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HOFFMAN, JAMES ELLIS

AN ANATOMICAL COMPARISON AMONG SEVERAL SPECIES OF ACANTHIA (PROSOBRANCHIA: MURICACEA) WITH AN EXAMINATION OF THE RELATIONSHIP BETWEEN A. ANGELICA AND A. LUGUBRIS

THE UNIVERSITY OF ARIZONA M.S. 1983

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AN ANATOMICAL COMPARISON AMONG SEVERAL SPECIES OF *ACANTHINA* (PROSOBRANCHIA: MURICACEA) WITH AN EXAMINATION OF THE RELATIONSHIP BETWEEN *A. ANGELICA* AND *A. LUGUBRIS*

by

James Ellis Hoffman

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In Partial Fulfillment of the Requirements
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Walter B. Miller
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13 July 1983
Date

PREFACE

There has been some difference of opinion regarding the validity of the three species *Acanthina lugubris* (Sowerby, 1822), *Acanthina tyrianthina* Berry, 1957, and *Acanthia angelica* Oldroyd, 1918. R. Tucker Abott (1974) referred to *A. angelica* as *Acanthina lugubris angelica* and said it was "Similar to and intergrading with *lugubris* but more elongate with a more angular shoulder. . .", and went on to describe *tyrianthina* as a form of *A. lugubris angelica*. James H. McLean (in literis 1983) considers *A. tyrianthina* to be a southern subspecies of *A. lugubris*, in turn related to *A. angelica* at the subspecies level. . . ." Keen (1971) and Morris (1966), however, have subscribed to the more traditional view, that each is a separate species.

Each of the above mentioned species was described using characteristics of the shell alone. Since then drawings of the radulae of two of these species have been published (Wu 1968, Hemingway 1975a), but not in a way that they can be directly compared. The anatomy of the reproductive system of *A. angelica* was studied (Houston 1976), but results were drawn schematically and measurements not shown, thereby precluding their use for comparative purposes. In fact there has been no definitive study conducted to determine what relationships exist among these three taxa, and the extent of their relationships has been primarily a matter of conjecture or intuition.

With this thesis, I proposed to elucidate these relationships by producing a definitive comparison of the anatomies of these three snails and comparing them with others. In addition, I propose to provide anatomical information that will prove useful for future studies involving these snails and for comparison with others.

I gratefully acknowledge the help and advice of the members of my committee, Drs. Walter B. Miller, Albert R. Mead, and Nicholas P. Yensen. I would particularly like to thank Dr. Miller for his encouragement, and his helpful advice on the subject of subspecies. I would also like to thank Ray Armstrong, Jennifer Titley, Curt Lively, Pete Raimondi, Dr. Walter Miller, and Dr. Richard Reeder for collecting material for me or providing me with preserved material that they had collected. In addition, I would like to thank Rick Kretzinger and Tom Marriam of Union Carbide for providing me with technical grade "Sevin", without which dissections would have been far more difficult. Dr. Barry Roth of the California Acadamy of Sciences and Dr. James H. McLean of the Los Angeles County Natural History Museum lent me specimens in their collections for which I am very grateful. I also gratefully acknowledge Donald Sayner and his Scientific Illustrations group in the General Biology Department at the University of Arizona for the use of their equipment and much helpful advice. I would also like to thank Peggy Turk for making the facilities at Centro de Estudios de Desiertos y Oceanos available to me and Dr. Carl C. Christianson for proof reading this thesis.

I am particularly grateful to my family for putting up with a part-time husband and father, and very special thanks is due to my mother-in-law, D. June Watt, for performing many of the chores that I was not there to do. She was, therefore, indispensable to this project.

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ABSTRACT

Acanthina lugubris (Sowerby), Acanthina l. tyrinathina Berry, and Acanthina l. angelica Oldroyd, formerly held to be separate species, are shown to have only subspecific differences. Acanthina brevidentata (Wood), on the other hand, shows major anatomical differences, and is considered to be another species.

Penis shape and the shape of and number of cusps on rachidian teeth were major factors used in combining the subspecies of Acanthina lugubris and in determining that Acanthina brevidentata is a separate species.

Shapes of shells and sculpturing on them were the major factors used to differentiate the subspecies of Acanthina lugubris.

MATERIALS AND METHODS

Acanthina species were collected at sites in the intertidal areas of the Pacific coast of Panama, and Baja California, Mexico, as well as the Gulf of California. When possible they were collected alive and maintained in aquaria until ready for dissection. The snails were then relaxed using 1-napthyl N-methylcarbamate ("Sevin") dissolved in acetone as suggested by Carriker and Blake (1959) and then killed by the gradual addition of ethanol.

In order to kill the *Acanthina*, the best method found was to put one to several snails in 30 ml of sea water. To this was added 0.1 g "Sevin" crystals dissolved in 15 ml of acetone. Within 30 min., the snails began to relax. After one hour, 5 ml of 90% ethanol was added gradually without disturbing the water. Five ml of 90% ethanol was then added every half hour for the next two and one-half hours. Each snail was then removed from the mixture, shell parameters were measured using dial calipers, and the shell was removed using a bench vise and forceps. Each snail was then placed in a separate container with 20 ml of sea water mixed with 10 ml of the "Sevin"-acetone solution and the ethanol level was brought gradually to approximately 60% over a period of four hours, at which point the snails ceased to respond and they were fixed for dissection. This method was developed after trying many others and was the only one to produce relaxation in A. *angelica* sufficient to cause the proboscis to extend. This method may be shortened somewhat for other intertidal snails that relax and die more quickly.

The snails were then fixed, in some cases with 70% ethanol and in some with Bouin's fluid mixed according to Galigher and Kozloff (1964). Those fixed with ethanol showed colors and natural relationships. Snails fixed in Bouin's fluid, on the other hand, were easier to cut in a controlled manner, the nervous systems were easier to trace (Davis and Carney 1973), and they took stains easily, but the natural markings of the animals were obscured, as well as the colors of their organs.

Some animals were collected for me, or were from collections made available to me. These were all preserved in the retracted state within their shells in 70% ethanol. The shells were measured and removed using a bench vise and forceps. The animals were sexed, their opercula measured, and were then returned to 70% ethanol.

Shells in dry collections were made available to me from the University of Arizona Invertebrate Collection, the California Academy of Sciences Collection, and the Los Angeles County Natural History Museum Collection. These shells were measured, and in some cases photographed, then returned to the collections.

Radulae were prepared by dissecting the buccal bulb from the snail, warming the bulb in 10% sodium hydroxide solution until the soft tissues were dissolved, and drying in absolute ethanol; then the radula was mounted on a microscope slide with Euparol and observed with the aid of a compound microscope. Representative unworn teeth were drawn.

All of the major organ systems were examined, drawn, and measured. The drawings were made on "Albanane" tracing paper with pen and india ink. Measurements were made (depending on the size of the object to be measured) using dial calipers, a small metric scale, a stage micrometer, or an eyepiece micrometer that had been calibrated on the microscope through the use of a stage micrometer.

Shell measurements were made using a hard plastic dial caliper graduated in 0.1 mm. Shell height and width, and aperture height and width were measured in the manner shown in Figure 1. Only adult shells were used for these measurements. In adult shells, the embryonic whorl was, in most cases, eroded away or overgrown by smaller invertebrates or calcareous algae, therefore height measurements are of necessity, approximate. This problem is encountered to about the same degree in all of the species studied, therefore, I feel that the use of height for comparison among species is valid.

The method for measuring the length of the organism is shown in Figure 2. Measurement was made from the edge of the mantle to the tip of the digestive gland, the foot and the opercular region were excluded from this measurement because their length was found to vary depending on whether the snail died in the relaxed or the contracted state.

The organs and organ systems are drawn to scale and their dimensions are indicated by the scale on the drawings. In some cases

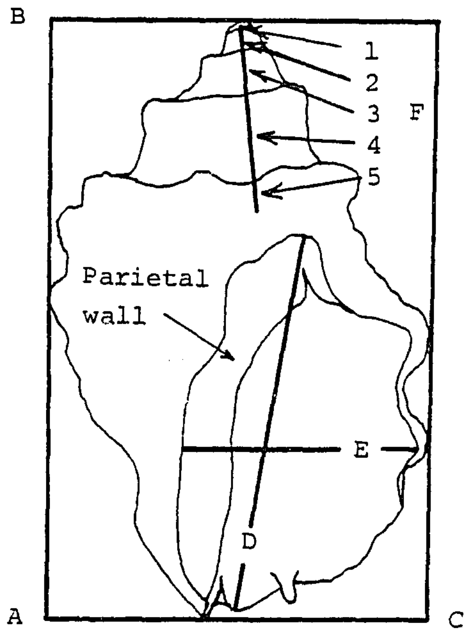


Fig. 1. Conchological measurements. -- A diagram to show the method of measuring: A-B, height; A-C, width; D, height of aperture; E, width of aperture; F, count.

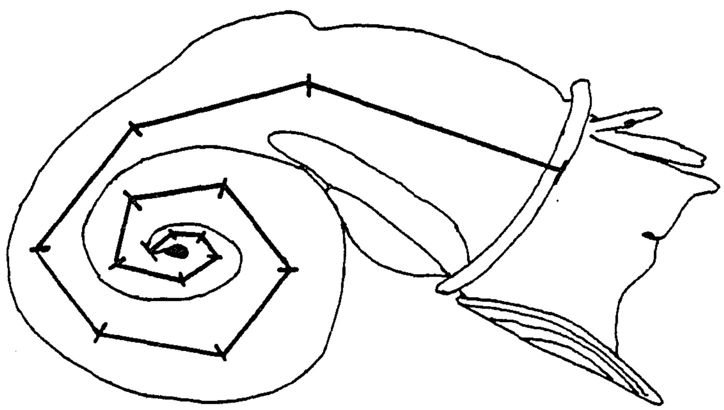


Fig. 2. Method of measuring the length of the snail. -- The animals were measured from the mantle edge to the tip of the visceral mass in segments. The lengths of all segments were then added.

the drawings are a composite of a number of individuals, but in most, they are of an individual that is typical of the members of its species and sex.

RESULTS

Description of Characteristics Studied

Four *Acanthina* species which inhabit rocky intertidal waters of the eastern Pacific Ocean are herein compared. The species were: *A. lugubris*, *A. tyrianthina*, *A. angelica*, and *A. brevidentata*. *A. brevidentata* occurs from Mazatlan, Mexico to Paita, Peru (Keen 1971). The north end of its range as well as the ranges of *A. lugubris*, *A. tyrianthina*, and *A. angelica* are shown in Figure 3.

Shell morphology was first examined because it was the sole basis for the original species descriptions. Digestive systems were also examined because variations in them would be expected to be produced by evolutionary differences, as well as by environment and variation in diet. The nervous system was likewise observed. Most importantly, however, differences in reproductive systems can be expected to provide direct evidence about relationships on the species level, and were, therefore, observed in detail. The muscular system was not examined except for a general examination of the buccal mass. The circulatory system was observed only generally and no obvious differences were noted, therefore, it will not be discussed. Opercula were examined and found not to vary in any substantial way among the taxa examined.

The soft parts of *Thais emarginata* were studied along with those of the *Acanthina* in order to provide examples of variation

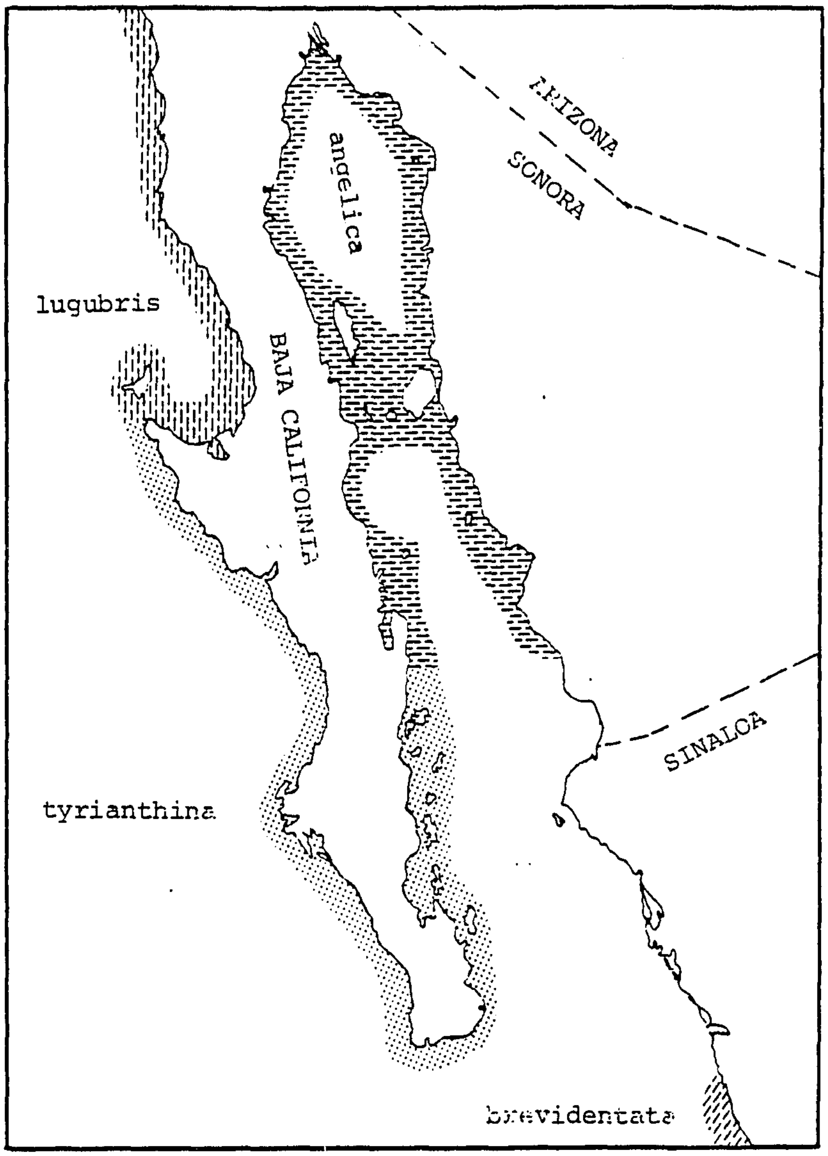


Fig. 3. Map of Acanthina distributions. -- The map shows the allopatric distributions of four eastern Pacific species of Acanthina: A. lugubris (Sowerby 1822), A. tyrianthina Berry 1957, A. angelica Oldroyd 1918, and A. brevidentata (Wood 1828).

in thaids at the genus level so that the importance of variation between the species of Acanthina could be more accurately gauged.

Shell

Members of the genus Acanthina have a rather solid, dextrally coiled shell of four to six whorls having no, or only slight sculpturing. The aperture is generally ovate, its height is approximately two-thirds the shell height and it has a short anterior canal. The interior may have one to several rows of denticles, and the outer lip invariably has a spine just posterior to the anterior canal.

Acanthina lugubris (Sowerby 1822) has a short spired shell with a relatively wide aperture (Figure 4 and 8-10). Its aperture may have none, one, or more axial rows of apertural denticles. These characteristics may be mixed in a single population. The shell varies from almost white to olive in color and is mottled with brown or black spots or wavy stripes paralleling the growth lines. The interior of the aperture is buff to brown with occasionally some purple tint.

Acanthina tyrianthina Berry 1957 is similar to A. lugubris, but it usually has a higher spire; is somewhat lighter in color; and has a narrower aperture (Figures 5 and 11). The spire height and the coloration vary from population to population, amnd also clinally, being similar to A. lugubris on the Pacific side of Baja California and more like A. angelica on the Gulf side. The presence of apertural denticles varies as in A. lugubris. The only really consistent difference is that A. tyrianthina has

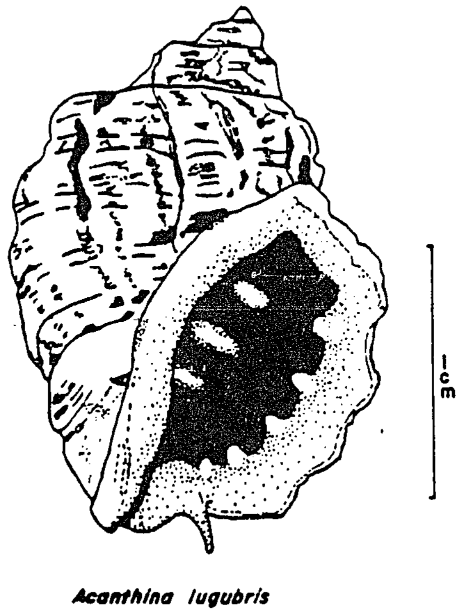


Figure 4. Acanthina lugubris (Sowerby, 1822).

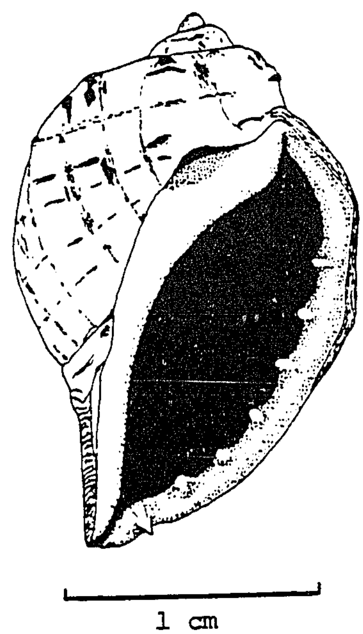


Figure 5. Acanthina tyrianthina Berry, 1957.

a consistently narrower aperture than _A_. _lugubris_ and has a concomitantly smaller angle at the shoulder. The difference in aperture shape was tested using a Student's t test to compare the ratio of height and width of the apertures of _A_. _tyrianthina_ from several lots collected in the Magdalena Bay area with the same ratios for _A_. _lugubris_ from two collections, one from Punta Banda and the other from Ensenada. The differences proved to be significant; but when a test for coefficient of difference (Mayr, 1969) was performed, it was found that there was an 80% nonoverlap between _A_. _lugubris_ and _A_. _tyrianthina_ for this characteristic (Table 1).

Acanthina angelica Oldroyd 1918 usually has a higher spire than either _A_. _lugubris_ or _A_. _tyrianthina_ and lighter coloration (Figures 6 and 12-14). The interior usually has some purple coloration, but may also be buff or brown. Like _A_. _lugubris_ and _A_. _tyrianthina_, the presence of denticles in the aperture of _A_. _angelica_ is completely variable; but the characteristics that set _A_. _angelica_ apart from the other snails discussed thus far are its degree of sculpturing, including tubercles or varicies, and its tendency to have a much higher shoulder.

The shells of juveniles of all of the snails whose shells have been discussed thus far have spiral rows of minute rectangular pits. By the time they mature these are normally filled in by calcareous algae or barnacles. They are, therefore, not a good characteristic for differentiating these organisms. Another characteristic that

Table 1. Ratio of height to width of aperture compared between *Acanthina lugubris* and *A. tyrianthina*.

	X_{ij}	N	$\bar{X}$	S^2	Calc t	Tab t	CD
lugubris	48.06	30	1.60	0.01			
tyrianthina	63.87	36	1.77	0.01			
					8.5	3.449	0.85*

*0.85 indicates an 80% joint nonoverlap (Mayr 1969).

Figure 6. Acanthina angelica Oldroyd, 1918.

has been used to differentiate these organisms is shell size. All three of these groups vary tremendously in size between one collection site and another, and though _A_. _tyrianthina_ tends to be smaller than either _A_. _angelica_ or _A_. _lugubris_, individuals of some lots of adult _A_. _tyrianthina_ are larger than adults in many lots of _A_. _angelica_ and _A_. _lugubris_.

Acanthina brevidentata (Wood 1828) has a brownish shell with greyish-white spots on very short nodes. It has very low shoulders, giving the apex a smooth pointed appearance. The interior is creamy white except for the inner margin of the outer lip which is dark brown or black. The interior may also contain spiral rows of denticles. The outer lip has a series of very small teeth along its length and also has a spine that is usually shorter than those of the species previously discussed. _A_. _brevidentata_ is unique among the _Acanthina_ discussed in that its aperture has a small posterior notch (Figures 7 and 15).

The shells of _Acanthina spirata_ and _A_. _pancilirata_ are examined even though the animals were not collected, and they appear in no other section of this thesis. This was done in order to develop a better concept of what constitutes the genus _Acanthina_ and how its species vary. The only species in this genus that is not compared is _A_. _punctulata_, examples of which I did not examine.

Acanthina spirata (Blainville) has an elongate shell about 25 to 30 mm high with little sculpturing, though individuals often have a conspicuous spiral keel. The shell is white in color with spiral rows of short brown lines. The interior is white, and every

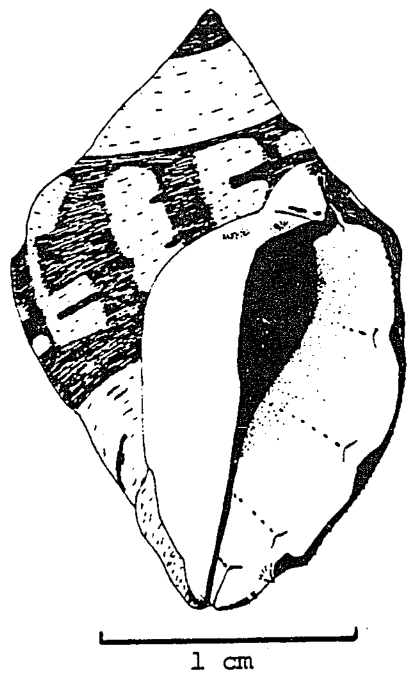


Figure 7. Acanthina brevidentata (Wood, 1828).

individual I have seen has a heavy axial row of white denticles below the inner margin of the lip. A characteristic that separates this species from the other Acanthina is the presence of a longer anterior canal (Figure 16).

Acanthina pancilirata (Stearns 1871) has the smallest shell among the observed Acanthina, about 16 mm high. It is very similar to A. lugubris in shape, but has external coloration similar to A. spirata. Its interior is buff to purple and may contain axial rows of denticles (Figure 17).

Operculum

Opercula are very similar in all of the Acanthina, though their shape varies slightly, probably due to variation in the shape of the aperture of the shell. The operculum of Acanthina is the horny, non-spiral type as discussed by Fretter and Graham (1962) and typical examples from A. angelica and A. lugubris are illustrated (Figures 18 and 19).

Digestive System

Radula

Radulae were removed from the following snails for comparison: Acanthina angelica. A. lugubris, A. tyrianthina, A. brevidentata, and Thais emarginata. In addition, radulae were removed from A. angelica collected at different times in the same location and from another location to determine the range of intraspecific variation.

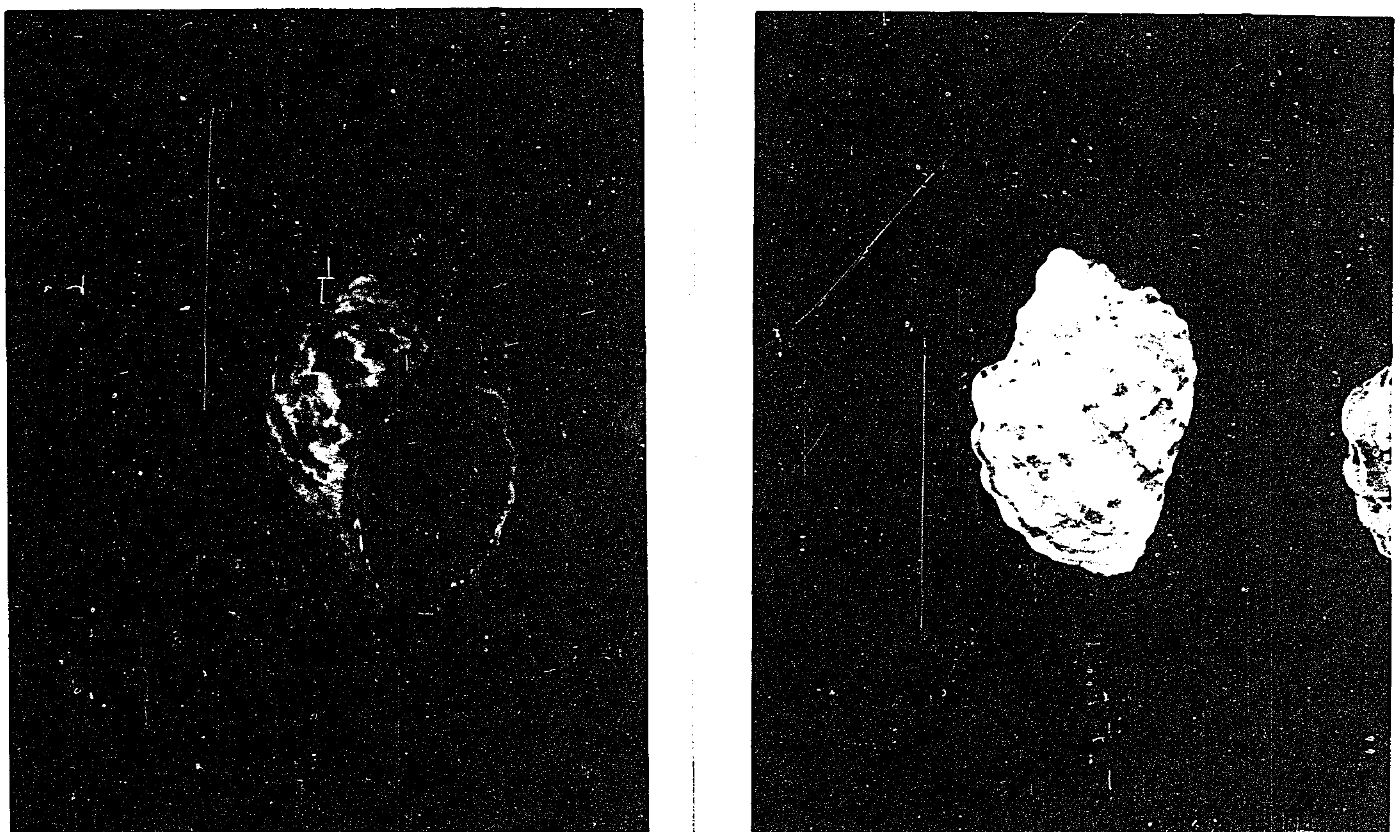


Figure 8. Acanthina lugubris (Sowerby, 1822) from Pta. Banda.

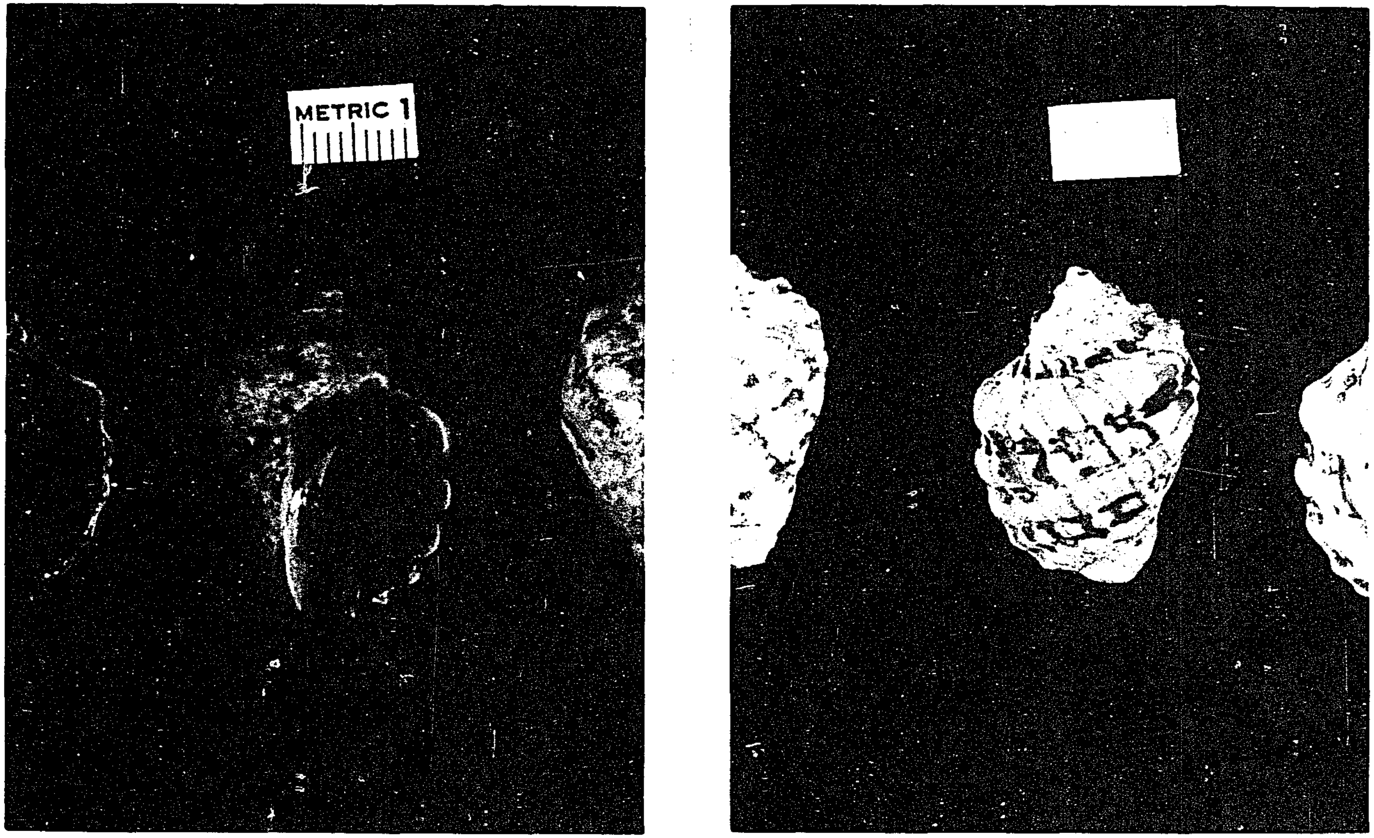


Figure 9. Acanthina lugubris (Sowerby, 1822) from Pto. Santo Tomas.

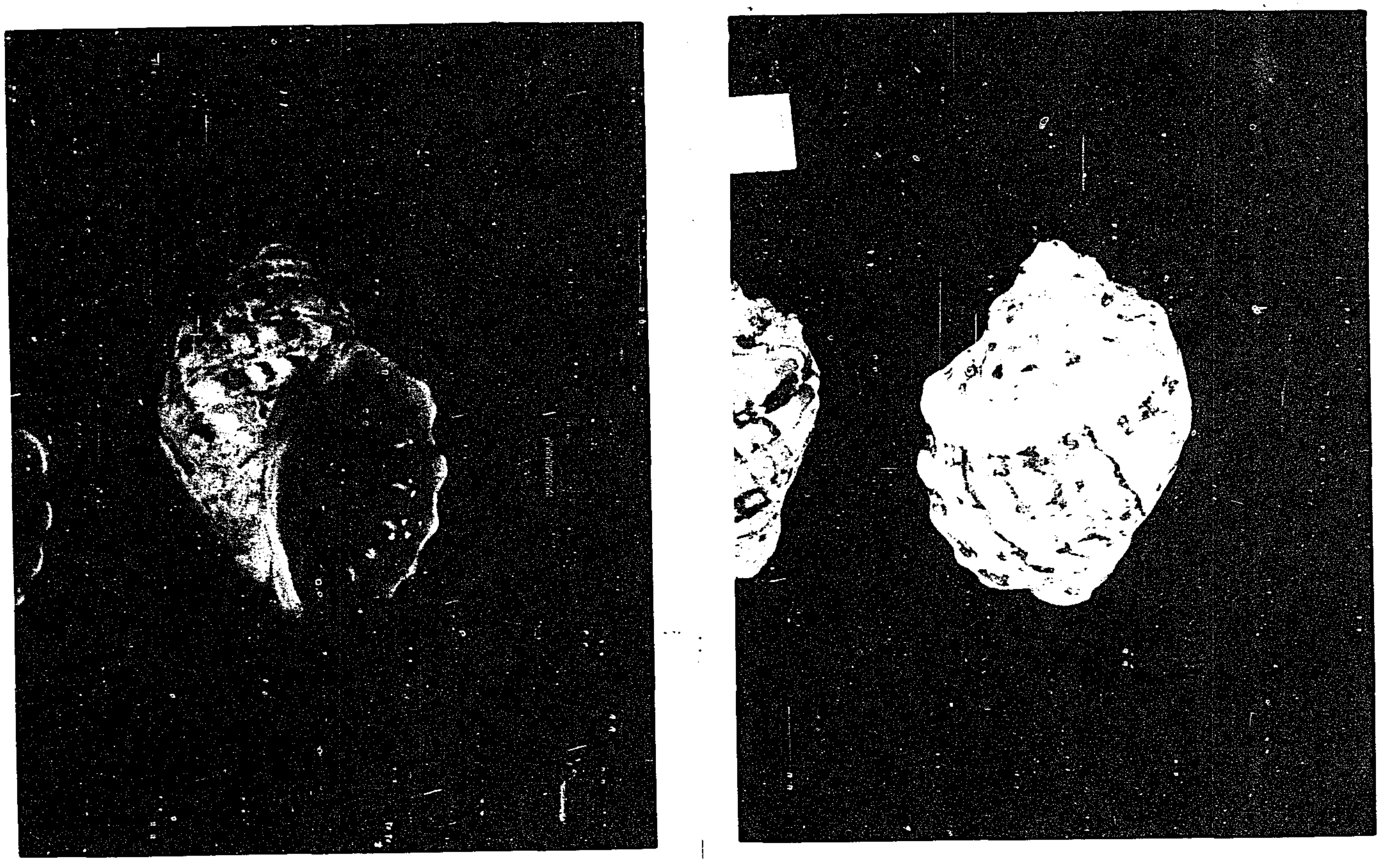


Figure 10. Acanthina lugubris (Sowerby, 1822) from Ensenada.

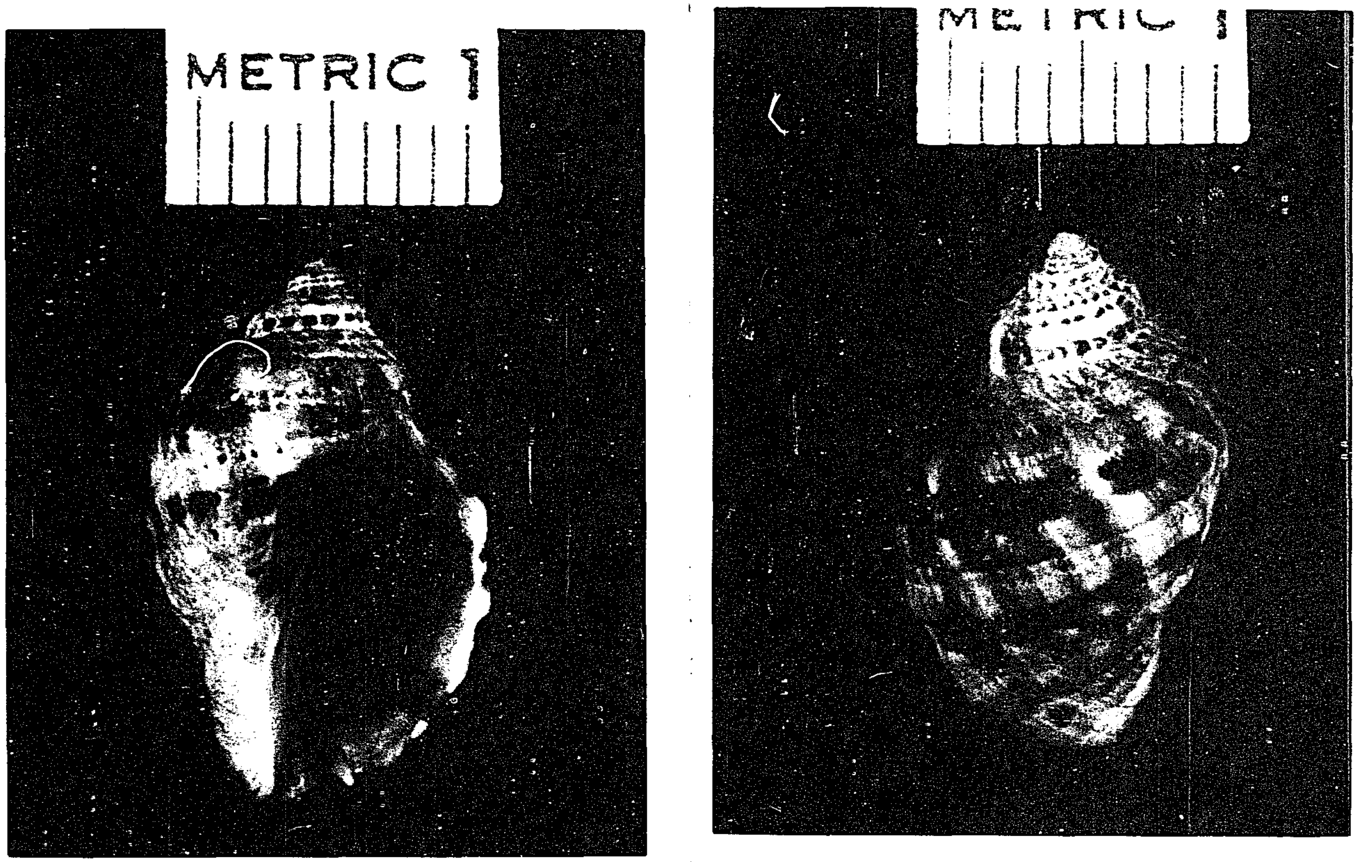


Figure 11. Acanthina tyrianthina Berry, 1957 from La Paz.

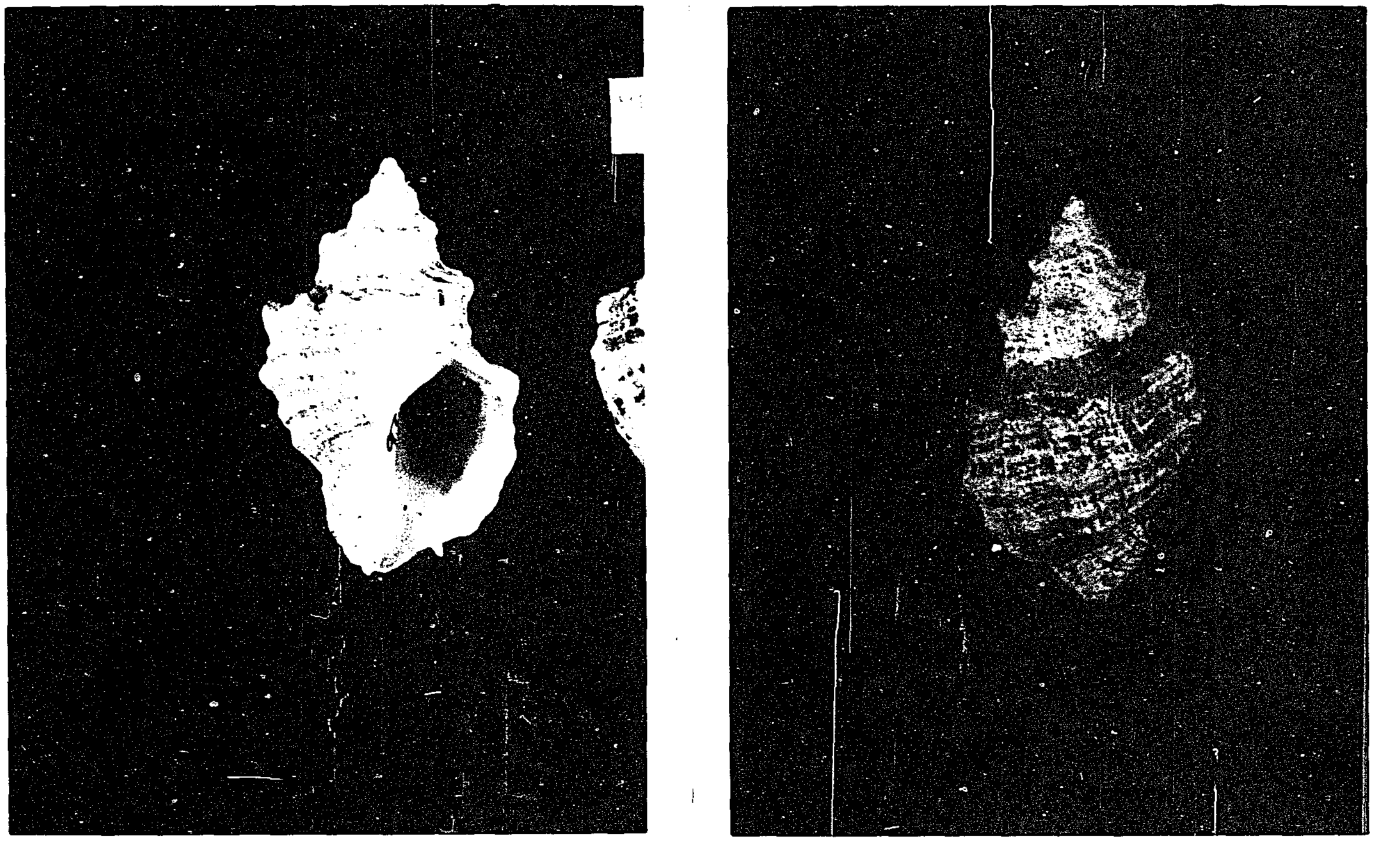


Figure 12. Acanthina angelica Oldroyd, 1918 from Puertocito.

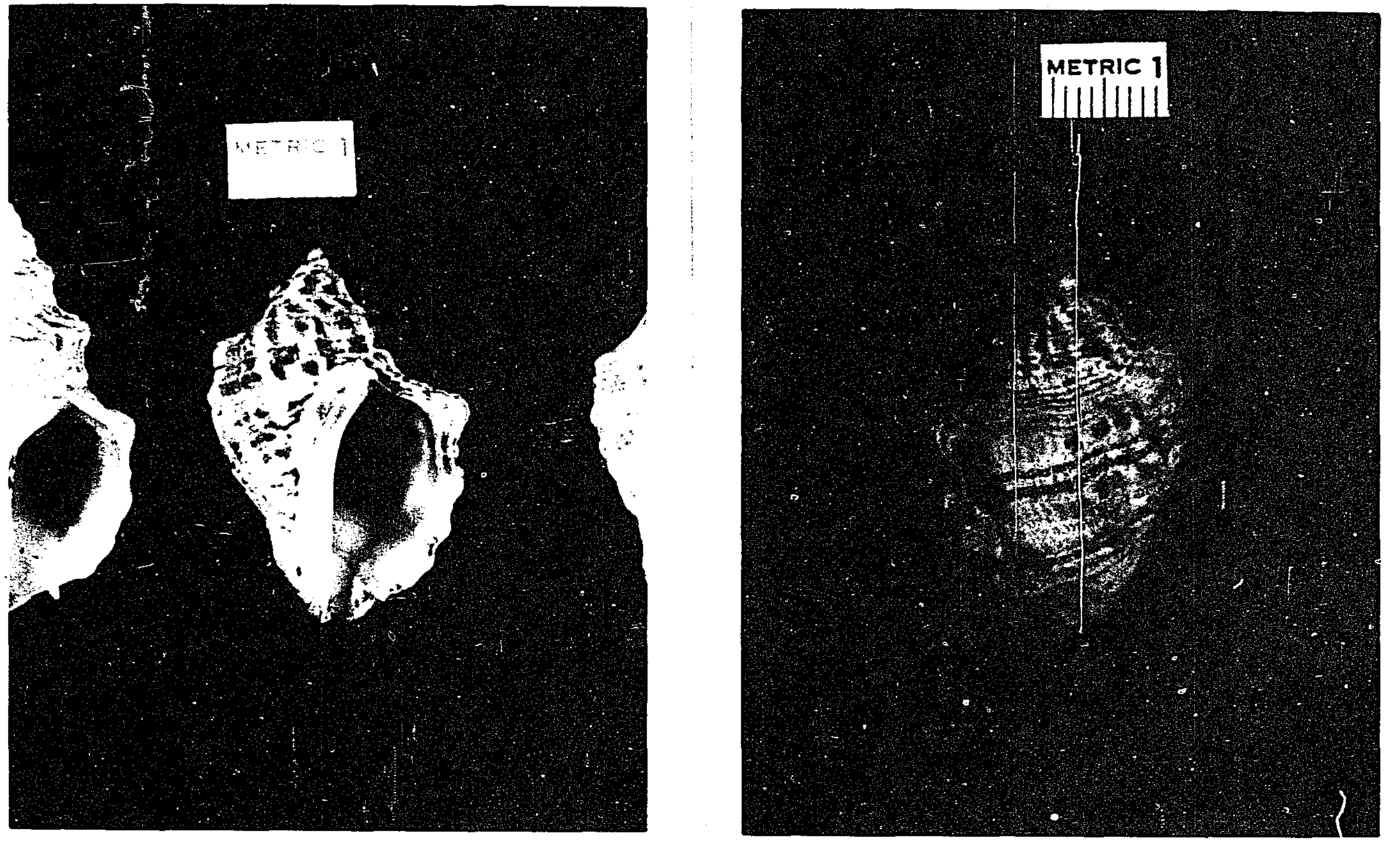


Figure 13. Acanthina angelica Oldroyd, 1918 from Puerto Penasco.

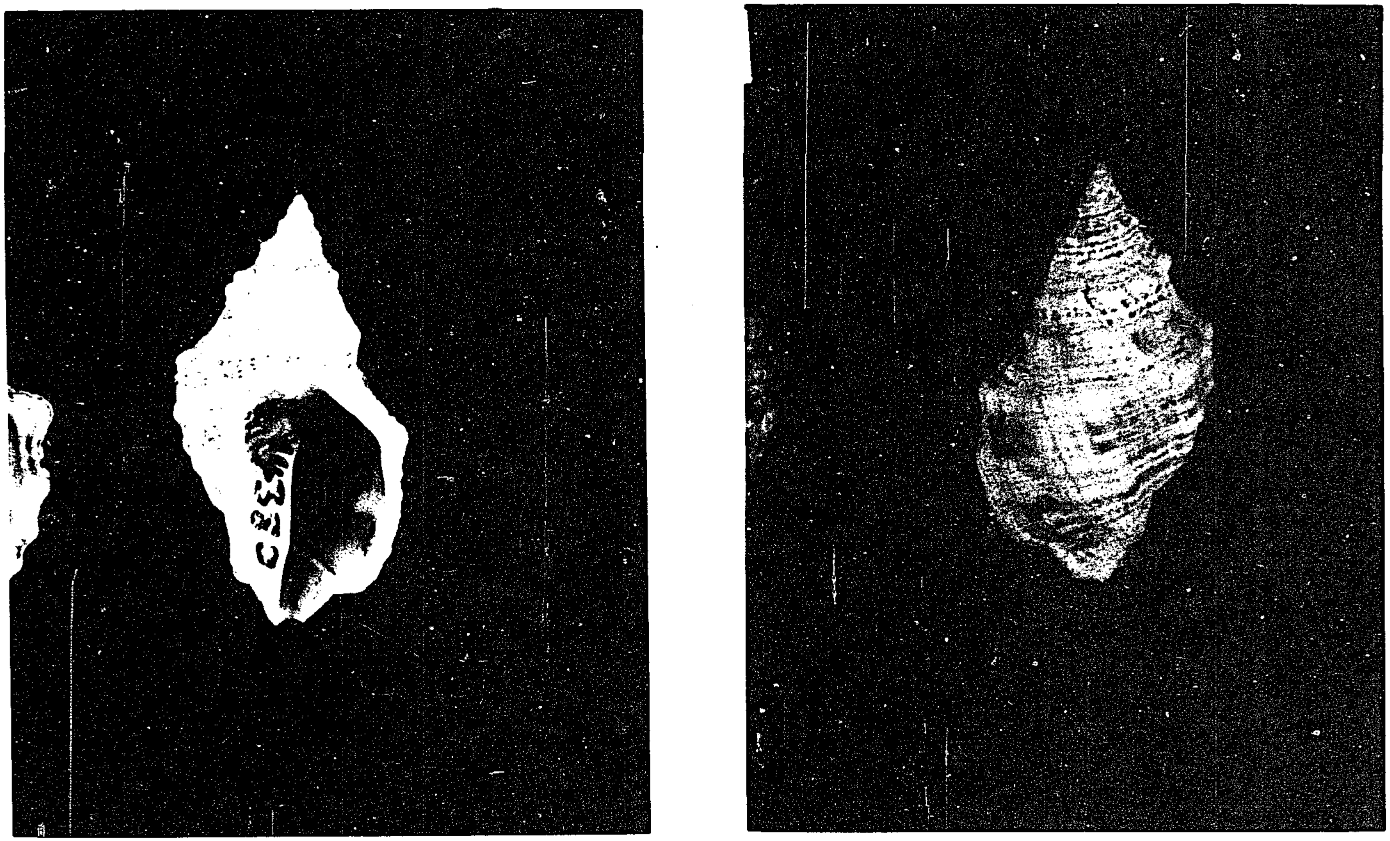


Figure 14. Acanthina angelica Oldroyd, 1918 from San Felipe.

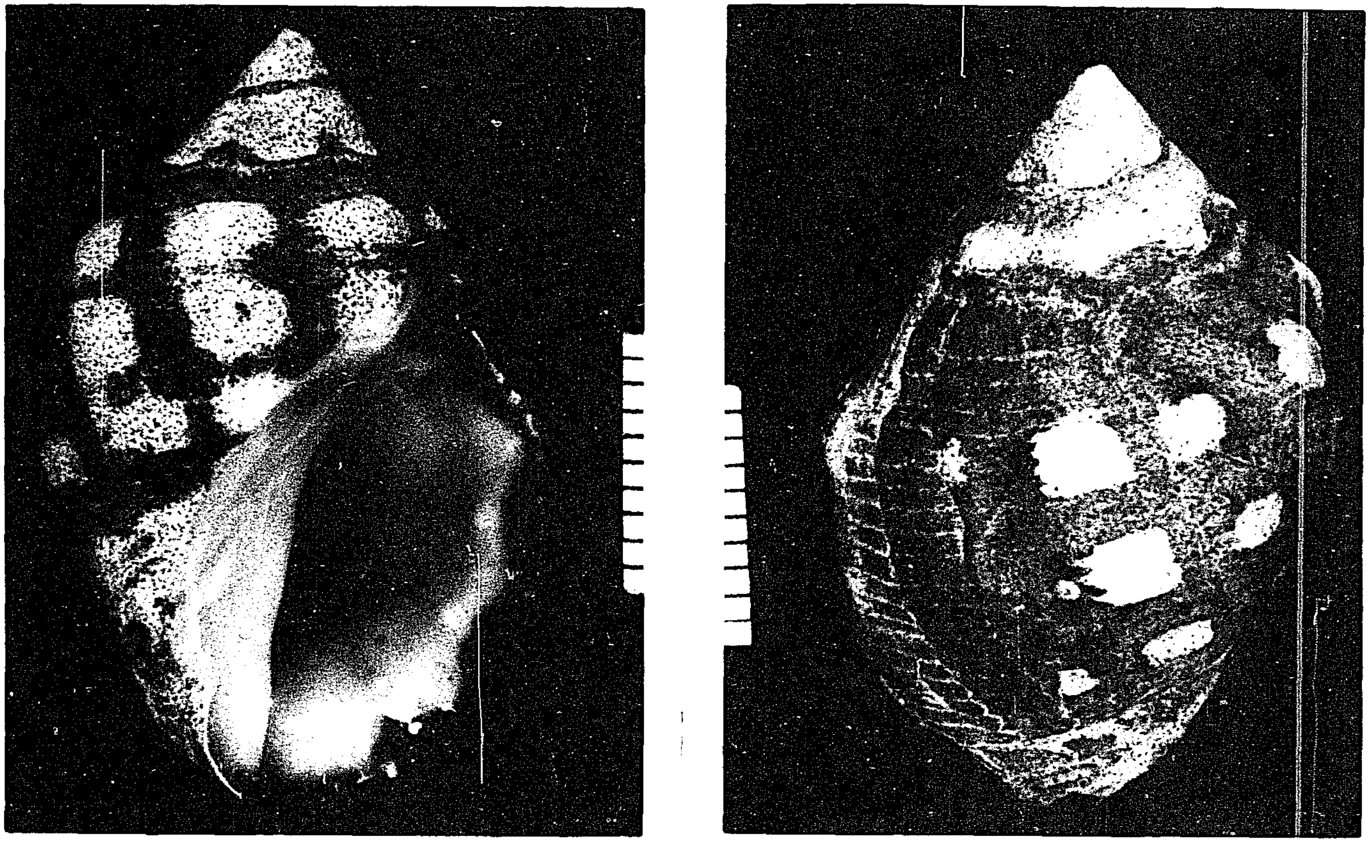


Figure 15. <u>Acanthina</u> <u>brevidentata</u> (Wood, 1918) from Venado Beach, Panama.

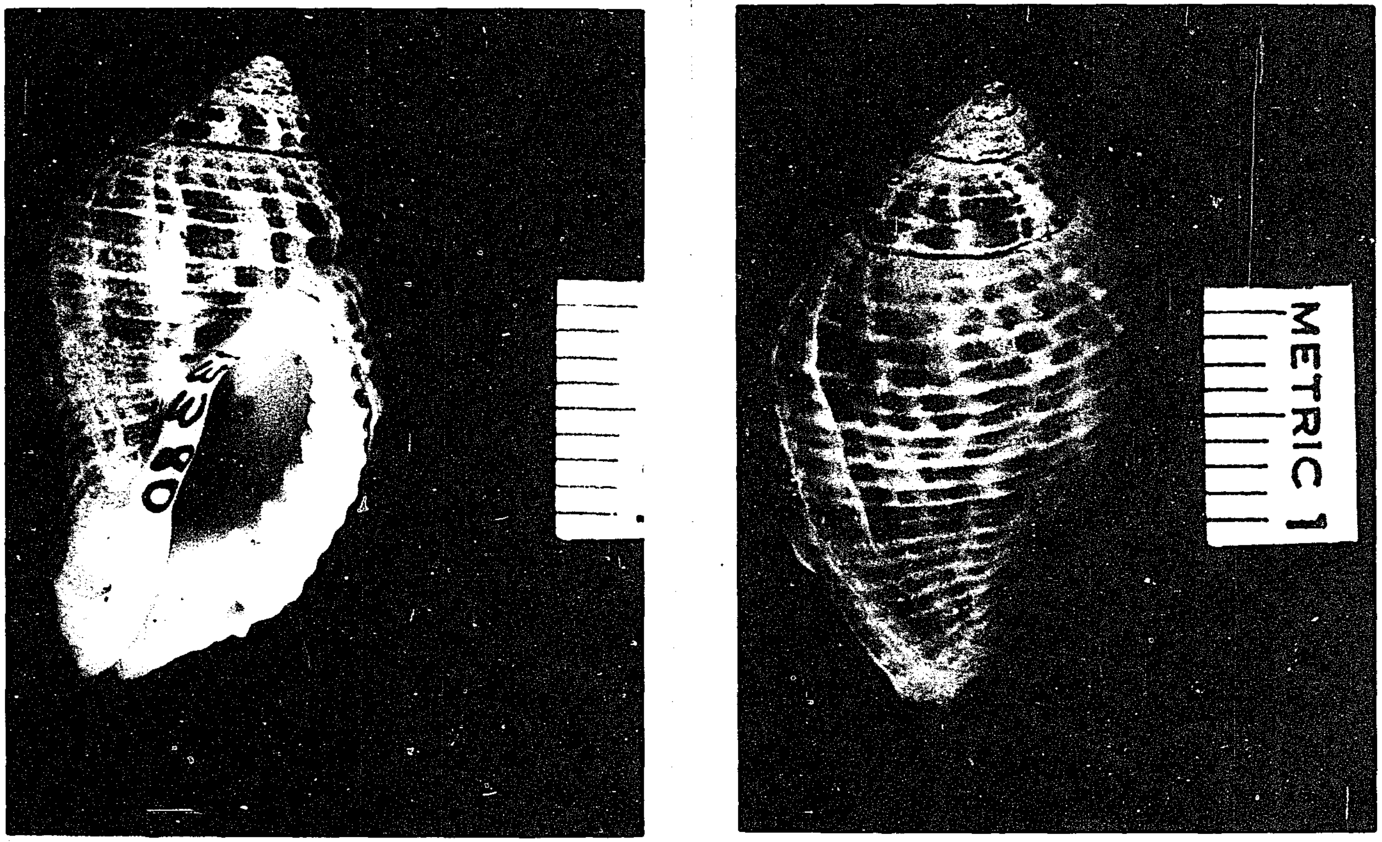


Figure 16. Acanthina spirata (Blainville).

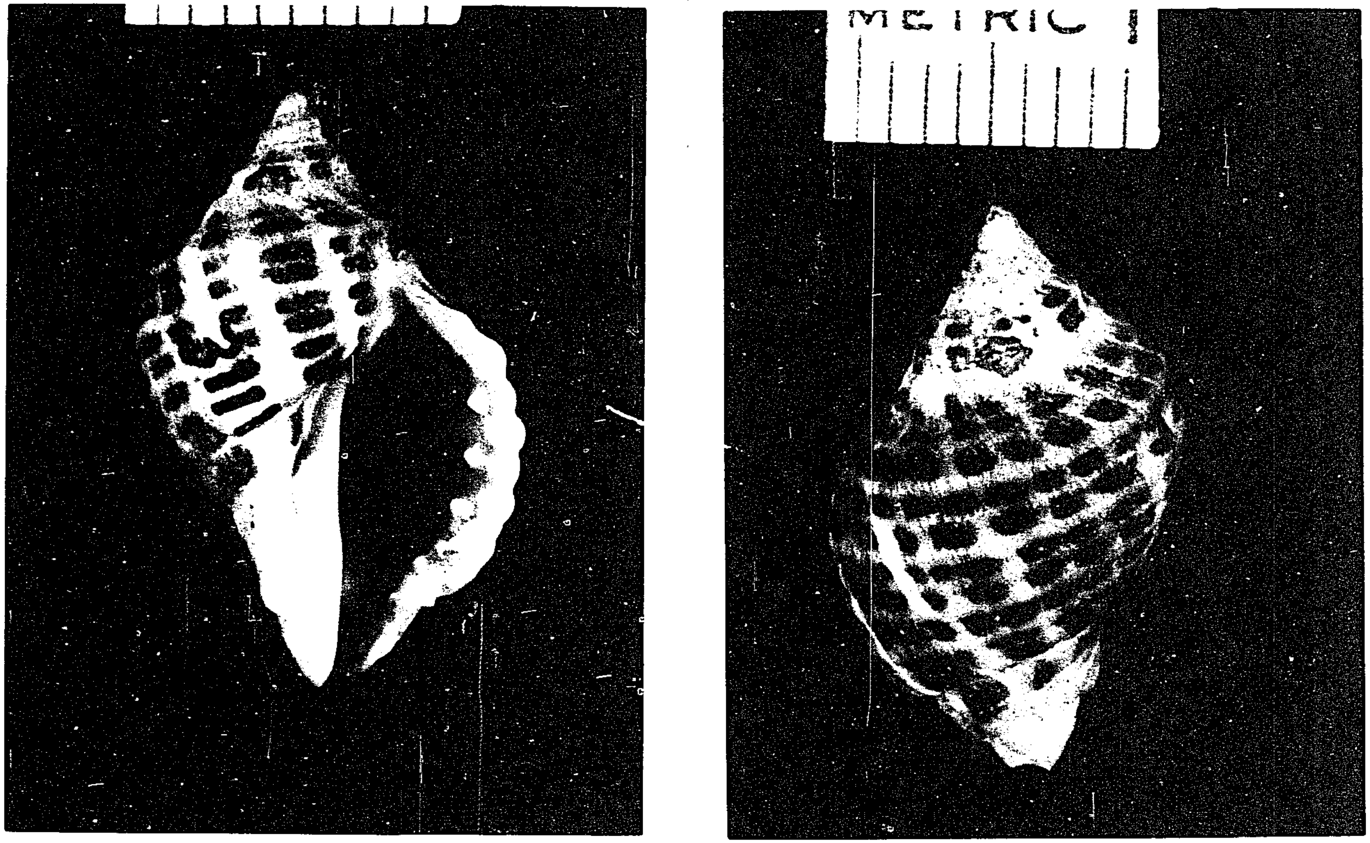


Figure 17. Acanthina paucilirata (Stearns, 1871).

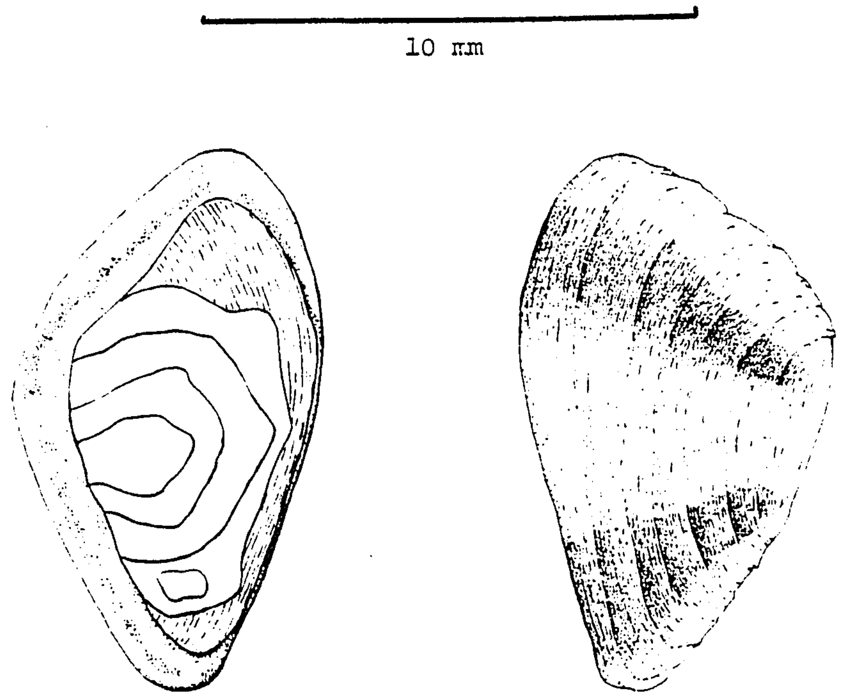


Figure 18. Operculum of Acanthina angelica.

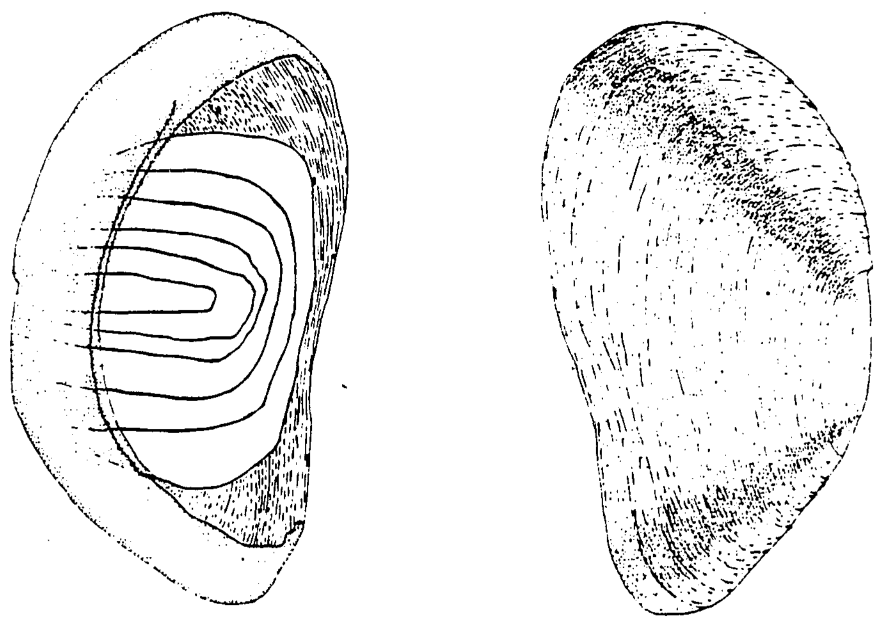


Figure 19. Operculum of Acanthina lugubris.

I also compared these with the dorsal view of the rachidian tooth drawn by Wu (1968).

Rachidian teeth of A. angelica are five-cusped, and all have similar medial denticles above the base of the lateral cusps although position and number of the lateral denticles varies considerably (Figure 20 a-c).

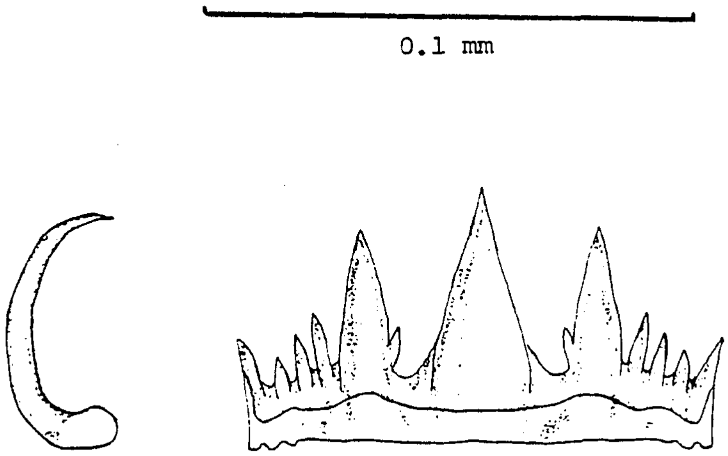
Rachidian teeth of A. tyrianthina and A. lugubris are very similar to those of A. angelica, the number and placement of the lateral denticles are the only points of variation (Figures 21 and 22).

The rachidian tooth of A. brevidentata is three-cusped with medial denticles high up on the lateral cusps. The central cusp is much larger and broader than those of the other species of Acanthina studied (Figure 23).

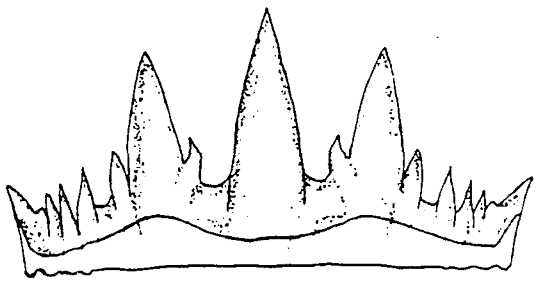
The rachidian tooth of T. emarginata is five-cusped with a basal plate that holds the cusps erect, a plate that observed species of Acanthina lack (Figure 24).

The lateral teeth of all of the observed species of Acanthina are similar in shape, however the length of the lateral teeth in A. brevidentata is approximately equal to the width of the base of the rachidian tooth, while those of the other species of Acanthina are equal to only about half the width of their rachidians (Figures 20-23).

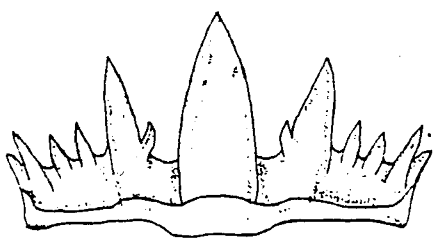
The lateral tooth of T. emarginata has a distinct hook at its tip and a web along its inner arc (Figure 24).



(a) From Pto. Penasco, Mexico.



(b) From Pto. Penasco, Mexico for comparison.



(c) From Punta Kino.

Figure 20. Radular teeth of Acanthina angelica.

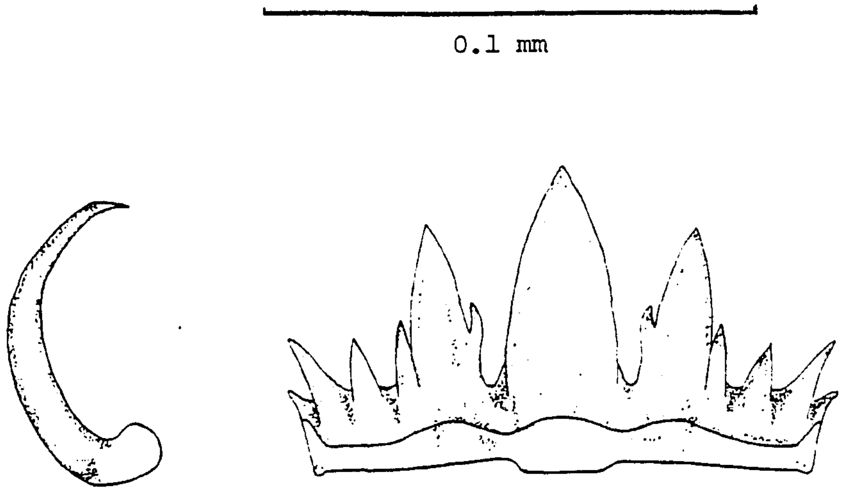


Figure 21. Radular teeth of Acanthina lugubris.

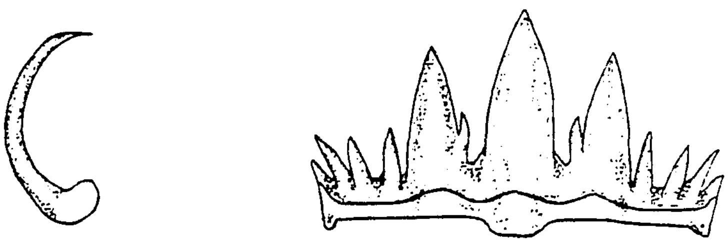


Figure 22. Radular teeth of Acanthina tyrianthina.

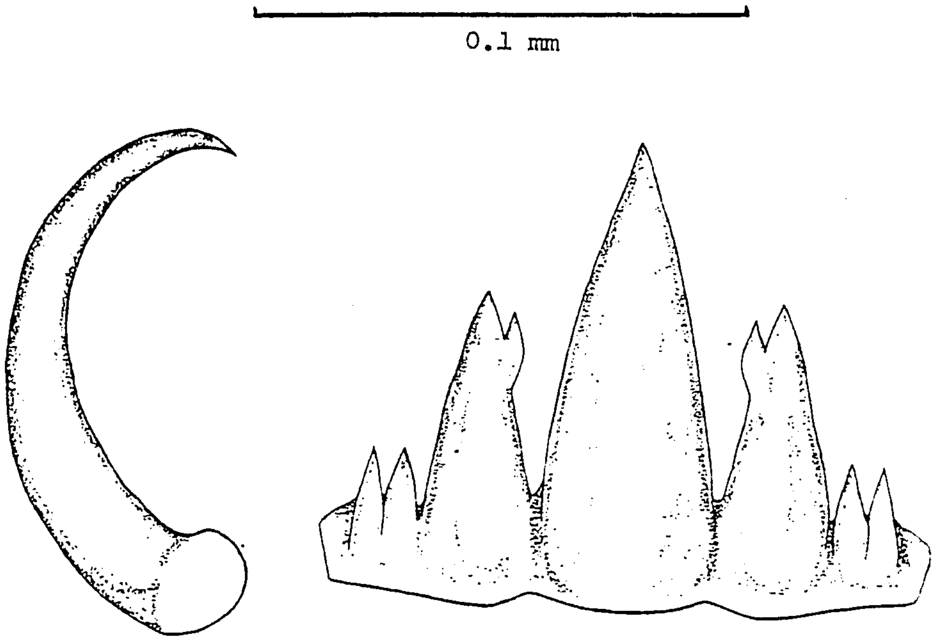


Figure 23. Radular teeth of Acanthina brevidentata.

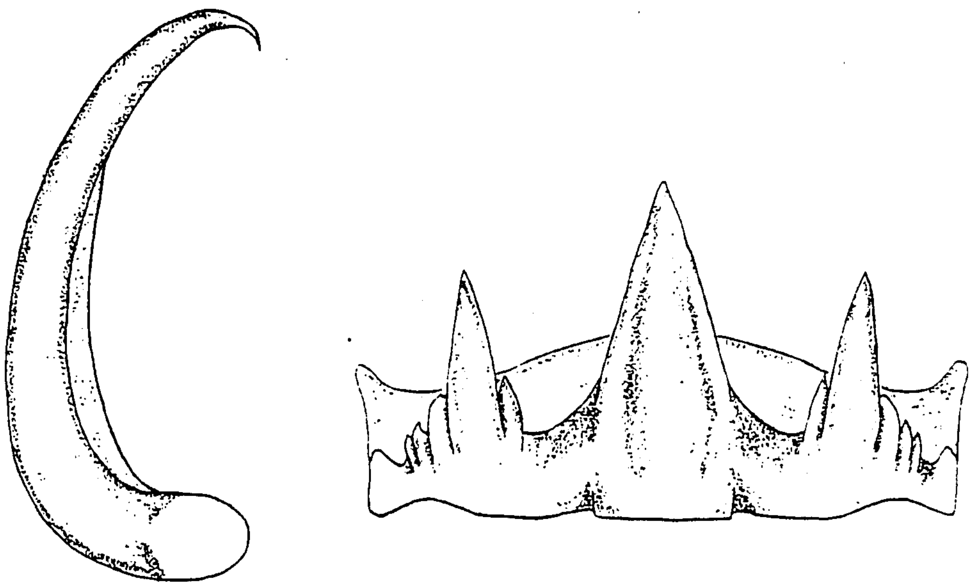


Figure 24. Radular teeth of Thais emarginata.

Buccal Mass

The buccal areas of Acanthina lugubris, A. tyrianthina, A. angelica, A. brevidentate, and Thais emarginata were dissected for comparison.

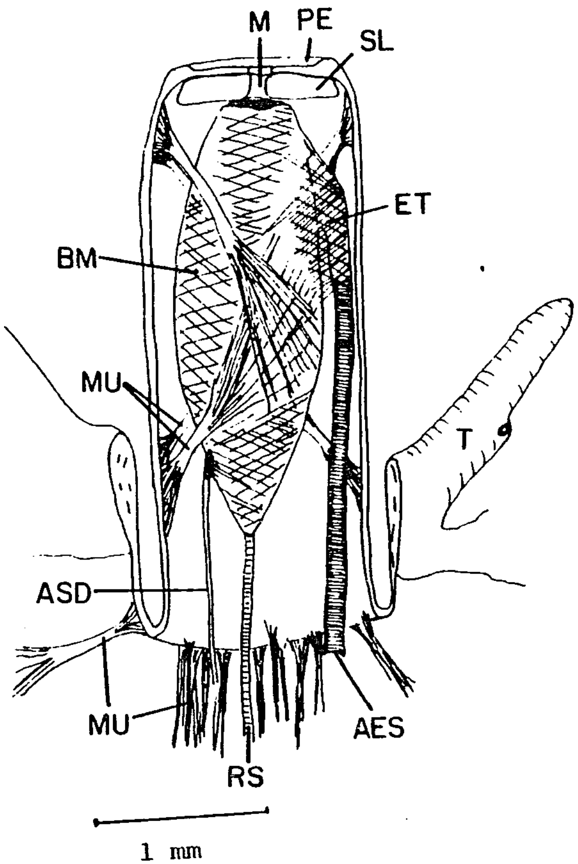
The proboscides of all of the species examined are the pleurembolic type (the rear of the proboscis is retracted first). Those of A. lugubris, A. angelica, and A. tyrianthina retract straight back while those of A. brevidentata and T. emarginata retract to the right of the midline of the animal in order to clear the acessory salivary glands and the gland of Leiblein. The right proboscis retractor muscle of A. brevidentata was considerably more massive than the left, unlike the other species examined.

The buccal masses of all of these species were very similar to one another and similar to Urosalpinx cinerea Say as described by Carriker (1943) (Figures 25-27).

Dimensions of the parts discussed above of typical examples of each species are given in Table 2. The proboscis length is based upon the length of eversion of the proboscides of properly relaxed examples of A. angelica (Figure 28), and the retracted proboscides of other snails were drawn out to about the same extent and measured. In fact, these proboscides may be eversable to 35 or 40 mm as in Urosalpinx (Carriker 1943).

Digestive Tract

Acanthina lugubris, A. angelica, A. brevidentata, and Thais emarginata were dissected to observe digestive organs caudal to the buccal



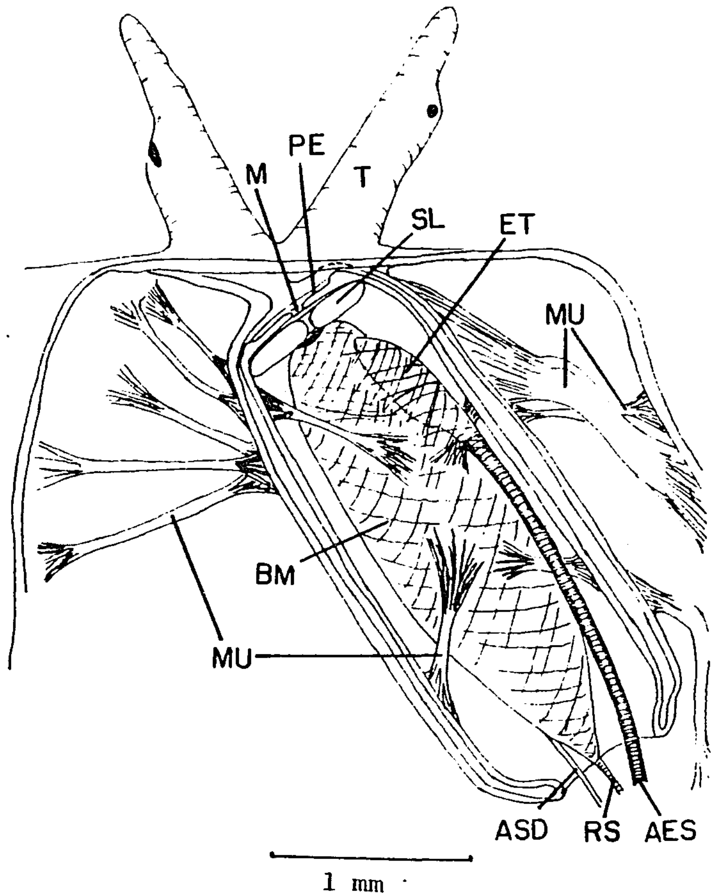


Figure 25. Bucccal mass of Acanthina angelica (those of A. lugubris and A. tyrianthina appear identical).

Figure 26. Buccal mass of Acanthina brevidentata.

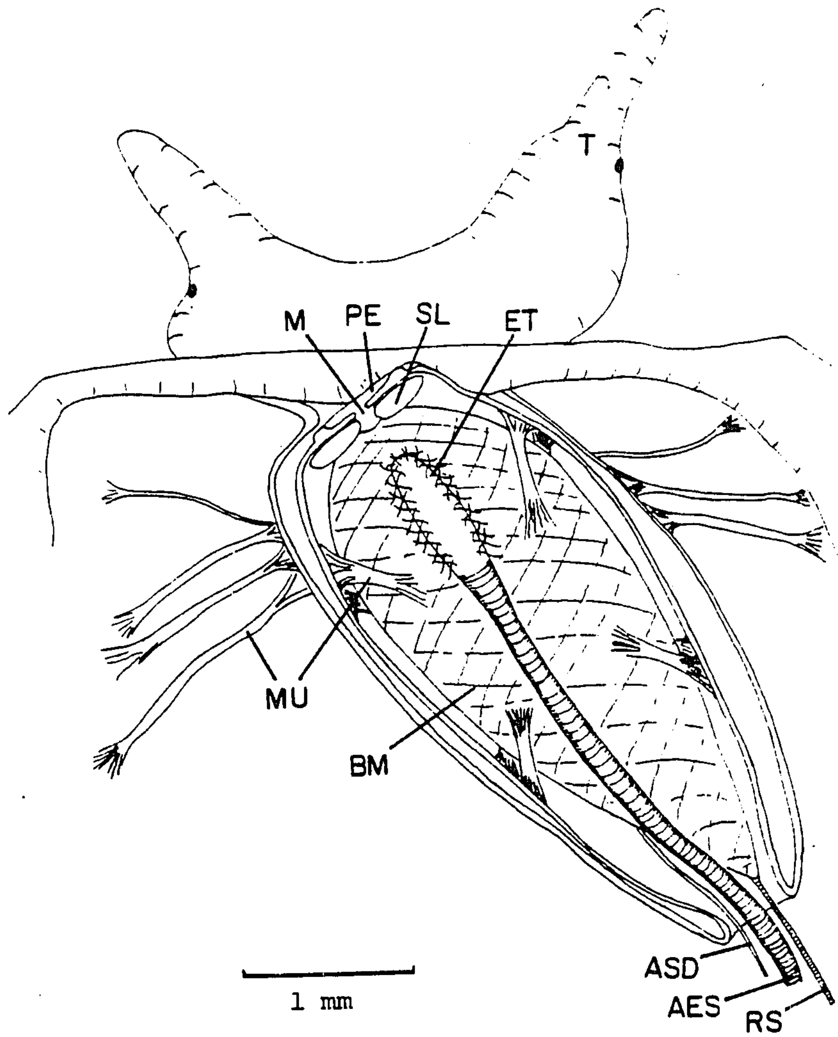


Figure 27. Buccal mass of Thais emarginata.

Table 2. Typical dimensions of the parts of the feeding apparatus in individuals of species used in this study (mm).

Species	Proboscis Length	Proboscis Diam	Buccal Mass Length	Buccal Mass Diam	Radular Sac Length	Body Length
<u>angelica</u>	4.3	1.1	2.4	0.8	8.5	21.8
<u>lugubris</u>	4.5	1.2	2.9	0.9	7.7	29.5
<u>tryianthina</u>	4.3	1.0	2.5	0.8	7.1	21.0*
<u>brevidentata</u>	3.6	1.0	2.5	0.7	2.6	29.1
<u>emarginata</u>	5.3	1.9	3.4	1.5	8.1	38.2

*This snail was badly decomposed. Therefore, the overall length was estimated from the part that could be measured.

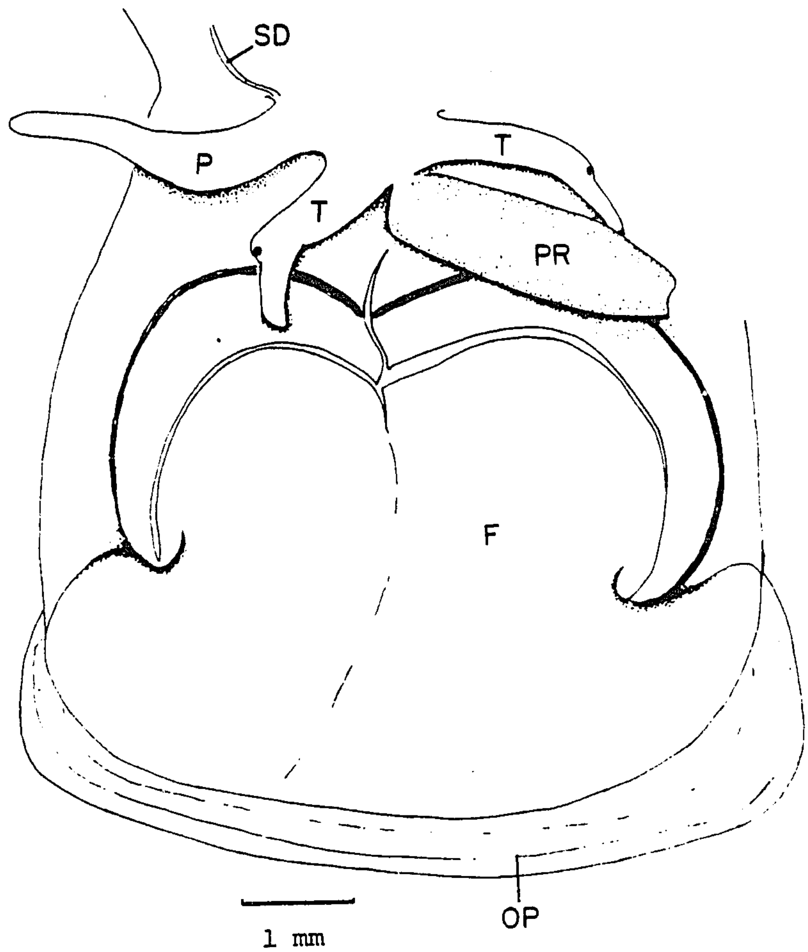


Figure 28. Head of Acanthina angelica showing everted proboscis.

mass. Acanthina tyrianthina was also observed to a certain extent, but the examples I was able to obtain were so badly decomposed that I was unable to make any observation or measurement of the posterior esophagus beyond the gland of Leiblein, the stomach, the intestine, or the rectum. The stomach and the inner surface of the rectum were somewhat decomposed in A. brevidentata also, but sizes and shapes of organs were still apparent. Since A. angelica, A. lugubris, and, so far as can be seen, A. tyrianthina have very similar digestive systems, I shall describe them together, and anything said about A. angelica will hold true for the other two unless otherwise stated.

In A. angelica, the anterior esophagus leaves the posterior end of the retracted proboscis and makes a vertical S-curve to reach the level of the nerve ring. Before it passes through the nerve ring, ducts of paired salivary glands enter the anterior esophagus at the point in which it enters the pharynx of Leiblein. The salivary glands consist of small masses of tubules covering the anterior face of the pharynx of Leiblein. In A. lugubris these seem to be somewhat larger than in the other two species, but due to the amorphous nature of these glands, they were not measured. The pharynx of Leiblein is spindle shaped and firm, with a maximum diameter of 1 to 1.4 mm. Upon exiting the pharynx of Leiblein, the esophagus passes through the nerve ring where a single duct attaches to the ventral side of the esophagus. This duct attaches to two accessory salivary glands, each of which consists of a single tube folded in such a way that it forms a large mass on either side of the retracted proboscis.

When stretched out, each of these tubes measures approximately 17 mm in length. The accessory salivary glands also have a duct that goes in the anterior direction without passing through the nerve ring and enters the underside of the buccal mass.

Shortly after it passes through the nerve ring, the posterior esophagus has a small (2 mm long) patch of glandular material, the glande framboisee, on its right side, after which it enters the gland of Leiblein (Figures 29 and 30).

The gland of Leiblein is a massive, multi-lobed organ about the color and consistency of cooked chicken liver, which takes up about two-thirds of the space in the cephalic hemocoel (Figure 31).

When the posterior esophagus leaves the gland of Leiblein, it immediately passes through the wall of the hemocoel into the digestive gland to the stomach. The stomach is "U" shaped with a groove running through it between the intestine and a duct to the digestive gland (Figure 32).

The intestine, not distinguishable from the rectum, runs directly to the anus which is normally closed off by a small papilla (Figure 33 and 48a).

The digestive system of _Thais emarginata_ is very similar to that of _A. angelica_ except that the accessory salivary glands are slightly shorter and each salivary gland is an enclosed lobe rather than a mass of tubules. There is also a mass of grandular material surrounding the posterior esophagus, posterior to the gland

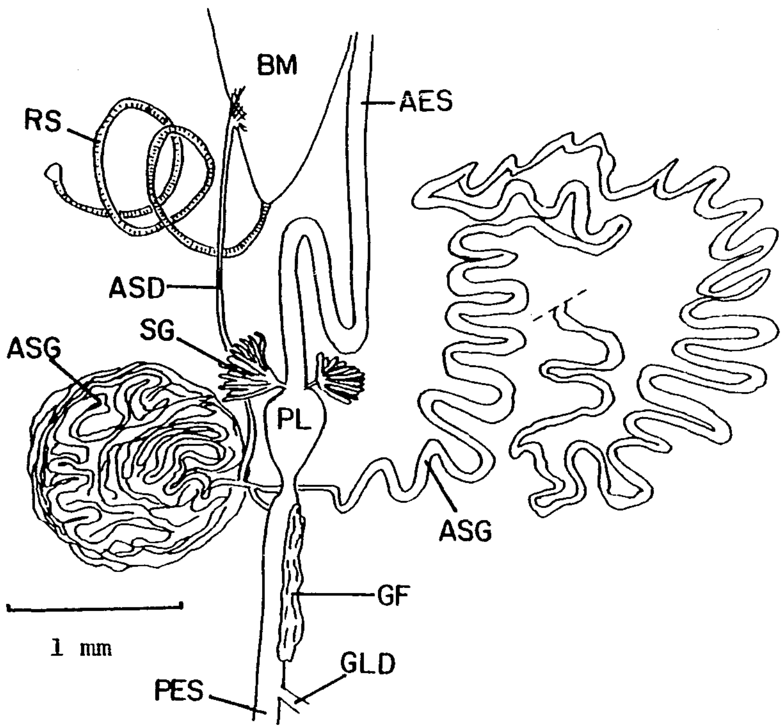


Figure 29. Anterior part of the digestive system of Acanthina lugubris.

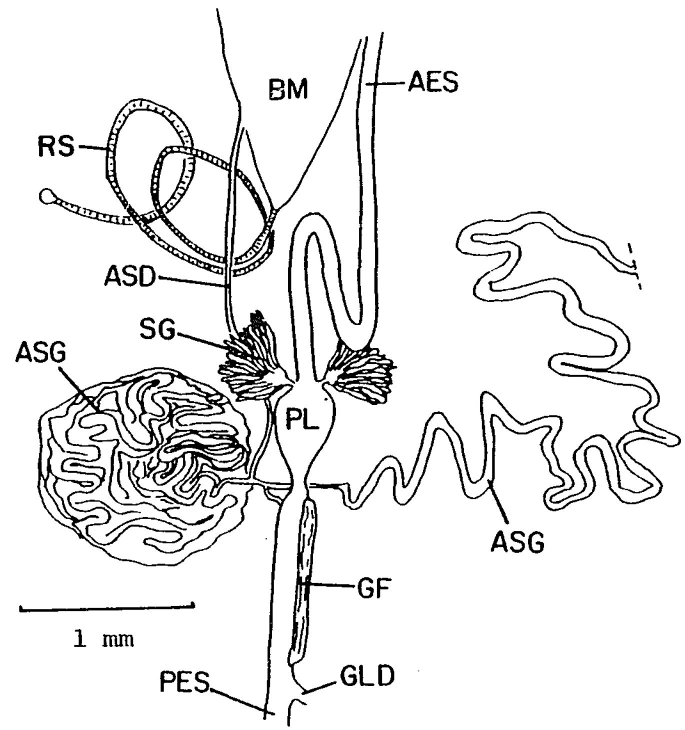


Figure 30. Anterior part of the digestive system of Acanthina angelica.

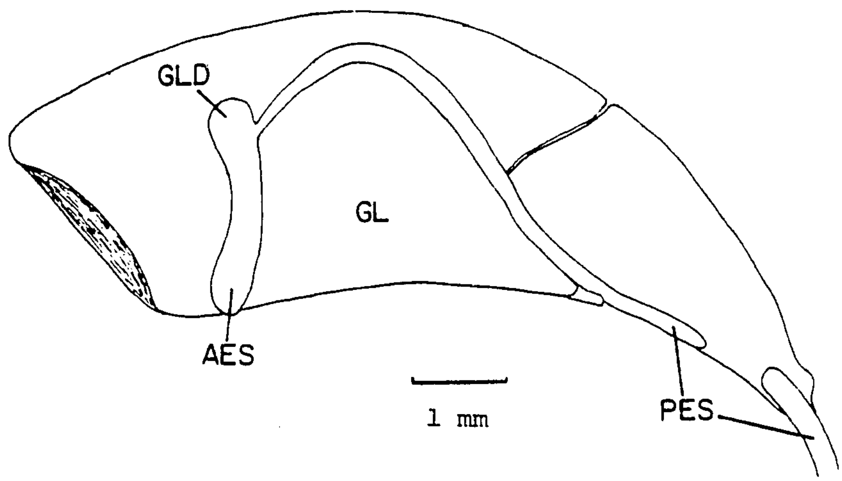


Figure 31. Gland of Leiblein of *Acanthina lugubris*.

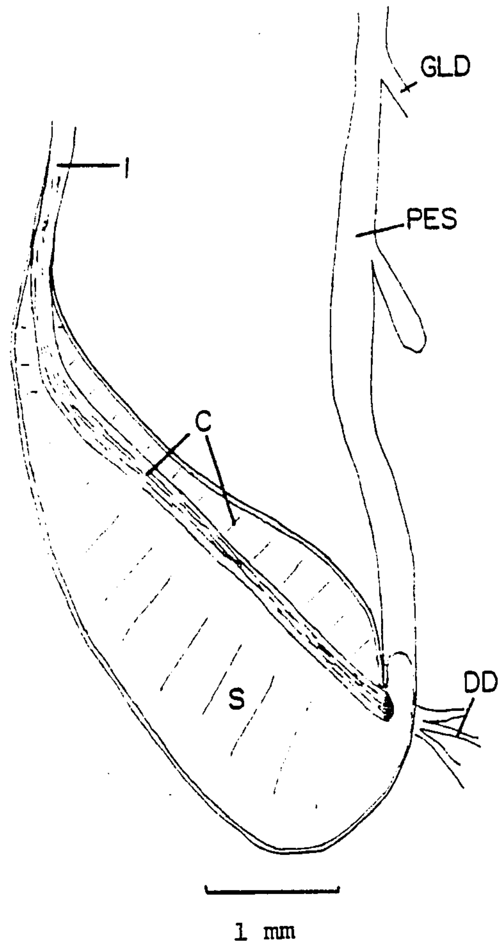


Figure 32. Stomach of <u>Acanthina</u> <u>angelica</u>.

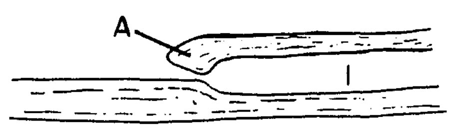


Figure 33. Sagital section of the anus of <u>Acanthina</u> angelica.

of Leiblein, which was not observed in _A. angelica_ (Figures 34 and 35).

The digestive system of _A. brevidentata_ differs in a great number of respects from the other _Acanthina_ as well as _Thais_. Its salivary glands are minute, making them very difficult to find. The pharynx of Lieblein is somewhat smaller than that in the other snails observed. The left accessory salivary gland is almost as large as that of the other snails measured (12 mm long), but the right one is short (2 mm long), possibly to make room for the retracted proboscis. The gland of Leiblein consisted of loose liver-colored material packed in white, very tough, muscular bags, very unlike these glands in the other snails observed. Beyond the gland of Leiblein was more glandular material along the esophagus which looks like more glande framboisée (Figures 36 and 37).

Accessory Boring Organ

Each of the snails dissected has an accessory boring organ located in the anterior portion of the foot. This is connected to the cephalic hemocoel by a channel and can be everted through a hole in the foot (Figures 38-40).

Reproductive System

Penis

The penes of _Acanathina angelica_, _A. lugubris_, _A. tyrianthina_, _A. brevidentata_ and _Thais emarginata_ were observed, measured and

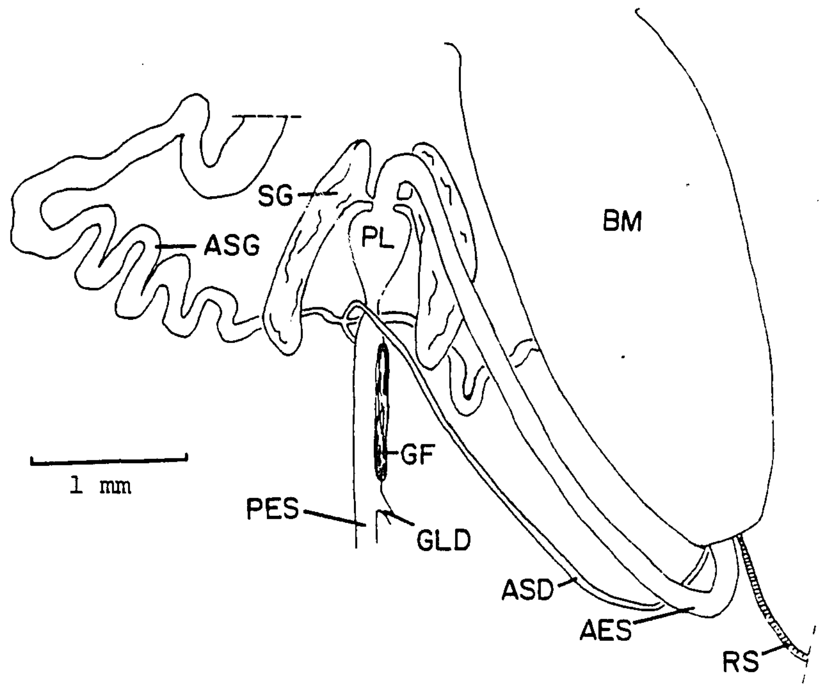


Figure 34. Anterior part of the digestive system of *Thais emarginata*.

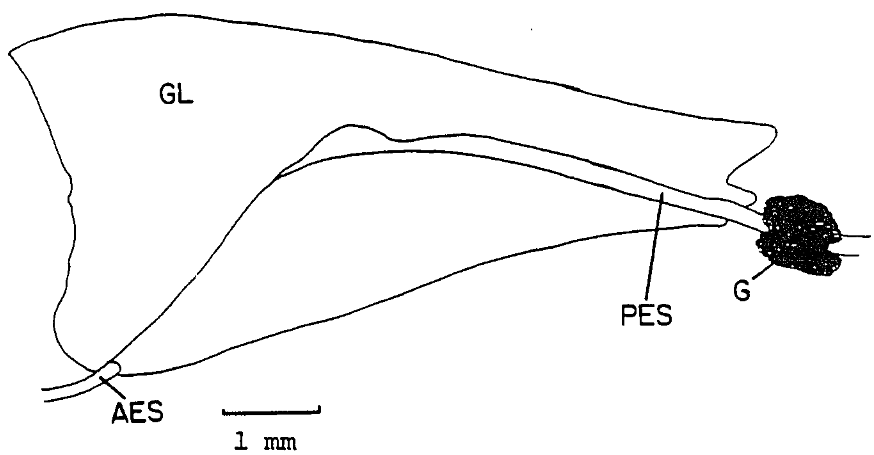


Figure 35. Gland of Leiblein of *Thais emarginata*.

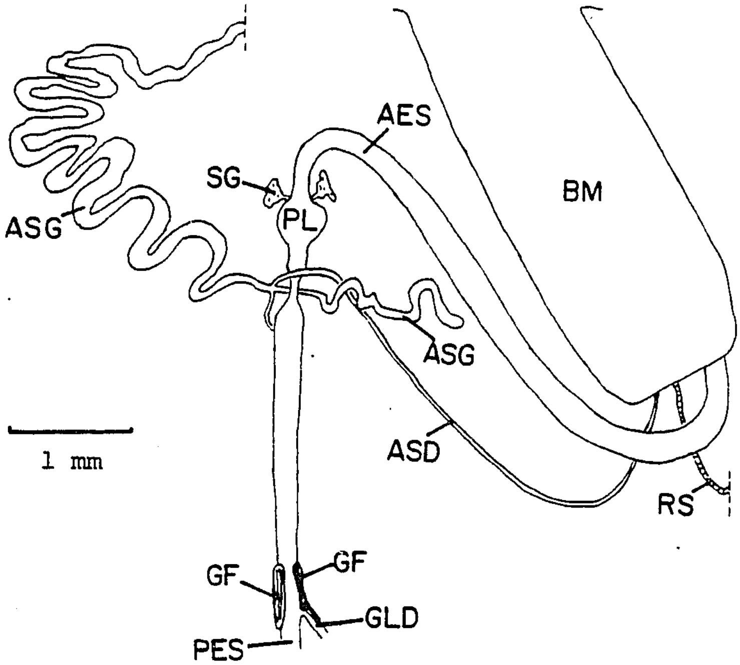


Figure 36. Anterior part of the digestive system of Acanthina brevidentata.

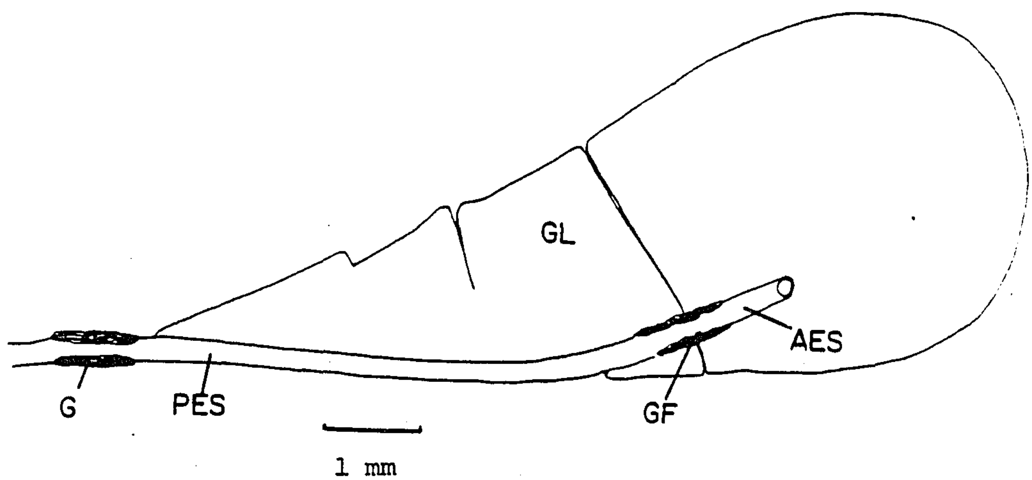


Figure 37. Gland of Leiblein of Acanthina brevidentata.

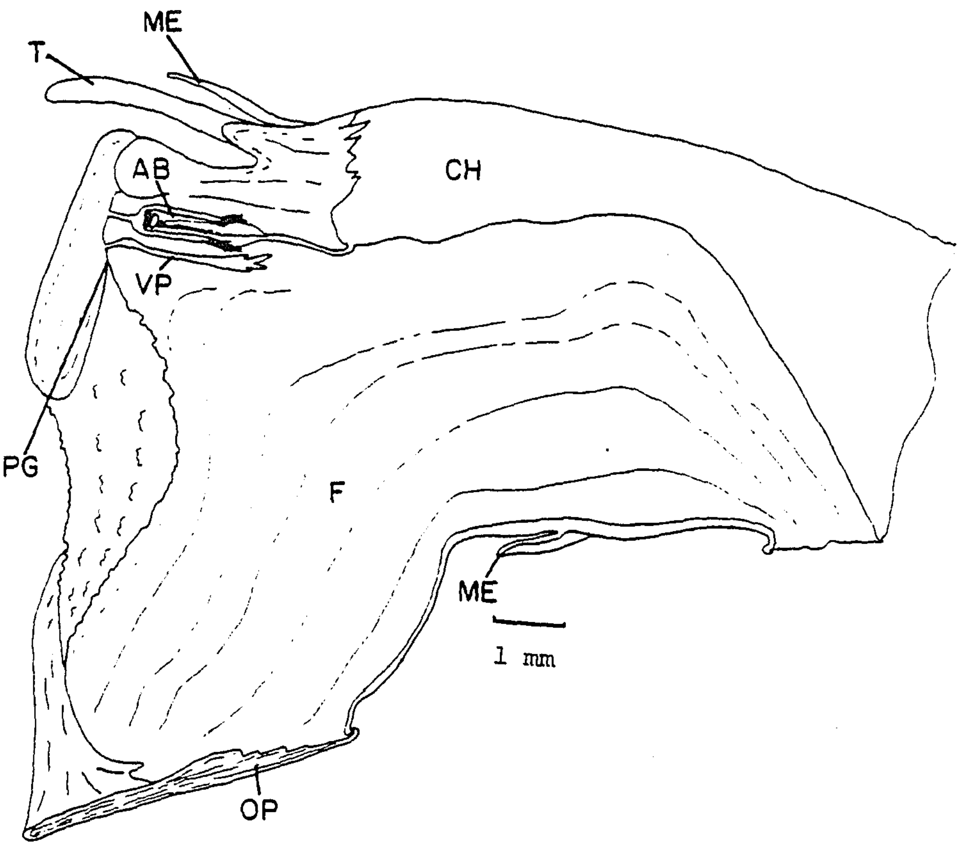


Figure 38. Accessory boring organ and ventral pedal gland of *Acanthina lugubris*.

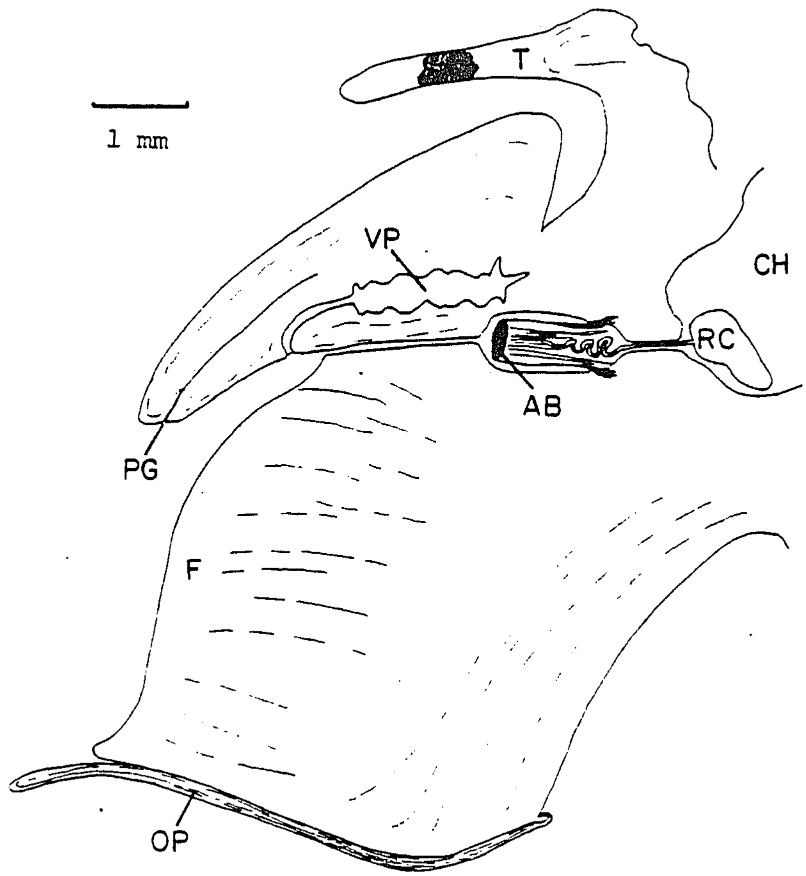


Figure 39. Accessory boring organ and ventral pedal gland of <u>Acanthina brevidentata.</u>

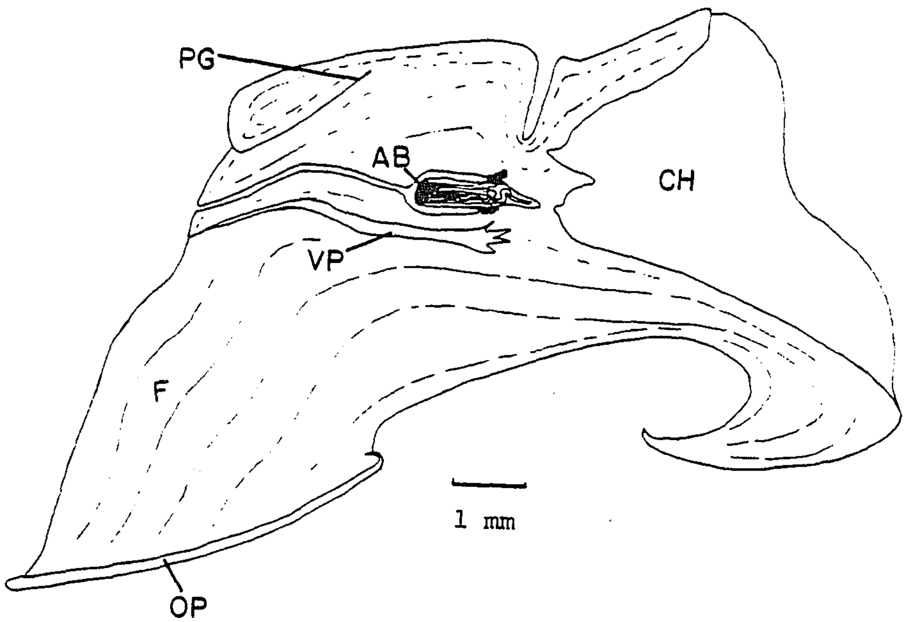


Figure 40. Accessory boring organ and ventral pedal gland of *Thais emarginata.*

sectioned. All penes are dorsoventrally flattened and have a similar cross section.

The penes of *A. angelica*. *A. lugubris*, and *A. tyrianthina* appear identical in shape (Figure 41) and show a certain amount of overlap in size (Table 3).

The penis of *A. brevidentata* is usually longer than those above and has a recurved tip that makes up more than one sixth of its length (Figure 42).

The penis of *Thais emarginata* is comparatively short and broad with a small anterior facing appendage through which the spermatic duct runs (Figure 43).

Male Ducts

The genital ducts, both male and female, have been described using the terminology of Fretter (1941).

The male genital ducts of *Acanthina angelica*, *A. lugubris*, *A. brevidentata*, and *Thais emarginata* were studied. The only male *A. tyrinathina* available for study proved to be too badly decomposed for useful observations.

Since all of the species observed had very similar male genital ducts, I shall describe the ducts of *A. angelica* and not mention the others except where they differ in some respect from *A. angelica*.

In *A. angelica*, the testes line the columellar side of the visceral mass, and from them an uncoiled vas deferens passes anteriad to the posterior margin of the prostate gland which lies along the right border of the mantle cavity. Before reaching the prostate,

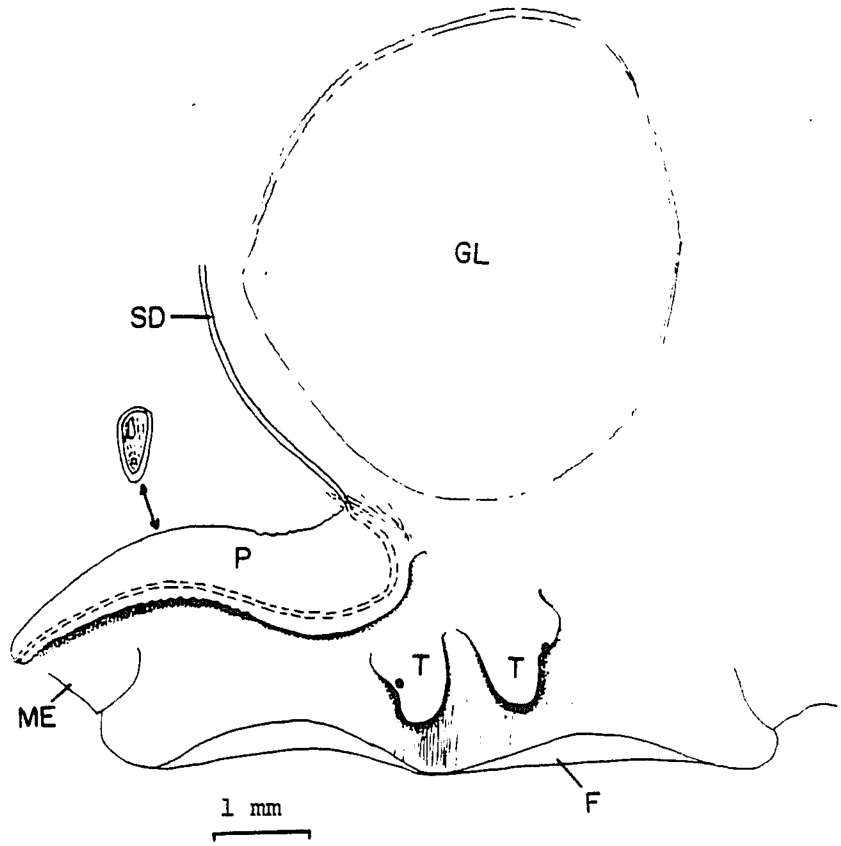


Figure 41. Head of male Acanthina angelica (A. lugubris and A. tyrianthina are similar).

Table 3. Penis size, animal size and shell length in individuals of species used in this study (mm).

Species	Penis Length	Animal Length	Shell Length	Ratio of Penis to Animal
angelica	3.1	21.8	--	0.14
	4.3	29.0	--	0.15
	4.3	31.7	--	0.14
	3.2	17.9	29.1	0.18
	3.9	26.5	--	0.15
lugubris	5.2	37.7	25.4	0.14
	3.6	31.3	22.3	0.12
	4.3	26.4	21.1	0.16
	3.9	29.9	--	0.13
	4.5	28.6	21.6	0.16
tyrianthina	3.9	21.0*	22.3	0.19

*This snail was badly decomposed. Therefore, the overall length was estimated from the part that could be measured.

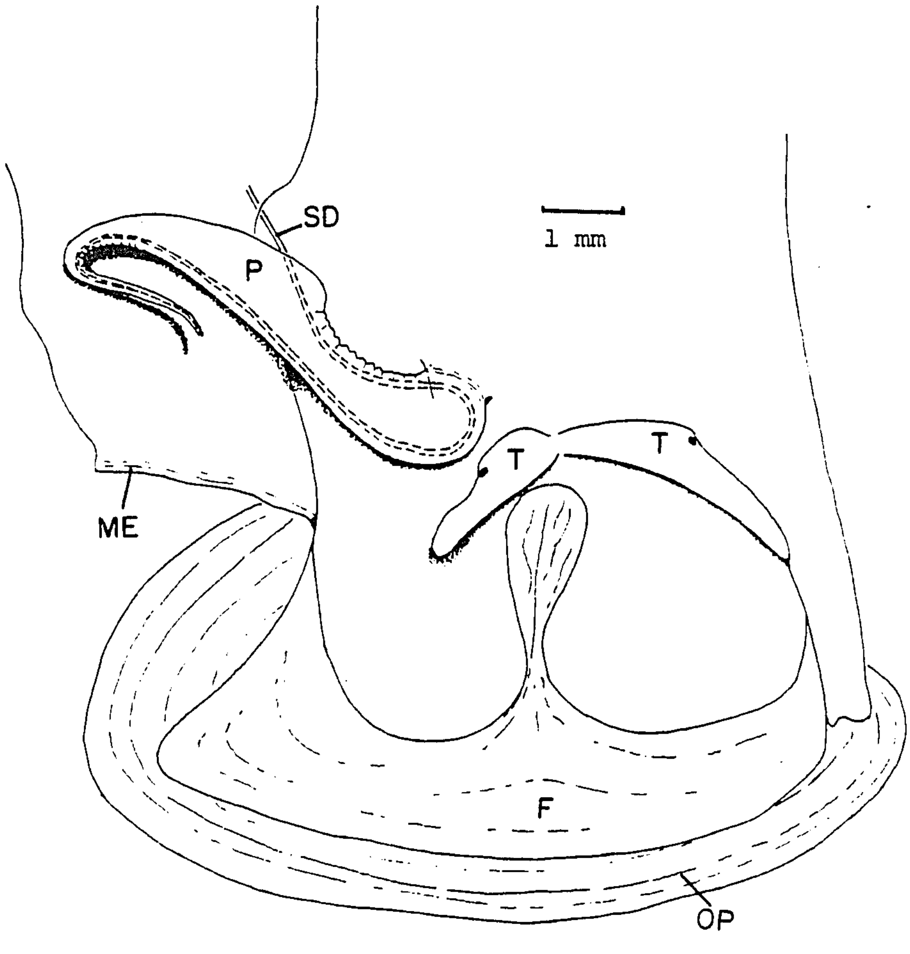


Figure 42. Head of male <u>Acanthina</u> <u>brevidentata</u>.

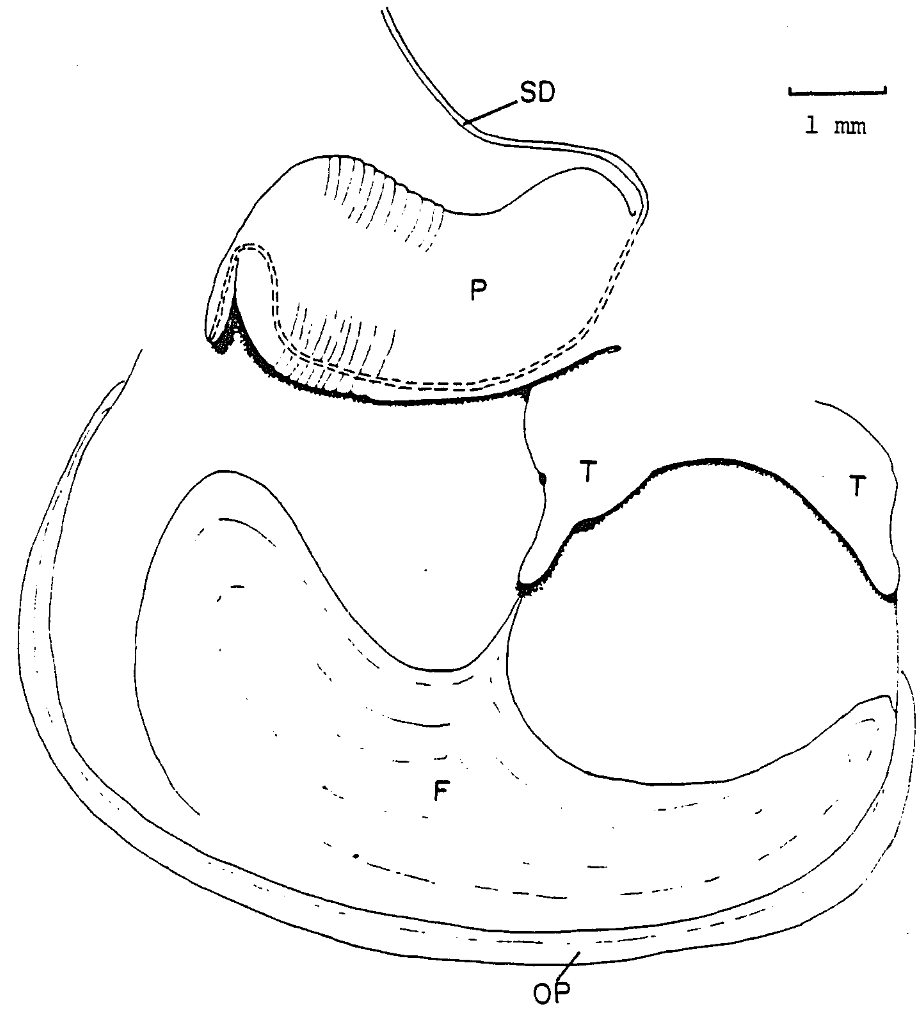


Figure 43. Head of male Thais emarginata.

the vas deferens in each species has a short connection with the pericardium, the gonopericardial duct (Figures 44-46). In each case, the walls of this vestigal duct are extremely thin and flaccid, and seem to be closed off permanently by the pressure of gravity and of the kidney surrounding them. Some or all of these may have been blocked, but if so, it was by a septum so thin that I could not explore the duct without destroying it.

The prostate glands of all species were similar in cross-section (Figure 47), but differed somewhat in shape and size. The prostates of A. angelica and A. lugubris have a very small slit shaped opening to the mantle cavity on the right side of the gland near the posterior end. This was slightly smaller in A. lugubris than in A. angelica (Figure 44). In A. brevidentata, there is a small oval opening to the mantle cavity at the posterior border of the prostate (Figure 45) appressed to the kidney. These openings would normally be tightly sealed by pressure from the mantle cavity or kidney. I could not locate an opening to the mantle cavity in the prostate gland of T. emarginata. If one is present, it is extremely small and obscure.

A duct runs from the ventral surface of the postate across the right side of the head to the base of the penis which is located behind the right tenticle. This duct runs behind the penis in A. angelica, A. lugubris, and T. emanginata and beneath it in A. brevidentata (Figures 41-43).

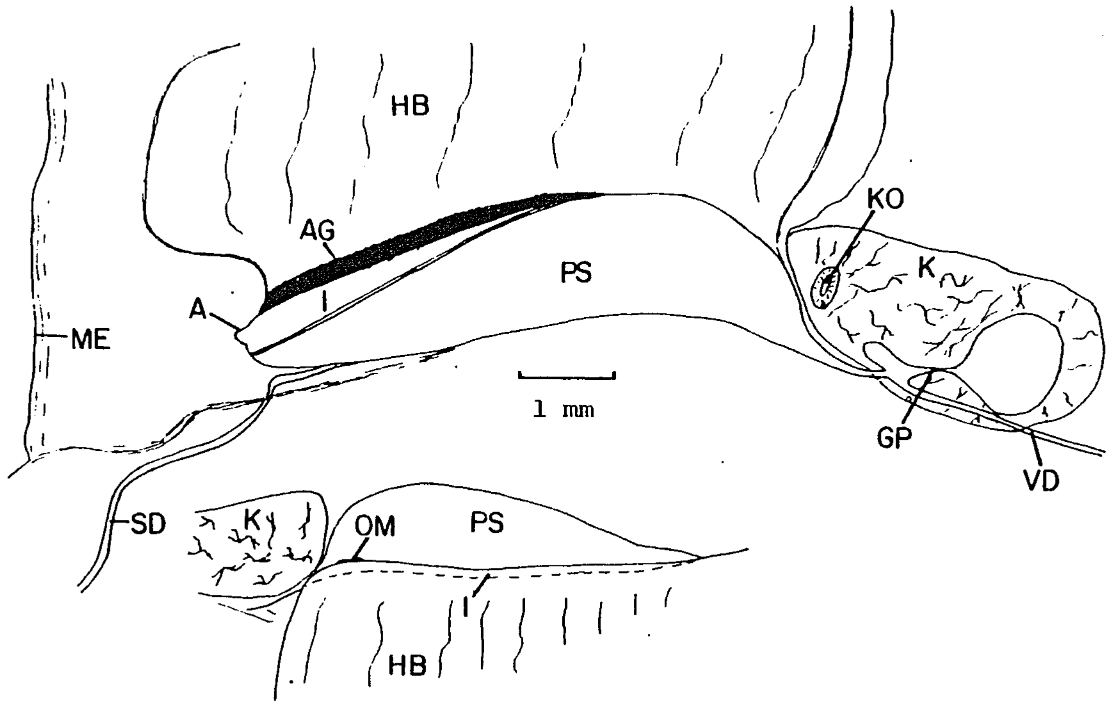


Figure 44. Male genital ducts of <u>Acanthina angelica</u>.

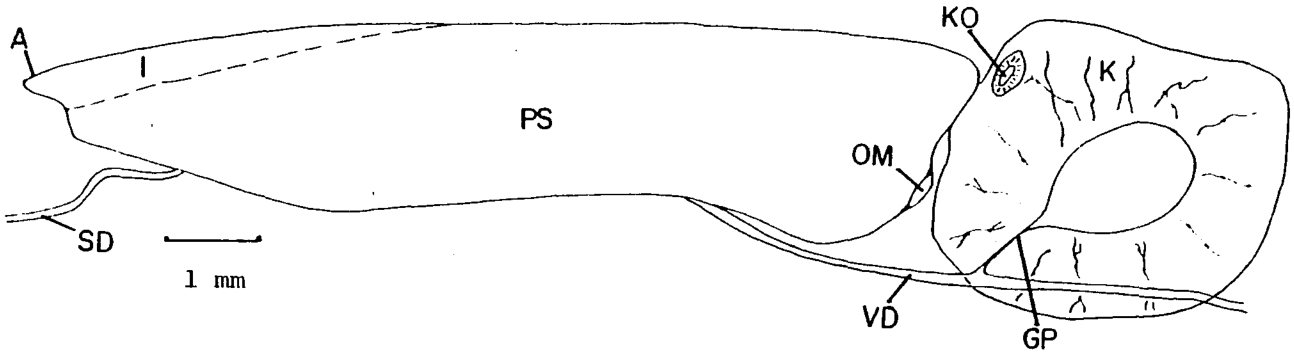


Figure 45. Male genital ducts of Acanthina brevidentata.

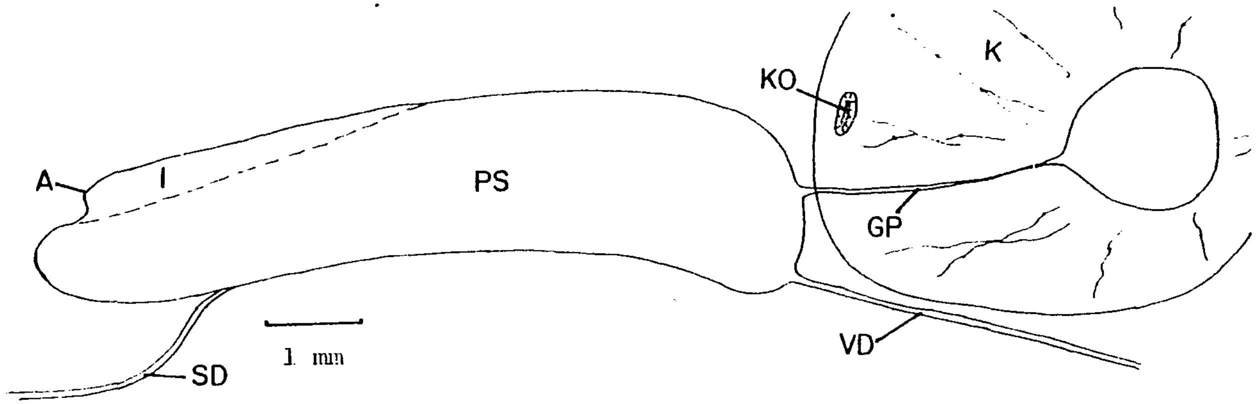


Figure 46. Male genital ducts of Thais emarginata.

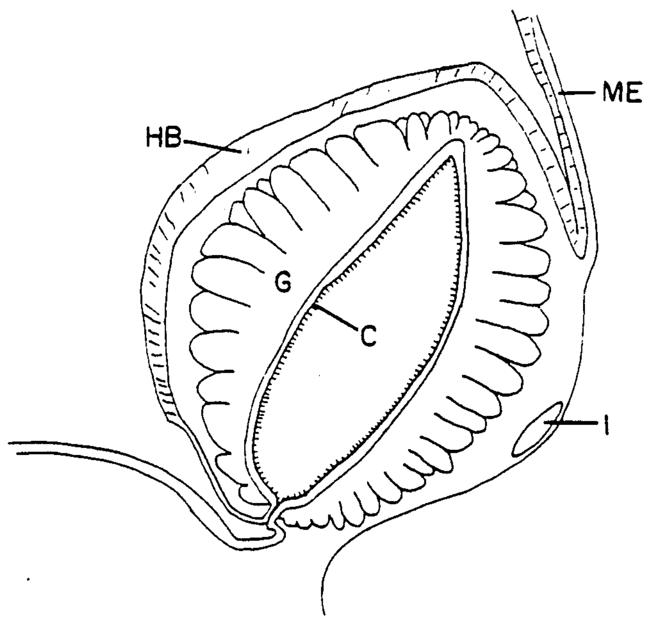


Figure 47. Cross section of typical prostate gland.

Female Ducts

The female genital ducts of Acanthina angelica, A. lugubris, A. brevidentata, and Thais emarginata were dissected out and examined. The two female A. tyrianthina from near Cabo San Lucas that I observed were too badly decomposed to yield useful information about this system.

T. emarginata, A. lugubris, and some A. angelica were apparently collected during breeding season since their vaginae were large and in each the bursa copulatrix was distended with packed sperm. Also, their ingesting glands were dense and black. A. brevidentata and some A. angelica had minute vaginae and much smaller bursae that were devoid of sperm; their ingesting glands were light brown.

The ovaries in all species examined were variable in extent, covering much of the surface of the digestive gland. The oviduct runs anteriad along the columellar surface, eventually reaching the capsule gland. Before reaching the capsule gland, the oviduct has a gonopericardial duct arising from it, and then it passes through the base of the albumen gland. The position and shape of the albumen gland, and the position of the gonopericardial duct relative to it, vary from species to species (Figures 48-50).

The female genital ducts of A. angelica and A. lugubris are very similar and will be described together. The inside diameter of the oviduct increases at its junction with the gonopericardial duct and attains its greatest diameter at its junction with the albumen gland.

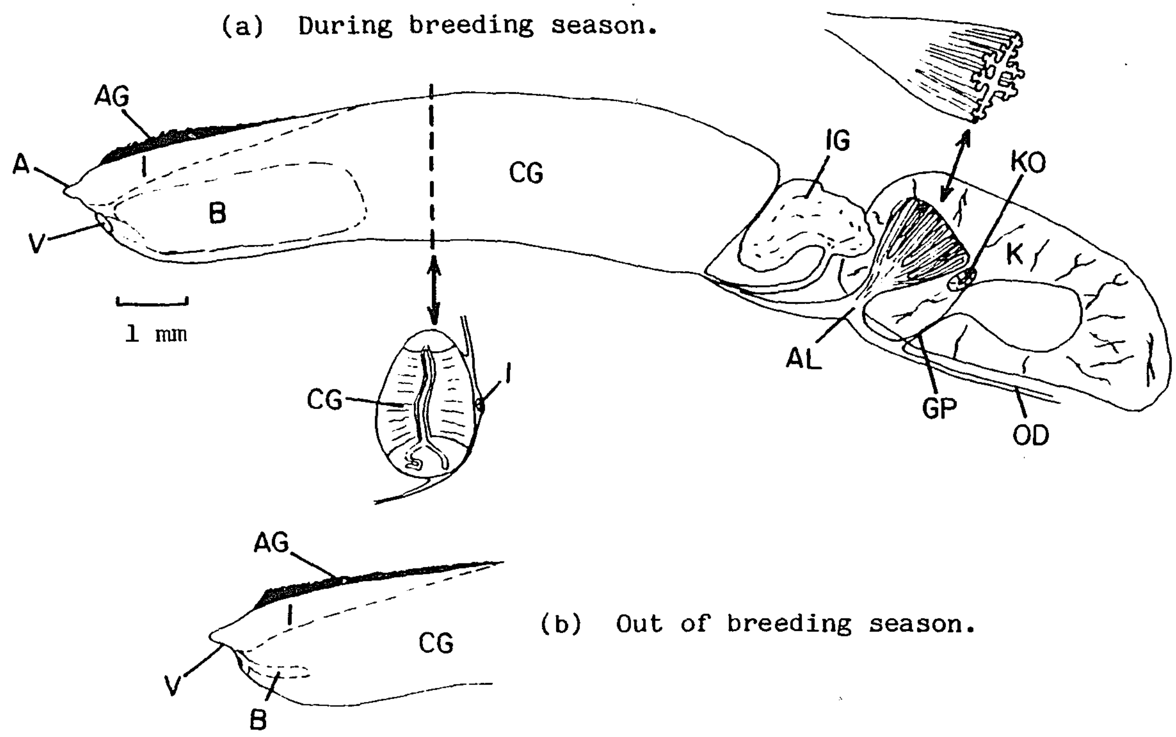


Figure 48. Female genital ducts of <u>Acanthina</u> <u>angelica</u>.

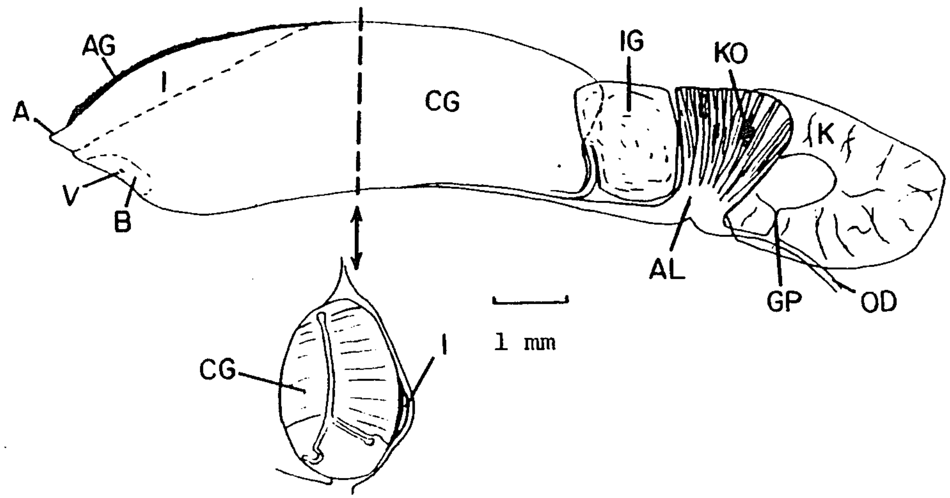


Figure 49. Female genital ducts of Acanthina brevidentata.

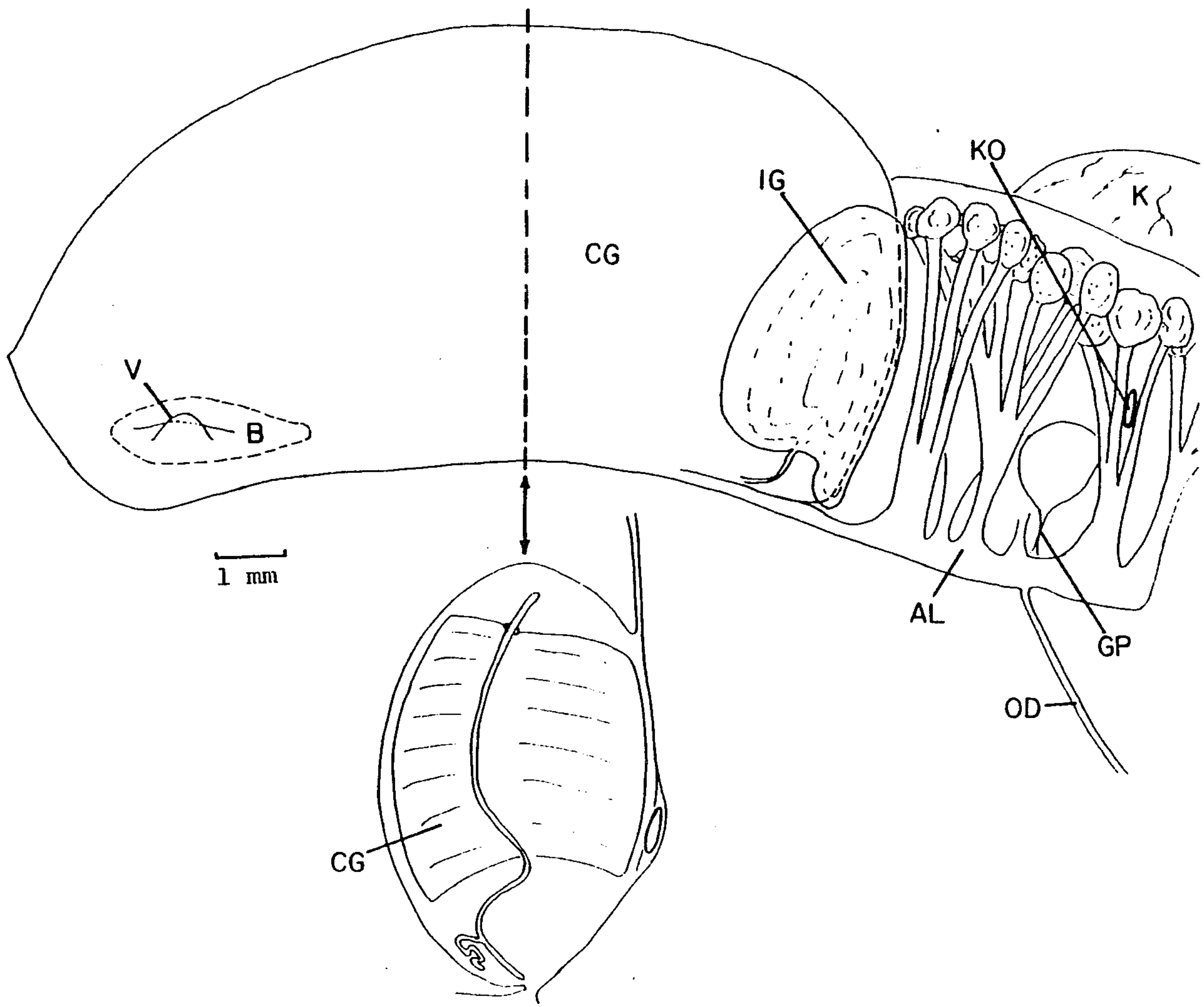


Figure 50. Female genital ducts of Thais emarginata.

the oviduct. The ingesting gland in this species, on the other hand, is extremely small forming a layer on the left-posterior of the capsule gland. The capsule gland is much larger and more massive, the vagina is on the anterior left side of the capsule gland, and the opening of the vagina forms a horizontal slit with a papilla in front of it (Figure 50). The capsule gland itself has a somewhat different cross section.

One immediate and obvious difference between the *A. angelica* group on the one hand and *A. brevidentata* and *T. emarginata* on the other, is that in the former the kidney opening has moved laterally from is position in the male and opens directly in the mantle cavity. In the latter, the kidney opening has retained its position and now forms a duct through the albumen gland (Figures 48-50).

For histology and function of both the male and female ducts in *A. angelica* see Houston (1976).

Ventral Pedal Gland

Examples of female *Acanthina angelica*, *A. lugubris*, *A. tyrianthina*, *A. brevidentata*, and *Thais emarginata* were sectioned along the sagittal plane in order to observe the ventral pedal gland of Fretter and Graham (1962) embedded in the anterior part of the foot. This gland (actually more of a muscular pouch) shapes the egg capsule and attaches it to the substrate.

Though the ventral pedal glands of *A. angelica* and *A. lugubris* appear identical (Figure 38) and both are about 24 mm deep when not in use, their egg capsules differ somewhat in shape and size, those

The albumen gland itself is composed of a series of lobes inside a sac. These lobes have an unusual shape not found in the other species (Figure 48a). The diameter of the ovaduct is reduced anteriorly until it enters the posterioventral part of the capsule gland. Along side of the oviduct at this point, another duct exits to the ingesting gland. This gland seems to be slightly more extensive in *A. angelica* than in *A. lugubris*.

The capsule gland lies along the right side of the mantle cavity just ventral to the rectum and is composed of three lobes (see cross section, Figure 48). The capsule gland of *A. lugubris* is usually slightly larger than that of *A. angelica* (typically 9 mm vs. 8 mm long) but is in no other way substantially different.

At the anterior end of the capsule gland are the bursa copulatrix, the vestibule, and the vagina. The latter is an oval shaped opening facing forward, just ventral and posterior to the anus.

The female ducts of *A. brevidentata* are similar to those described above except that the albumen gland is much larger than that of *A. lugubris* (approximately four times) and shaped differently (Figure 49), and the vaginal opening is moved slightly toward the proximal side of the anterior end of the capsule gland. Since the dissected specimen was not breeding, the bursa copulatrix was not packed with sperm, and was, therefore, much smaller than that shown for *A. lugubris*.

In *T. emarginata*, the albumen gland is a very large structure that completely covers the face of the kidney. The gonopericardial duct arises from the base of this gland opposite the entrance of of A. lugubris averaging 8.64 mm long while those of A. angelica average 6.66 mm in length (Wolfson 1970).

The ventral pedal gland of A. tyrianthina appears identical to those of A. angelica and A. lugubris. These glands are slightly posterior and to the right of the accessory boring organs in these organisms.

The ventral pedal gland of A. brevidentata is about the same size as those of the other Acanthina observed but is located slightly anterior and to the left of the accessory boring organ (Figure 39).

The ventral pedal gland of T. emarginata is in the same position with respect to the accessory boring organ as A. lugubris, but is approximately twice as large (Figure 40).

Other Sexually Determined Characteristics

An attempt was made to find a method to determine the sex of the specimens studied without killing them or breaking the shell. To this end, an attempt was made to observe the ventral pedal gland in individuals of Acanthina angelica as they crawled across a glass slide, and to find any secondary sexual characteristics such as a dichotomy in size or pigmentation that might help with sex determination. The only species that exhibited any dichotomy was Acanthina brevidentata, the female of which has irregular brown bands on its tenticles which the male lacks (Figure 51). In no species observed was size of any value in predicting the sex of an individual (Appendix B), and the only way to sex the species other than A. brevidentata would be to check for the penis using the method of Hargis (1957).

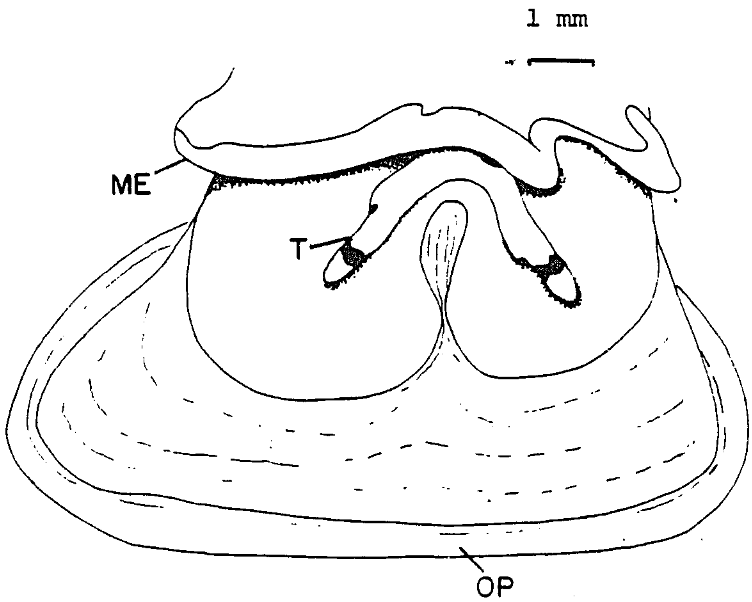


Figure 51. Head of female <u>Acanthina</u> <u>brevidentata</u>.

Nervous System

The nerve ring and associated ganglia and nerves were observed in Acanthina angelica, A. lugubris, A. tyrianthina, A. brevidentata and Thais emarginata. The nerve rings of both the males and females of each species were observed but only those of the females were drawn, and since there were no obvious differences among the nervous systems of A.angelica, A. tyrianthina and A. lugubris, only one illustration was made which represents all three species.

The only difference noticed between the nervous systems of the male and female in each species was that the nerve that travels from the right cerebral ganglion to the albumen gland in the female is replaced by one travelling from the right cerebral ganglion to the penis in the male.

A. brevidentata seems to have the most compact nervous system, and everything seemed to be moved far forward in the cephalic hemocoel. T. emarginata seemed to display an intermediate amount of cephalization, and the nervous systems of the other three species of Acanthina seemed least cephalized (Figures 52-54).

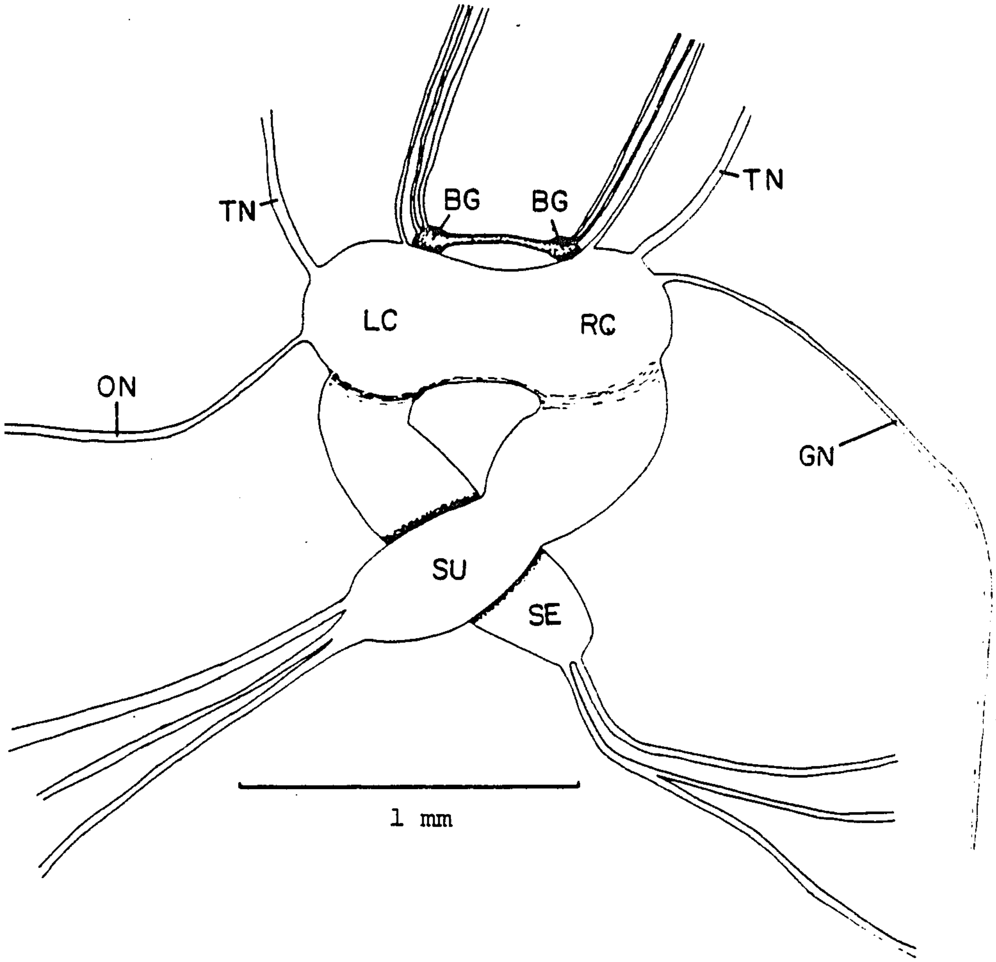


Figure 52. Nervous system of female Acanthina lugubris.

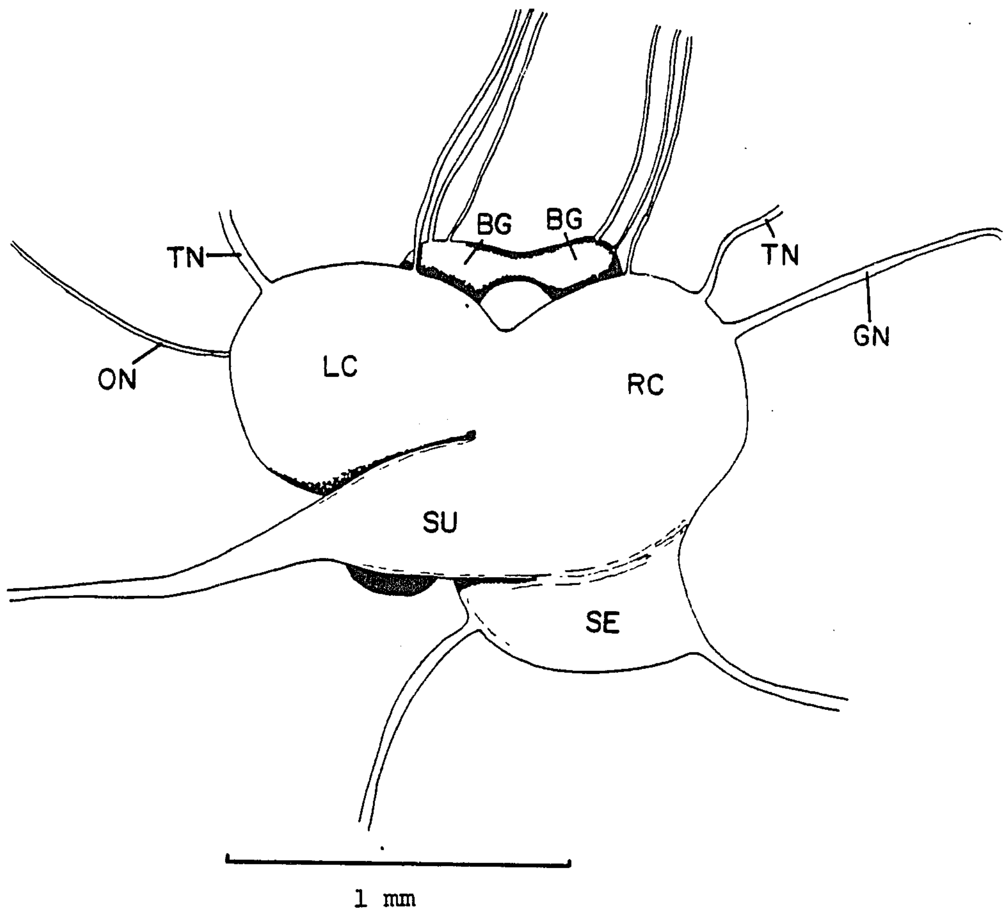


Figure 53. Nervous system of female Acanthina brevidentata.

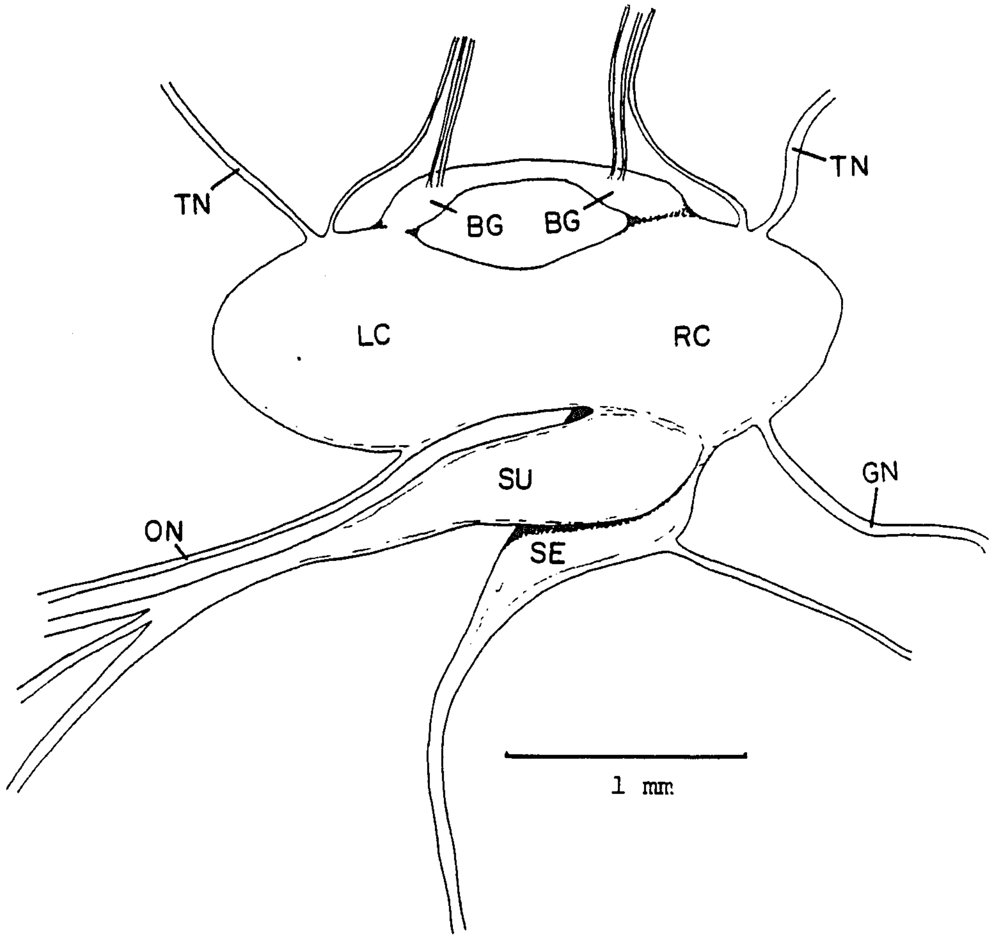


Figure 54. Nervous system of female Thais emarginata.

DISCUSSION

Physical Characteristics

The most obvious and striking feature of the _Acanthina_ shell is the spine that it bears on the outer lip; in fact this is the one characteristic that has been used to separate it from other thaids. There has been much study and debate concerning the use of this spine in feeding and workers have come to opposite conclusions while observing the same species. A case in point is that Paine (1966) observed that _Acanthina angelica_ at Puerto Peñasco, Mexico does not place its spine between the scutes of barnacles, but invariably drills them. Yensen (1979), on the other hand, has observed that _A. angelica_ in the same location almost invariably wedges open barnacles scutes with its spine, drilling only on rare occasion. Having observed this species extensively at Puerto Peñasco, I agree with Yensen, but do not feel that this feeding method can, necessarily, be attributed to this species or other species in this genus at other locations, or under different conditions.

All _Acanthina_ observed in this study have been shown to specialize in the eating of barnacles, but all occasionally drill molluscs for food (Hemingway 1975a and b, Paine 1966, Yensen 1979). The only exception to this is _A. tyrianthina_ which has not yet been observed feeding, but which appears so closely related to _A. lugubris_ and _A. angelica_, that its diet is probably similar.

A number of workers feel that the shell is not the best characteristic to use as the basis for taxonomic determinations. For instance, Cernohorsky (1969) found that taxonomic relationships deduced from the shape of the radula often conflict with those deduced from the shape of the shell, and felt that those based on the radula were usually more accurate in muricids and thaids. He has also described a snail using the radula and the penis (Cernohorsky 1966). Wu (1973) has said that radulae and reproductive systems are important taxonomically, but the digestive system is not, since it is more subject to environmental factors and diet.

In the radulae of rachiglossans, each row consists of three teeth, a central rachidian tooth which is used primarily for drilling, and the marginals, which, pulled back during drilling, are later brought forward in order to slice up the prey (Carriker 1943, Carriker et al. 1974).

The rachidian tooth of *Acanthina brevidentata* is vastly different from those of the other three *Acanthina* observed (Figures 20-23). Wu (1973) refers to the *brevidentata* type of three-cusped tooth as a *Murex* type and makes a strong distinction between it and the five-cusped *Thais* type of the other three *Acanthinas*. While the marginal teeth of *A. brevidentata* match those of the other *Acanthina* in shape, they are much longer compared to the width of the rachidian than are the marginals of the others. These factors would seem to indicate that the relationship between *A. brevidentata* and the other three *Acanthina* is not very close.

To recount the points of difference between A. brevidentata on the one hand, and A. lugubris, A. tyrianthina, and A. angelina on the other, we can go down the list of things discussed in the Results section of this thesis: 1) the shell of A. brevidentata has a posterior notch, which the other lack, 2) the radula of A. brevidentata is vastly different from those of the other species, 3) the digestive tract is also different from those of the other species, and 4) the reproductive system differs from those of the other species, and though a different penis shape and location of the vagina would be expected in order to produce a mechanical barrier in order to avoid wasting gametes, and the layout is basically the same, the large size of the albumen gland, and the fact that the kidney opening passes through it, in my judgment appear to be major distinctions.

Gene Flow

Penis shape and size as well as the shape and size of the vaginal opening seem adequate to prevent gene flow between Acanthina lugubris and Thais emarginata and between Acanthina angelica and A. brevidentata if they are or should become symptatric. But what about flow between Acanthina lugubris and A. tyrianthina where their territories abut one another, and A. tyrianthina and A. angelica where their boundaries meet?

There is admittedly a certain amount of difference between these snails, but many of the characteristics including the size and shape of the genitalia overlap considerably. By observing shells collected from areas near the boundaries, one finds that they are usually intermediate in characteristics between the shells on either side.

During the Quarternary, there was a southward displacement of isotherms, making the water temperature at Magdalena Bay approximately the same as the temperature that now occurs at Cedros Island (Jordan 1924). I conjecture that the snail that has evolved into these three groups was living at that time around the tip of Baja California and part way up both coasts; in fact Jordan (1924) found a shell identified as _A. lugubris_ in Quarternary deposits at Magdalena Bay. As the isotherms moved north to their present position, some snails moved northward on each coast evolving into the _A. lugubris_ and _A. angelica_ types. As the territories of these two groups moved northward, a remnant, left behind, without competition from other warm-adapted snails that would have migrated northward if there had been a southward connection to land, adapted to the warmer conditions, becoming what is now known as _A. tyrianthina_.

At present, the water temperatures in San Diego, at the northern end of the range of _A. lugubris_ vary between 10.6 and 22.2°C, those in Puerto Penasco near the northern end of the range of _A. angelica_ vary between 11.1 and 32.8°C, and the water temperature range at La Paz, within the range of _A. tyrianthina_, varies from 16.7 to 33.3°C (U.S. Coast and Geodetic Survey 1952). Note that the low temperature for _A. angelica_ and _A. lugubris_ is very similar. During this time, _A. angelica_ breeds and lays eggs (Turk 1981) and _A. lugubris_ collected in December, when the water there was near its coldest, proved to have their bursae packed with sperm indicating that they were breeding also.

Wolfson (1970) noted differences in mating behavior between *A. angelica* and *A. lugubris*. She said that she had observed two female *A. lugubris* depositing eggs in a cliff crevice, quite unlike the large breeding aggregations of *A. angelica*. It is hoped that further observations will be made of breeding in *A. lugubris* so that it can be more confidently compared with what is known about *A. angelica*.

CONCLUSIONS

Because of the great similarity of three of the groups of Acanthina discussed, particularly in genital structure, I must conclude that they are all members of the same species. However, because of the differences, particularly in the shape of the shells, I feel that they exhibit subspecific differences. I therefore propose, since the name lugubris has priority, that they be known as Acanthina lugubris lugubris (Sowerby, 1822), Acanthina lugubris tyrianthina Berry, 1957, and Acanthina lugubris angelica Oldroyd, 1918. I do not consider Acanthina brevidentata (Wood, 1828) to be particularly closely related to A. lugubris and therefore consider it to be a full species. I feel that A. paucilirata, Acanthina spirata, and A. punctulata should be dissected in order to determine the relationships of all of the species in this genus.

Though Acanthina l. lugubris and Acanthina lugubris angelica are probably genetically rather far apart for subspecies, I think it likely that they would produce viable offspring if they were bred together. At any rate, as two ends of a cline of allopatric populations, they should still be considered to be members of the same species (Mayr 1969).

Making Acanthina lugubris tyrianthina a subspecies separate from Acanthina l. lugubris also presents a problem since they appear very closely related. To this end the ratio of height to width of the aperture of 36 adult A. l. tyrianthina in 7 collections from the Magdalena Bay area were compared to 30 shells in 2 collections of A. l. lugubris from the Ensenada area, and though the difference proved to be significant at the .001 level using a Student's t test, it proved to have only an 80% joint nonoverlap when tested for coefficient of difference. A 90% nonoverlap is considered to be the minimum allowable for a good subspecies (Mayr 1969). In spite of this, I feel that A. l. tyrianthina is a good subspecies based on the shape of the aperture and the steepness of the shoulder, and even though these could not be readily measured, the differences are obvious to the eye and the subspecies can be easily discriminated.

APPENDIX A

LIST OF LETTER SYMBOLS USED TO LABEL ANATOMICAL DRAWINGS IN THIS THIS

A Anal Papilla

AB Accessory Boring Organ

AES Anterior Esophagus

AG Anal Gland

AL Albumen Gland

ASD Anterior Duct of Accessory Salivary

ASG Accessory Salivary Gland

B Bursa Copulatrix

BG Buccal Ganglion

BM Buccal Mass

C Cilia

CG Capsule Gland

CH Cephalic Hemocoel

DD Duct to Digestive Gland

ET Esophageal Tensors

F Foot

G Glandular Tissue

GF Glande Framboisee

GL Gland of Leiblein

GLD Duct of Gland of Leiblein

GN Genital Nerve

GP Conopericardial Duct

HB Hypobranchial Gland

I Intestine or Rectum

IG Ingesting Gland

K Kidney

KO Kidney Opening

LC Left Cerebral Ganglion

M Mouth

ME Mantle Edge

MU Muscle

OD Oviduct

OM Opening to the Mantle Cavity

ON Osphradial Nerve

OP Operculum

P Penis

PE Peristomal Rim

PES Posterior Esophagus

PG Pedal Groove

PL Pharynx of Leiblein

PR Proboscis

APPENDIX A--Continued

PS	Prostate
RC	Right Cerebral Ganglion
RS	Radular Sac
S	Stomach
SD	Spermatic Duct
SE	Sub-Esophageal Ganglion
SG	Salivary Gland
SL	Spongy Layer
SU	Supra-Esophageal Ganglion
T	Cephalic Tentacle
TN	Tentacular Nerve
V	Vagina
VD	Vas Deferens
VP	Ventral Pedal Gladn

APPENDIX B

COLLECTION LOCATIONS, SEX, AND SHELL MEASUREMENTS OF SNAILS USED IN THIS STUDY

Subspecies	Location	Sex	Length	Width	Spine Length
angelica	Pto. Penasco*	F	31.4	20.3	4.1
		M	29.1	17.1	2.2
		F	33.6	21.3	2.8
		F	30.1	18.6	2.5
		F	30.3	20.6	3.4
		F	30.4	13.0	3.3
		M	27.5	18.3	3.0
		F	30.6	18.9	4.7
		F	32.3	17.6	4.7
		M	31.8	19.3	4.2
		M	30.4	18.5	3.6
	Estero Rosa	F	31.1	18.1	2.1
		F	26.3	11.1	1.7
		F	27.8	17.9	1.7
		F	26.2	16.2	1.8
	Punta Rosa	?	30.1	18.5	2.4
		?	32.5	20.6	1.6
		F	30.4	19.1	1.7
		F	30.7	19.8	2.0
	Libertad	M	32.4	23.8	Broken
		?	30.6	22.3	4.2
		F	30.6	19.7	2.1
		F	29.4	20.4	2.2
	Punto Kino	F	32.3	20.3	2.4
		M	28.8	18.7	1.5
		F	30.2	18.7	2.3
		F	32.1	18.3	1.9

Subspecies	Location	Sex	Length	Width	Spine Length
lugubris	Punta Banda	F	25.3	16.5	3.0
		M	25.4	18.3	3.3
		M	21.1	14.5	2.8
		F	26.7	19.4	3.2
		F	23.5	11.3	2.4
		M	24.7	12.3	3.0
		F	25.0	17.1	3.0
		F	23.4	15.5	3.6
		M	-	-	-
		F	22.4	15.2	Broken
		M	21.6	14.1	Broken
		M	22.3	15.4	2.1
		M	23.3	16.0	2.8
		F	26.3	18.5	4.7
		M	23.1	15.8	3.1
		F	23.3	16.4	2.6
tyrianthina	Cabo San Lucas	F	27.6	19.0	2.4
		F	21.0	14.1	1.5
		M	22.3	15.1	1.2
brevidentata	Venado Beach	F	30.3	21.0	2.2
	Panama	F	32.4	22.8	1.7
		F	32.0	21.2	2.0
		M	33.2	22.0	1.8
		F	31.4	20.2	1.9
		M	32.0	20.6	1.4
		F	34.9	22.0	1.6
		F	33.4	23.5	1.7
		F	29.2	19.5	2.7
		M	30.2	21.1	2.0

Dimensions in mm

*Many other snails dissected from this location were not measured.

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