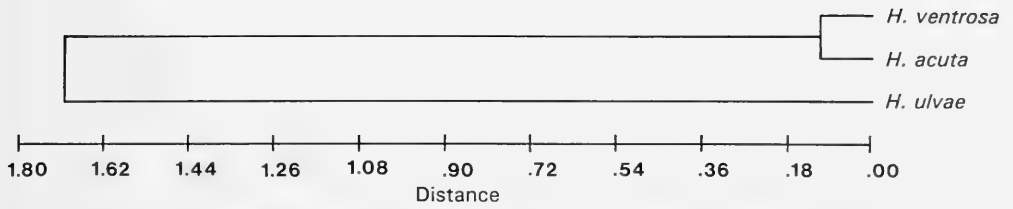


FIG. 4. UPGMA phenogram based on Nei's (1978) unbiased genetic distance.

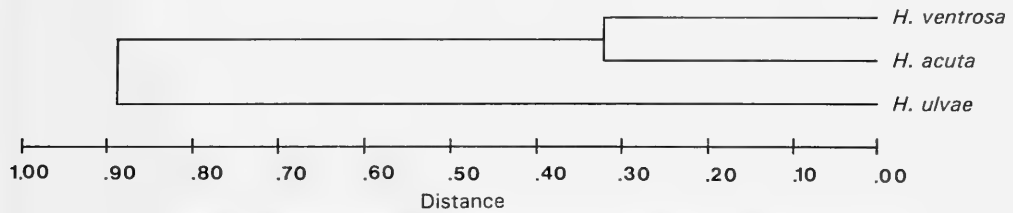


FIG. 5. UPGMA phenogram based on Cavalli-Sforza & Edwards's (1967) arc distance.

these three populations reflect the true relationships between the three species. Thus, a separation of *H. ulvae* from the other two species based on allozymes, ecological and developmental data can well be justified. Because the general anatomical organization of all three species is practically identical, a separation beyond the subgenus level would be unwarranted. Consequently, the genus *Hydrobia* Hartmann, 1821, can be subdivided into the subgenera *Hydrobia s. s.* and *Peringia* Paladilhe, 1874, and *Ventrosia* Radoman, 1977, has to be considered synonymous with *Hydrobia*. This synonymy is based on natural arguments, which demonstrate that Boeters's (1984) purely taxonomic attempt discussed in the introduction is unnecessary and also therefore to be rejected.

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DIVERGENCE OF ACTIVITY PATTERNS IN COEXISTING SPECIES OF LAND SNAILS

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ABSTRACT

The activity patterns of the land snails *Mesodon normalis* and *Triodopsis albolabris* were examined. These species share microhabitats (leaf litter) and food (fungi) in the Appalachians. Their patterns of daily activity showed striking dissimilarities in both natural and laboratory conditions of light and temperature. The activity of *M. normalis* was more or less crepuscular, whereas *T. albolabris* was strictly nocturnal. These distinctive patterns were maintained whether the two species were kept together or in isolation. Thus, the differences are not due to their direct interaction; the activity patterns have diverged evolutionarily. The temporal separation of the two species previously demonstrated in the wild results from this divergence of activity patterns.

Key words: activity pattern, temporal separation, *Mesodon normalis, Triodopsis albolabris, Neohelix,* Polygyridae, Pulmonata

INTRODUCTION

In terrestrial communities, molluscan guilds are mostly composed of pulmonates, which show a great deal of ecological diversity coexisting in a large variety of habitats (Machin, 1975; Riddle, 1983). Although niche differentiation in general can be realized in its fundamental dimensions, such as food, space, and time (Hutchinson, 1957), relatively few studies have documented temporal separation of coexisting molluscs on land.

In pulmonates, some daytime activities may be found in the field (Ingram, 1940; Blinn, 1963), initiated by the changes of physical conditions, such as temperature, humidity, and precipitation (Dainton, 1954a,b; Karlin, 1961; Webley, 1964; Dainton & Wright, 1985; Rollo, 1991). In many species, however, the regular patterns of daily activities have been shown to be nocturnal; the slugs *Arion* (Lewis, 1969a), *Deroceras* (Newell, 1966; Morton, 1979), *Limax* (Rollo, 1982; Ford & Cook, 1987), and *Milax* (Barnes & Weil, 1945), and the snails *Arianta* (Abdel-Rehim, 1983), *Cepaea* (Cameron, 1970), *Helix* (Bailey, 1975; Gelderloos, 1979), and *Monadenia* (Szlavecz, 1986), and *Triodopsis* (Henne, 1963). Several of the above species evidently possess endogenous rhythms of activities (Lewis, 1969b; Sokolove et al., 1977; Morton, 1979; Bailey, 1981; Ford & Cook, 1987).

On the other hand, only a few studies have addressed the question of interspecific diversity of activity patterns in pulmonates. Barnes & Weil (1942, 1945) noted differences of activity times in slugs. Cameron (1970) documented the variation of activity patterns among the sympatric snails, *A. arbustorum* (L.), *C. nemoralis* (L.), and *C. hortensis* (Müller) in the laboratory. Daily activities of these species commonly showed unimodal distributions but differed in the degree of nocturnality. *Cepaea nemoralis* and *C. hortensis* show different patterns of activity in field enclosures (Tilling, 1986).

Mesodon normalis (Pilsbry) and *Triodopsis albolabris* (Say) are sympatric in many places in the southern Appalachian Mountains (Hubricht, 1985). These mycophagous snails share food and microhabitat on the forest floor, and show striking similarity in shell morphology (Pilsbry, 1940, Asami, 1988). Among coexisting molluscs, these species are distinctively abundant and large in body size (approximately 30 mm in diameter). In mark-recapture experiments in sympatric populations, *M. normalis* is captured on the forest litter more frequently than *T. albolabris* in the daytime, whereas this relationship is reversed at night (Asami, 1988), suggesting that the two species appear and forage on the litter at different times of the day. I conducted the present study to examine the daily patterns of activities of *M. normalis* and *T. albolabris* and to test whether their different activity patterns bring about temporal separation in the wild.

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MATERIALS AND METHODS

Taxonomy

Because of extreme conchological similarities, the taxonomy of the current species and related taxa has been often confused (Pilsbry, 1940; Solem, 1976; McCracken & Brussard, 1980; Emberton, 1988, 1991). *Mesodon* Rafinesque and *Triodopsis* Rafinesque are in separate subfamilies, the Polygyrinae and Triodopsinae, respectively, of the Polygyridae on the basis of penial structure (Pilsbry, 1940). Examination of shells, genitalia, and allozymes suggest that the conchological similarities between *Mesodon* and *Triodopsis* are due to convergence (Pilsbry, 1940; Emberton, 1988, 1991). In the revision of the Triodopsinae, Emberton (1988) has raised the subgenus *Neohelix* to generic rank. *Mesodon normalis* and *T. albolabris* are one of a number of species pairs in these subfamilies that show striking similarity in shell morphology in spite of their taxonomic positions. Voucher specimens of the taxa studied here are deposited in the Academy of Natural Sciences of Philadelphia (catalog nos. 369306 and A12179 for *M. normalis,* and A12094 for *T. albolabris*).

Study Site and Sample Maintenance

These experiments were conducted at the Mountain Lake Biological Station, 1167 m in elevation, Giles County, Virginia, USA. Adults of *M. normalis* and *T. albolabris* were collected from an area of 200 × 10 m, 0.5 km west of the station (approximately 37°22″N, 80°31″W). The collected snails of each species were maintained separately in field enclosures (12 mm metal mesh, 46 cm diameter and 23 cm height, approximately ten animals per enclosure), established in a deciduous forest near the collection site, for about two months prior to the experiment.

Activity Recording

Except in those experiments examining individual interactions, experimental animals were individually isolated in plastic containers (84 mm diameter, 37 mm height) and fed oatmeal with powdered natural chalk on moist paper towels. Humidity inside the containers was close to 100% for the whole period. Containers were horizontally arranged on a platform 0.8 m above the substratum or floor. Each animal was transferred to a clean container with new food every other day, and locations of the containers were randomized at this time. During the complete course of the experiments, a 40 w red bulb 1.2 m above the animals was kept on, enabling night observations. Prior to recording activity patterns, the animals were conditioned to the experimental treatment for 5 days. Each individual was then scored for activity every hour for 24 h beginning 2 h after the routine maintenance, unless indicated otherwise below. Activity was defined as moving the head with extended antennae, creeping, feeding, or cleaning the shell as reported by Ingram (1944).

Experiments were conducted under both natural outdoor conditions and controlled laboratory conditions. For the former, the containers were shaded by a shelter and experienced natural changes of temperature and light (Fig. 1A). In the five-day conditioning period, the air temperature changed daily in a clear cycle (9 to 22 °C). Daylight lasted from 4:30 a.m. through 6:30 p.m. including dawn and dusk. On the recording day, however, the weather was overcast, resulting in a rather obscure pattern of temperature change.

For the indoor experiments, the animals were conditioned to the day-length and temperature cycle typical for July at the study site, light from 4:30 a.m. to 7:30 p.m. and temperature ranging from 18 to 25°C daily (Fig. 1B). No natural light was admitted to the experimental area. Two fluorescent lamps (34 w each, placed 1.2 m above the samples) were used to produce the light phase. There was no dawn or dusk. To create a daily cycle of temperature similar to the natural one, an electric heater was turned on at 6:00 a.m. and off at 1:00 p.m.

Test of Interaction Between Individuals

In order to test the effects of interactions between conspecific individuals and between individuals of different species, the activity patterns of paired animals were examined, with those of single animals as controls. All the animals were conditioned to the same laboratory conditions described above. To provide them with the same amount of space per individual, each pair was maintained in a container twice as large as that used for single individuals. Scoring was carried out as described above.

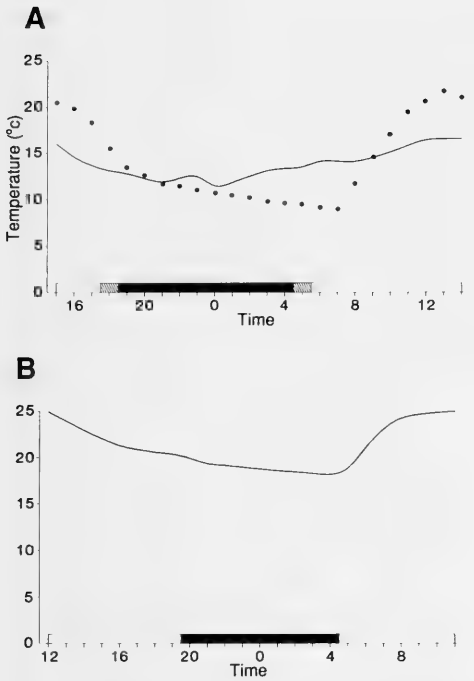

FIG. 1. Temperature and light conditions during the experiments. A. Outdoor experiment. B. Indoor experiment. Solid line: the temperature pattern on recording day. Interrupted line: the pattern of mean temperature in the conditioning period. In the indoor experiment, the same temperature pattern was repeated on the recording day as in the entraining period. The straight bars indicate the light conditions; Open bar: daytime or light phase; hatched bar: dusk or dawn; filled bar: nighttime or dark phase.

Statistics

Analyses were designed to test the differences in the degree of nocturnality, which was defined as the proportion of nocturnal activity in each 24-h period. Values of nocturnality were calculated by dividing the total scores for the dark phase by those for 24 h. The Mann-Whitney test or the Kruskal-Wallis two-way test was used in each test of the homogeneity of the mean nocturnalities and total scores for 24 h between treatments. For testing interactions between conspecifics and between species on nocturnality or the total score, the mean of the two individuals was used as an independent observation for each pair.

RESULTS

Interspecific Variation of Activity Pattern

Under natural conditions of light and temperature *Mesodon normalis* and *Triodopsis albolabris* showed notable differences in their daily patterns of activity (Fig. 2A). The pattern of *T. albolabris* was strongly nocturnal, whereas that of *M. normalis* was nearly crepuscular, showing no activity at 11 p.m. Although *T. albolabris* showed high activity at 6 p.m., this was reduced immediately thereafter, and most of its activity was confined to the night. The pattern of *M. normalis* differed from that of *T. albolabris.* After the first peak around dusk, activity steadily diminished until 11 p.m. and then increased to form the morning peak. The same individuals of *M. normalis* were often active in both periods in a single 24-h cycle; there were not two behavioral types of individuals corresponding to the two peaks.

The results of the outdoor experiment were corroborated by the indoor experiment (Fig. 2B). As in natural light and temperature, *T. albolabris* was strictly nocturnal. In contrast, *M. normalis* showed a drastic reduction in activity in the middle of the dark phase when *T. albolabris* was most active.

In both species, there were some differences in activity patterns between the outdoor and indoor experiments. Indoors, *T. albolabris* showed an increase of activity towards the end of the dark phase. In *M. normalis,* the relatively large activity was observed at dusk outdoors, but in the early morning indoors. For statistical evaluation of the differences in activity time between species and between the outdoor and indoor conditions, the distributions of individual nocturnalities were compared (Fig. 3). In both indoor and outdoor experiments, nocturnality of *M. normalis* was significantly less than that of *T. albolabris* (Kruskal-Wallis two-way test, $P < 0.0001$), and the results were consistent between experiments ($P > 0.25$). It was concluded, therefore, that *T. albolabris* and *M. normalis* have distinct patterns of daily activities and that *M. normalis* is substantially less nocturnal than *T. albolabris.*

Effects of Individual Interactions

There was no significant difference in mean nocturnality between isolated and paired conspecifics of either species (Fig. 4A; $P > 0.7$

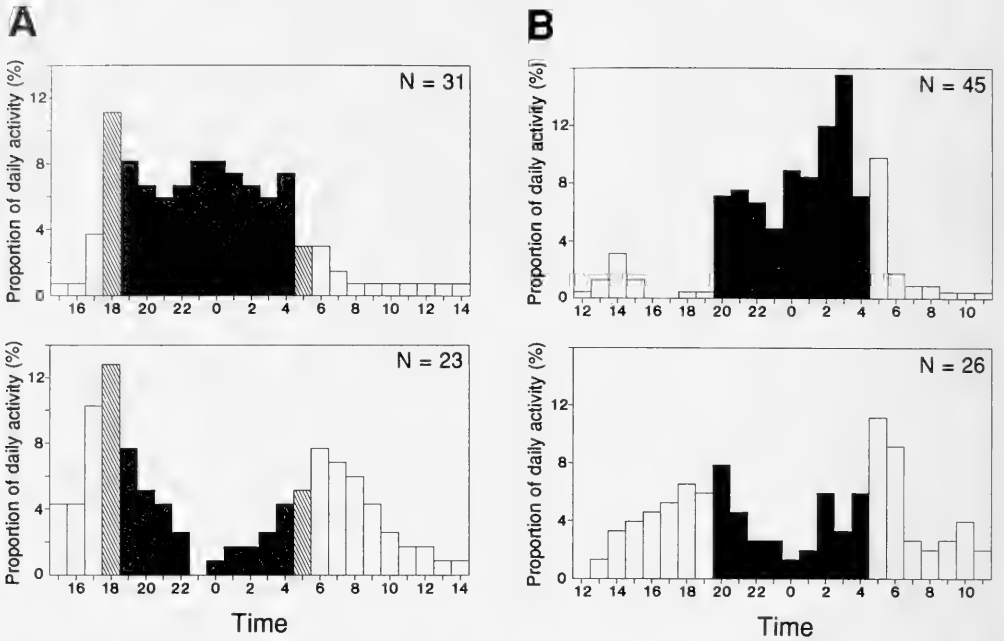

FIG. 2. Activity patterns of *T. albolabris* (upper) and *M. normalis* (lower). A. Outdoor experiment. B. Indoor experiment. Each bar shows the mean hourly percentage of the 24-h activities. Black bar: nighttime. Open bar: daytime. Hatched bar: dusk or dawn. N: sample size.

for *M. normalis,* $P > 0.5$ for *T. albolabris*). Because coexistence of conspecifics might affect overall activity levels, the total scores for 24 h were compared between the treatments in each species. As shown in Figure 4B, paired individuals of *M. normalis* were more active than isolated individuals ($P < 0.003$), whereas there was no difference for *T. albolabris* ($P > 0.7$). The 24-h activity of paired individuals was higher in *M. normalis* than in *T. albolabris* ($P < 0.005$), but there was no difference between species in the activity of single individuals ($P > 0.2$). These results suggest an interaction between individuals of *M. normalis* that causes increased activity.

In the experiment to test for interspecific interaction, there were no significant differences in nocturnality between single and paired individuals in either species (Fig. 5A; $P > 0.2$ for *M. normalis,* $P > 0.2$ for *T. albolabris*). In addition, neither species showed any effect of treatment on overall 24-h activity (Fig. 5B; $P > 0.7$ for *M. normalis,* $P > 0.5$ for *T. albolabris*). These results of pairing experiments indicate that *M. normalis* and *T. albolabris* retain their distinct nocturnalities, even when allowed to encounter conspecifics or other species as they would in the wild. Also, their coexistence does not lead to direct inhibition or enhancement of the activity of either species.

DISCUSSION

Evolutionary Divergence of Activity Patterns

Pulmonates are considered to be nocturnal in general to avoid high daytime temperature and reduced humidity, which may cause problems with body-water retention and osmoregulation (Cameron, 1970; Schmidt-Nielsen et al., 1972; Machin, 1975; Ford & Cook, 1987). The present study has demonstrated, however, that *Mesodon normalis* and *Triodopsis albolabris* have distinct patterns of daily activities. *Mesodon normalis* has two activity peaks in the daytime, near dawn and dusk, whereas *T. albolabris* shows strong nocturnality, with unimodal distribution of activity, the pattern usually considered typical for pulmonates.

The slight differences between activity pat-

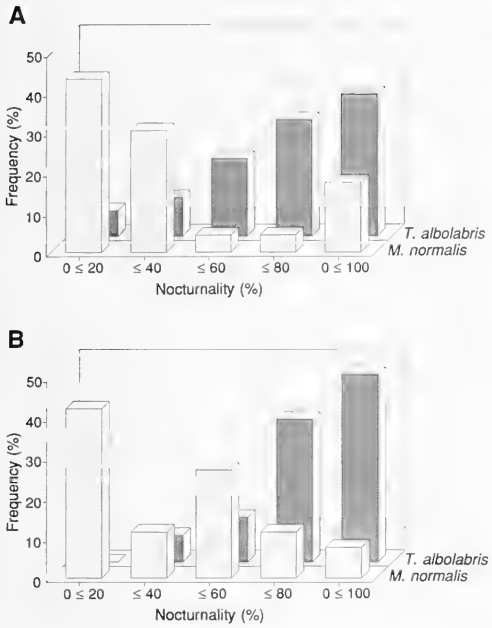

FIG. 3. Distributions of individual nocturnalities in *M. normalis* and *T. albolabris.* A. Outdoor experiment. B. Indoor experiment. The vertical axis indicates the frequency of individual nocturnality.

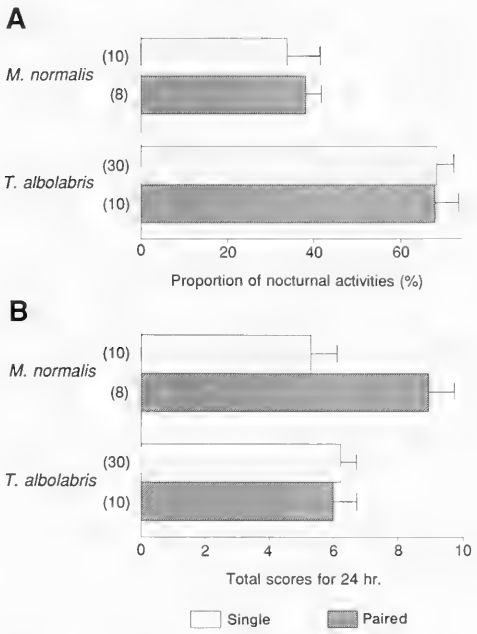

FIG. 4. Test of the effect of conspecific interaction on nocturnality and activity. A. Mean nocturnalities and standard errors. B. Mean total activity scores for 24 h and standard errors. Number of replicates is indicated in parenthesis.

terns in the outdoor and indoor experiments may be related to the limitations of simulating natural conditions in the laboratory. For instance, indoors there was no gradual change of light intensity, while the animals outdoors experienced dawn and dusk. Outdoors both species showed high activity at 6 p.m. Indoors, however, *M. normalis* was most active at 5 a.m., and *T. albolabris* showed nearly 10% of its total activities at the same time. In the field, *T. albolabris* burrows under litter just before dawn. It is possible that *T. albolabris* showed an increase of activity after light-on because no shelter was provided in the experiments. This type of post-dark activity in artificial light cycles has been found in other pulmonates (Sokolove et al., 1977; Gelderloos, 1979; Wareing & Bailey, 1985; Ford & Cook, 1987). Except for these differences, equivalent results were obtained outside and inside the laboratory. Therefore, the present results show that the activity patterns of *M. normalis* and *T. albolabris* are distinct, especially in the degree of nocturnality.

Interspecific separation in activity time cannot be due to direct reactions between the two species. The samples of *M. normalis* and *T. albolabris* were maintained in separate enclosures for two months prior to the experiments. They were then individually isolated for the entraining periods and experiments. These molluscs are not likely to have determined activity patterns so rigidly by learning or habituation prior to collection from the wild that they could retain those patterns through these experimental periods. Besides, the interspecific pairing experiments showed no effect on nocturnality or the total activity of either species. Therefore, the present results strongly suggest that the divergence of activity patterns between the two species is evolutionary, as in *Cepaea* (Cameron, 1970; Tilling, 1986; Cowie & Jones, 1987).

Mesodon normalis is usually abundant in mountainous areas in the southern Appalachians, whereas *T. albolabris* is much more widely distributed at lower altitudes as well as in sympatry with *M. normalis* (Hubricht, 1985). Cameron (1970) suggested that hot and dry habitats are occupied by more nocturnal species. Low nocturnality of populations that inhabit high altitudes, where the climate is

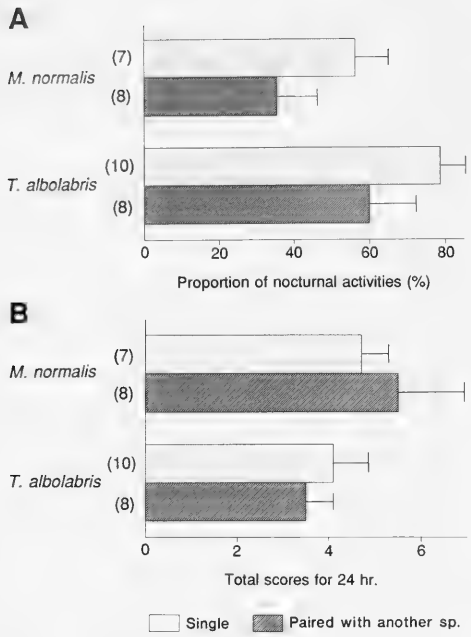

FIG. 5. Test of the effect of interspecific interaction on nocturnality and activity. A. Mean nocturnalities and standard errors. B. Mean activity scores for 24 h and standard errors. Number of replicates in indicated in parenthesis.

cooler and wetter, could be predicted by this hypothesis. This does not explain, however, why *M. normalis* shows a reduction of activity at night, in contrast to *T. albolabris,* in areas where they occur in the same microhabitats (Asami, 1988). Moreover, *M. normalis* is much inferior in water retention and survival of juveniles in low humidity to *T. albolabris* (Asami, in press). Their adults similarly show clear differences in desiccation tolerance (Asami, in preparation). Thus, the diurnal activity of *M. normalis* is not explicable by a relatively large tolerance of dry and warm daytime conditions.

Evaluation by Field Experiments

In repeated searches for snails on the forest litter, 75% of the animals captured at night were *T. albolabris,* whereas 78% of those in the daytime were *M. normalis* (Fig. 6). As these ground-dwelling snails are likely to appear on the litter for foraging or mating, the ratio of animals captured per search between nighttime and daytime would correspond to

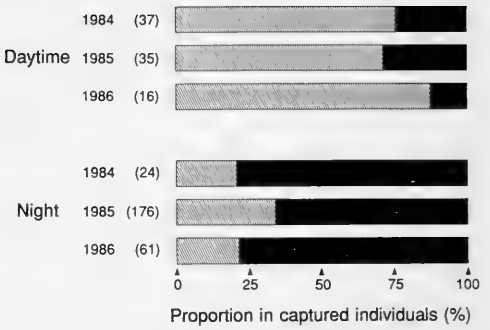

FIG. 6. The relative discovery rates (proportions in yearly captures) of *M. normalis* (hatched) and *T. albolabris* (black) in natural habitats. Number of yearly captures is given in parenthesis (after Asami, 1988).

the daily proportion of nocturnal activity (nocturnality) in the field. Thus, by comparing the interspecific ratios of nocturnalities between the field observation and present experiments, it can be examined whether their difference in activity patterns explain temporal separation of the two species in the wild. The mean nocturnalities of field captures in three years were 48% in *M. normalis* and 91% in *T. albolabris,* a ratio of 0.53 (Asami, 1988). The interspecific ratios of nocturnalities observed in the present outdoor and indoor experiments (0.56 and 0.45, respectively) are closely comparable to the ratio from the wild, indicating that the present results are a good representation of the relative activity patterns of the two species in nature.

Nevertheless, comparison of nocturnalities in the wild and in the present experiments suggests that both species tend to be more nocturnal in the wild. This difference could be due to the high humidity maintained in the experiments. In the natural habitats, the humidity is typically 100% from midnight to noon in summer, whereas it was kept at that level inside the containers for the entire experimental periods. The daily change of temperature was often larger outdoors than in the laboratory. The daily shifts of the physical conditions were, accordingly, greater in the field than in the experiments. Hence, their nocturnalities may well be higher in the wild on fine days than those observed in this study.

In the treatment of pairing individuals, the density of animals needs to be considered as existence of one individual could have an effect on another. In the present paring treatments, the density was higher than in nature.

Thus, the effect of individual interaction would be enhanced if it exists. There was, however, no significant difference in either nocturnality or the total activity between paired and isolated snails, except for *M. normalis,* which showed higher activity in conspecific pairs. *Mesodon normalis* might be more sensitive to high density or might tend to respond to conspecifics more promptly than *T. albolabris,* although no courtship was observed in these experiments. The absence of pairing effects, between and within species, on nocturnality also indicates that individual isolation in the experiments did not cause significant artifacts in activity patterns, relative to the field situation where snails could encounter each other.

This study has demonstrated substantial separation of activity times in coexisting species of land snails. Further studies are needed to understand the ecological and evolutionary causes of this divergence.

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THE LOTTERY OF BIBLIOGRAPHICAL DATABASES: A REPLY TO EDWARDS & THORNE

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We understand that our finding that over 20% of new molluscan genus-group names are omitted by *Zoological Record* (*ZR*) has caused surprise to the editors of this journal, as it has surprised us and many of our colleagues, all of us being regular users of this inescapable and valuable bibliographical tool. Indeed, the prevailing intuitive opinion is that approximately 5–7% of the names are omitted. In our answer to Edwards & Thorne (*Malacologia,* 35: 153–154), we want to emphasize two points:

(1) Omission affects all sorts of journals, including high-profile international journals;

(2) the high rate of omission and other nomenclatural defects highlight the risks and problems of establishing a "List of Available Generic Names in Zoology" based on Neave's *Nomenclator Zoologicus* and *ZR,* as is being currently considered by the International Commission on Zoological Nomenclature (ICZN).

Which Names Get Omitted?

Most of the taxonomists with whom we have discussed this question seemed to believe that names that escape *ZR* were originally published in very obscure sources. In discussions, these scientists often frankly suggest that omission from *ZR* and nomenclatural oblivion are, after all, probably deserved and that the authors of such names are themselves responsible for the ill fate of their names. These beliefs are wrong, as we show below.

To supplement the data provided in our paper (*Malacologia,* 34: 75–86), we have analyzed the place of publication of 370 genus-group names omitted from *Nomenclator Zoologicus* and *ZR.* These are names starting with the letters A-K, mostly published between 1940 and 1975. Places of publication were divided into three categories:

(a) books and collections of books,

(b) main-stream scientific journals,

(c) little-known and obscure journals.

Admittedly, it is a matter of personnal opinion whether one should rank a journal as main-stream or little-known. Our appreciation is best explained by a series of examples. Among main-stream journals, we have ranked: *Memoir of the Geological Society of America; Mémoires de l'Institut Royal des Sciences Naturelles de Belgique; Trudy Zoologicheskogo Instituta; Sarsia; Malacologia* (the very journal where this paper is published! Omitted names: *Globicarina* Waterhouse, 1965, *Malacologia,* 3(3): 374; *Calibasis* and *Idabasis* Taylor, 1966, *Malacologia,* 4: 41, 42); *Oceanologia et Limnologia Sinica;* etc.

Among little-known and obscure journals, we have ranked: *Science Reports of the Tohoku University; Bulletin du Muséum d'Histoire Naturelle de Marseille; Vestnik Moskovskogo Universiteta; Gastropodia; Leaflets in Malacology; Bulletin of the Department of Geological Sciences, University of California Publications;* etc.

The first category, books and collections of books, is itself a mixed category, and includes both main-stream and little-known titles. Examples are Habe, 1961, *Coloured illustrations of the shells of Japan; Fossils of central southern China;* Nordsieck, 1972, *Die miozäne Molluskenfauna von Miste-Winterswijk; Das Tierreich; Galathea Report;* Starobogatov, 1970, *Fauna molliuskov i zoogeografiskoe rajonirovanie kontinentalnits vodoemov zemnogo shara;* etc.

Our results show that 141 omitted names (38%) were published in books and series; 153 names (41%) were published in main-stream journals; 76 names (21%) were published in little-known or obscure journals. If country of publication is considered, 98 names (26%) were published in books or journals of the former USSR; 91 names (25%) in USA; 48 names (13%) in Japan. Only 9 names (2%) were published in China, but this is because Chinese output did not start until after the end of the cultural revolution (1976), that is, later than the time span of our study. These results demonstrate that there is no correlation between omission from *Nomenclator Zoologicus* and circulation of a journal or book.

Most, if not all, of the journals, main-stream or obscure, cited above are in principle covered by *ZR.* Hence, obscurity is not the main reason for omission. On a number of occasions, we have found that four new names published in a paper are correctly gazetted in *ZR,* whereas a fifth name published in the same paper has been omitted. Or a whole paper published in a normally recorded journal has been omitted. We regret to say that carelessness seems to be a not infrequent source of omission. As our results show, names published in books constitute a major proportion of omitted names. Taxonomists have also noticed that many books and irregular series are recorded in *ZR* only several years after their publication, when most practicing scientists know of these books within a few weeks or months after their publication; often, book reviews have also been published in main-stream journals. We believe that the main reason for this regrettable situation is that there are few, if any, personal contacts between the recorders and bibliographers, on one side, and the people that write the books and monographs, that is, the malacologists and taxonomists, on the other side. In our era of frequent and easy travel, we regret that, to our knowledge, the staff of *ZR* has attended only once (in Edinburgh, 1986) an International Malacological Congress, which are held every three years in Europe. We believe that attendance of such and other similar congresses in USA and Russia would greatly enhance the efficiency of *ZR,* when malacologists could identify the Mollusca section of *ZR* with the face of a person whom they have personally met.

The Risks of a "List of Available Generic Names in Zoology" Based on *Nomenclator Zoologicus* and *ZR*

Stability of names has become a much debated topic, both in botanical (Hawksworth, 1991) and zoological (Ng, 1991) nomenclature. The International Commission on Zoological Nomenclature resolved at its University of Maryland meeting "to enter into negotiations with Biosis with a view to developing a data base of generic names as a list of available names" (Anonymous, 1990). The report (Anonymous, 1991) of the Amsterdam meeting of the Commission further stated that "Biosis has made good progress in the preparation of a draft list of generic names published between 1758 and 1990, based on Neave's *Nomenclator Zoologicus* and *Zoological Record.*"

Indeed, all taxonomists including ourselves would dearly like to have a complete nomenclator of generic names under a single cover, and it was precisely for lack of such a catalogue that we started compiling our own, albeit limited to Mollusca. However, we seriously question the value of the Biosis nomenclator when up to 23% of recently published names are omitted.

More importantly, we want to stress the risks of making this list a formal List of Available Generic Names in Zoology. In an unofficial report of the 1990 ICZN meeting, Savage (1990) suggested that "most importantly, only the generic names on this list would be available for use. Any other names, subsequently discovered or not, would not exist for nomenclatural purposes." This is what Savage calls "the statute of limitations for the resurrection of old names." We call it a receipe for injustice and chaos. By using such expressions as "resurrection of old names," Savage tends to suggest that names omitted by *Nomenclator Zoologicus* and *ZR* belong to the very obscure category, and that those zoologists discovering them are merely book archeologists that disrupt the work of real taxonomists. We have amply demonstrated that in malacology, and probably many branches of invertebrate (paleo)zoology and vertebrate paleozoology as well, there are literally thousands of nomenclaturally available names that get omitted by *ZR.* When, for example, *Aliomactra* Stephenson, 1952 (U. S. Geological Survey Professional Paper, 242: 125) or *Dancea* Zilch, 1960 (*Handbuch der Paläozoologie,* 6(2): 730) are omitted by *ZR,* should Stephenson and Zilch be blamed for that? Should *Aliomactra* and *Dancea* be deemed not to exist for nomenclatural purposes? We strongly reject this idea, as we reject the idea that an Official List of Available Generic Names in Zoology should be compiled on a commercial basis.

In his report of the ICZN 1990 meeting, Savage (1990) further suggested that "at the time of publication (e.g., 1996), the dates in the list (regardless of any subsequent findings) would be the final determinants of priority." Again, the rationale behind this point is probably to avoid changes of names as a result of bibliographical subtleties, an opinion that many taxonomists would defend. However, there are again hidden sides that have apparently been overlooked: we refer to the

listing of generic names by *Nomenclator Zoologicus* whereas some of these names are unavailable under ICZN Art. 13, which rules that genus-group names published after 1930 must have a diagnosis *and* a type species.

We will give two examples:

Hennocquia is listed in Neave and credited to Haber, 1932, *Fossilium Catalogus,* pars 53, 220. However, Haber designated a type species but omitted a diagnosis, and *Hennocquia* is unavailable under Art. 13a(i). Wenz, 1938, *Handbuch der Paläozoologie,* 6(1): 219, first provided a diagnosis and type species. *Hennocquia* should thus be credited to Wenz (1938). *Pseudohelenoconcha* is listed in Neave and credited to Germain, 1932, *C.R. Congr. Soc. Sav. Sci.,* 1929, 7 (sic, should be 6). Germain failed to designate a type species, and the name is unavailable under Art. 13b. Zilch, 1959, *Handbuch der Paläozoologie,* 6(2): 215, provided a diagnosis and type species designation, and is the author of *Pseudohelenoconcha.* These examples should suffice to demonstrate the risks of binding too strongly the *Code of Zoological Nomenclature* and the databases operated and marketed by Biosis.

In conclusion, we want to outline briefly our suggestion to introduce a mandatory system of registration of new zoological names. We have proposed that the next edition of the *Code* adds a new article:

"A copy of every work containing the introduction of a new zoological name must be sent, by its author or publisher, to the International Commission on Zoological Nomenclature. Receipt of the publication by the Secretariat of ICZN is necessary to validate a new name.

When all other relevant provisions of the *Code* are satisfied, the date of validity of a new name is the date (day, month, year) when the publication containing its introduction is formally received by the Commission.

The International Commission on Zoological Nomenclature publishes every year a list of the new taxa received at its offices, together with complete bibliographical reference, and the date (day, month, year) of their availability."

When this proposal was submitted to ICZN by the senior author, he recommended that the *Zoological Record/Nomenclator Zoologicus* be associated with the compilation of these annual lists, which do not duplicate the current contents of the *Zoological Record.*

This proposal would clearly benefit the more professional journals over the more locally produced, unedited ones, or with editors not even aware that there exists a *Code of Nomenclature.* With time the authors will know their interest is to seek publication in those professional journals that offer a better service with regard to this provision of the *Code.* Those that do not comply can be ignored. But this will be the result of their own carelessness, not the result of the lottery of bibliographical databases.

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NOTE BY A CO-EDITOR

While I find convincing the argument by Bouchet & Rocroi for a greatly improved system to capture and publicly recognize valid new taxa, I find one aspect of the methodology they propose for doing so particularly troubling.

At the same time they call for improvement of the capture of new taxa by the laudable expedient of having journal editors (and authors) send all of them to a central repository for official recognition, they surrender the entire process and leave the dates of recognition in the hands of the most inefficient and frequently careless bureaucracy in the world, the postal authorities.

A name would, they propose, only be official when it arrives in the hands of the central authority and is suitably blessed. Even assuming that the costs of sending all issues of all journals and other works to the central authority is borne by the publishers and editors and the costs thus saved put into staff to do the extraction and blessing, this is bound to be a time-consuming and tedious task that will require much staff time. Perhaps this is a price that must be paid.

The weak link, however, is the postal system. I estimate that about a third of the things mailed from Latin America never reach their destinations. An "airmail" package from South America can take two months. I estimate based on recent experience that well over half of the materials going back and forth between the Far East of the Soviet Union and the West never reach their destinations at all. So, must we leave important taxonomic decisions and the all-important dating of taxonomic works in the hands of the Russian, Italian, or Colombian postal authorities? Are these bureaucrats to be new arbiters of priority and validity?

I would suggest that instead we rely upon the real dates of publication, and then make every effort to get the materials into the hands of the Commission of whatever central repository is chosen.

Eugene Coan, Co-Editor

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AWARDS FOR STUDY AT
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The Academy of Natural Sciences of Philadelphia, through its Jessup and McHenry funds, makes available each year a limited number of awards to support students pursuing natural history studies at the Academy. These awards are primarily intended to assist predoctoral and immediate postdoctoral students. Awards usually include a stipend to help defray living expenses, and support for travel to and from the Academy. Application deadlines are 1 March and 1 October each year. Further information may be obtained by writing to: Chairman, Jessup-McHenry Award Committee, Academy of Natural Sciences of Philadelphia, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103-1195, U.S.A.

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