COMPARATIVE ANATOMICAL STUDIES IN THE GENUS OLIVA (MOLLUSCA: GASTROPODA)

by

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ABSTRACT

Five Philippine and one Gulf of California marine snails of the genus *Oliva* were studied. Synonomy, shell description, comparative male genital anatomy, and a description of copulation are given. The basic anatomy of *Oliva miniacea* is given. A single species in this genus may show color forms in the same or in different localities. These color forms have led to much synonomy. The different species may be distinguished by the male genitalia. It is suggested that the present taxa, established and ranked on the basis of the color and form of the shell, be revised on the basis of the comparative anatomy of the male genitalia.

INTRODUCTION

The genus *Oliva* contains elongate, compact, porcellaneous, and beautifully colored and patterned shells that vary from one to five inches in length. The olives are active, living normally on sandy flats, where they burrow under the surface as the water retreats during low tides. Typically they are abundant inhabitants of tropical waters, principally of American and Indo-Pacific regions.

Most of the literature bases the classification of *Oliva* entirely on the shell structure and coloring. This is principally because European workers did the naming and they had no soft parts with which to work. Therefore, characteristics of the shells provided the only criteria. The manner in which the shell markings intergrade among the species is extraordinary. This has acted as an impediment in attempts to determine the true relative positions of the various forms and has caused confusion in the nomenclature. When the shells were first given names by the European investigators, different color variations of the same species were regarded as separate species, with the result that a considerable number of names are now synonyms.

With improved methods of preservation, the soft parts of the animals can be maintained with little distortion, and investigators can now work confidently on the soft anatomy of animals that have been preserved for long periods of time. Oliva were made available for the present study through the J. E. Norton Philippine Collection at The University of Arizona.

There have been purely anatomical works done on Oliva, and there have been works comparing the anatomy to other genera; but there has been no anatomical work comparing the different species of Oliva. It is with this thought in mind that an attempt has been made to find some characteristic of the soft parts which would serve as a basis for a more acceptable classification.

The genus Oliva contains a great number of species that are scattered throughout the world. It was considered clearly beyond the scope of this thesis project to attempt to discover for any large number of species anatomical characters that would contribute to a better understanding of their classification. Instead, the present project was limited to several species that are found in the Philippine Islands and one that is found in the Gulf of California, with the intent of determining the relative value of the various anatomical features to classification.

Because many species of molluscs within the same genus have distinctive radulae, this was an obvious place to start. It was found, however, that there was little intraspecific or interspecific variation in the radulae. This is confirmed by Burch and Burch (1967). Therefore other structures and systems were investigated.

The central nervous system of Oliva has been previously studied and reported on by Bouvier (1887: 309-312), Haller (1905: 653-658), Küttler (1913: 517-523), and Marcus and Marcus (1959: 118). After examining the nerve rings, however, no morphological differences to distinguish the several species could be found.

The alimentary tract has been studied previously by Küttler (1913: 494-511) and Marcus and Marcus (1959: 123-128). Some slight differences, especially in the anterior regions, were found in the several species examined in the present study; but the same structure or structures did not prove to be sufficiently different or stable to be of dependable value in taxonomy. It is possible that these differences may ultimately prove to be of some value in the species which are more difficult to distinguish by conventional means.

The kidneys of the specimens of Oliva examined were found to be less than adequately preserved in most cases to be used for this comparative study. However, those that were especially well preserved showed no distinctive structural differences that might be used as a means of classifying the different species of Oliva. Some previous works on the kidney of this genus have been done by Perrier (1889: 246-249), Haller (1905: 661), Küttler (1913: 530-540), and Marcus and Marcus (1959: 144-147).

In order to study the circulatory system effectively and to follow the blood vessels and sinuses, it would be necessary to have well fixed specimens so that the animals could be sectioned in toto. The rather considerable variation among individuals would probably make this system unfeasible for taxonomic purposes. The hearts and pericardial cavities of the different species are large and easy to investigate. Upon examination, however, there were found very few differences, and none that could be used as criteria for the classification of Oliva.

In studying the genitalia, it was found in previous studies by Schmidt (1885), Von Ihering (1892), Lang (1900), C.B. Boettger (1939), Mead (1950), and Miller (1967) that there is value in the use of comparative genital anatomy of other molluscan groups as a basis for taxonomy. The female genitalia of the species examined in this present study exhibited relatively little variation in structure; and therefore they proved to be of little taxonomic value in determining the different species of Oliva. The most striking differences were found to occur in the male genitalia. All males have the same basic pattern in their reproductive structures; but these structures vary in size, shape and appearance. This is particularly true of the penis and the vas deferens. The seminal vesicle shows some variation but it tends, along with the testis, to vary in shape and size with the seasons of the year, and therefore it is of no taxonomic value. The shape of the penis varies strikingly among the species and has a negligible amount of variance within a species. It is this difference in shape, along with the differences of the appearance of the vas deferens, that may be of some value in the taxonomy of this genus.

It is not the mission of this study to determine the taxonomic validity of each species, but rather to determine the degree in which the anatomy might prove to be of taxonomic value. Therefore only a synopsis of the synonymy of each species is given.

All anatomical directions are given in terms of the specimen; that is, "to the left" means "to the animal's left."

METHODS AND MATERIALS

All the species except *Oliva spicata* were collected in various localities in the Philippine Islands. The shells were collected by divers at a depth of five to thirty feet of water. *Oliva spicata* was collected at Cholla Bay, Sonora, Mexico. The Mexican snails were collected at low tide when the animals were left stranded in the mud and sand flats. Immediately after collection, the Philippine specimens were placed in 70 per cent ethyl alcohol. The alcohol was reportedly changed a second time within a week, a third time six months later, and then changed a final time a year after collection. Apparently there must have been occasional overcrowding because some of the specimens were found to be inadequately preserved.

Whenever possible, the animals were pulled gently from their shells; however, with this treatment the visceral mass had a tendency to break off. When the animal could not be removed in this manner, the shell was broken as carefully as possible by tapping with a hammer. When done properly this method allowed the animals to be removed without damage to the tissues.

Radulae were obtained from the animals by dissolving the tissues of the proboscis in warm 25 per cent sodium hydroxide. The radulae were then washed, dehydrated and mounted on slides in permount.

Sections of the male reproductive systems were taken at 10 micra and were stained with Mayer's hematoxylin and eosin. Spermatophores were found by making longitudinal cuts in the spermiduct and staining the exposed spermatophores with basic fuchsin. The spermiduct is a muscular duct in the penis that forms and transports the spermatophores.

Dissections were made under a dissecting microscope. The mantle was cut transversely anteriad to the kidney and was folded to the animal's left side. This exposed many parts of the digestive, reproductive and circulatory systems. The columellar surface of the visceral mass was exposed by cutting the connective tissue that connects the mass to the muscular portion of the body, and then unwinding the visceral whorls. Incisions were made with fine scissors and the overlying tissues were carefully teased away with fine forceps to expose the underlying structures.

Each species of *Oliva* investigated in this study is discussed with regards to its present classification, synonyms, and color forms. Because much of the anatomy in the genus was found to be fairly uniform, a general anatomical description has been given for only *Oliva miniacea*.

A description of the basic male reproductive system is given in order to define and describe the structures. The male genital anatomy of each of the species studied is then reported so that comparisons can be made. From the comparisons of the male genital anatomy, it can be seen that each species has its own form that distinguishes it from other species. The basic female anatomy is discussed. This is followed by a description of how copulation probably occurs. Since copulation has not been observed in the present study, it has had to be described by relating the functions of the structures of the two sexes.

TAXONOMY

Linnaeus (1758) divided the shells known as Olvidae into three species: *Voluta oliva*, *V. porphyria*, and *V. ispidula*. Gmelin (1791) added a few new species; and Lamarck (1811) extended the number to 62. Dillwyn (1817) reduced it to 18. Duclos (1835) figured 84 species he considered that 22 of the species which Lamarck described as distinct were only varieties of the other species. Reeve (1850) published figures of 100 species. In 1858, J. E. Gray published "An attempt to distribute the species of *Oliva* into natural groups," but this work did not meet with general acceptance by other authors. In 1870-1871, F. P. Marrat published his monograph of the Genus *Oliva* in which he figured 220 species (in Sowerby 1870-71). In 1883 George W. Tryon published volume V of the "Manual of Conchology," which contains his monograph of the Olividae. Tryon grouped related species and reduced the number of species to 55. More recently Johnson (1910-1911, 1915, 1928), Dautzenberg (1927), Dodge (1955), Olsson and Dance (1966), and Burch and Burch (1967) have published on this family.

The taxonomy of *Oliva* is as follows:

Phylum Mollusca

Class Gastropoda

Subclass Prosobranchia

Order Monotocardia

Suborder Stenoglossa

Superfamily Buccinacea

Family Olividae

Genus *Oliva*

SYNONYMS AND SHELL DESCRIPTION

Oliva miniacea (Röding, 1798)

The name *O. erythrostoma* (Meuschen, 1787: 376) was and is mistakenly referred to *O. miniacea*. The work of Meuschen was declared invalid by the International Commission on Zoological Nomenclature.

Burch and Burch (1967) believe that *O. sericea* (Röding, 1798) and *O. tremulina* (Lamarck, 1811) are species distinct from *O. miniacea*. Tryon (1883), however, called *O. tremulina* and *O. erythrostoma* varieties of *O. irisans*. Johnson (1910) believed *O. sericea* and *O. tremulina* to be forms of *O. miniacea*. Webb (1951) calls *O. sericea* and *O. erythrostoma* separate species, and *O. tremulina* a subspecies of *O. erythrostoma*.

Many authors have published illustrations of *O. miniacea*, for example Habe (1966), Kira (1962), and Webb (1951). A great deal of literature, even today, refers to *O. miniacea* as *O. erythrostoma*. Some authors use the name *O. porphyretica* (Martini, 1773), but this is invalid because the name was not established according to the international rules.

O. miniacea is composed of shells ornamented with wavy longitudinal lines and two more or less interrupted transverse bands, one encircling the top and one at the center of the last whorl. All, however, are yellow-white, and streaked and banded with blue, green or purple. The aperture is always a deep orange. Mature shells measure 50-75 mm. in length.

There are several color forms that have been given specific names, but these are merely synonyms of *O. miniacea*. It might be found, however, that some of these color forms are actually true species. Some of the potential species, now called color forms, are *O. efasciata* (Dautzenberg, 1927) which is a form that supposedly differs only by not having bands. It is reportedly common in many localities. *O. johnsoni* (Higgins, 1919) is dark brown to black in color with large white markings. This is common in many localities and is found in colonies that merge into other color forms. *O. marrati* (Johnson, 1910) is entirely dark brown to black and is found in many localities. *O. saturata* (Dautzenberg, 1927) is described as having darker longitudinal lines and having the bands colored in such a manner that the shell has a somber aspect. *O. sylvia* (Duclos, 1835) is orange-yellow with irregular lines, and has two bands of brown. This color form is usually smaller than the other color forms.

These shells show such great variation that it is easy to understand why there is much confusion concerning what is a variety and what is a species in this group of shells.

Oliva acuminata Lamarck, 1811

Oliva acuminata does not have the color variation that many olive species have. It has a fawn, ash-gray or yellowish background with irregularly marked zigzags and maculations. Sometimes the markings are faint or lacking. The suture sometimes has fasciculations which may be reduced to a row of spots. More frequently the sutures are without markings. The fasciole and fasciolar band are yellowish or fawn color and sometimes have faint, close, orange-red striations. The columella and the interior of the aperture are white with the lip-border maculated with chestnut. The length of the mature shell varies from 35 mm. to 75 mm., the body of the shell being slender and the spire high.

There are several possible synonyms listed by Tryon (1883) for this species: O. subulata Lamarck, O. annotata Marrat, O. carito Marrat, and O. barthelemyi Ducros.

Oliva mustellina Lamarck, 1811

The shell of Oliva mustellina is a pale yellow, covered with light chestnut figurations. The interior of the aperture is varying shades of violet. The shell is cylindrical, the aperture long and narrow, and the spire short and sharply pointed. The length of the mature shell is 25-33 mm. The shell is most easily distinguished by its cylindrical form, light coloring, and violet interior, However, many specimens have been assigned to this species in error, especially specimens of O. elegans. Variation in this species and several related species should be taken into consideration when trying to identify this group of shells.

A probable synonym of this species is O. pacifica Marrat. Weinkauff(1878) accepted this as a species and placed O. arctata Marrat (1867) as its synonym. Tomlin (1953) believed O. arctata to be a young specimen of O. pacifica. Other probable synonyms are O. caroliniana Duclos, O. angustata Marrat, O. laevis Marrat, O. scitula Marrat, O. cana Marrat, O. neostina Marrat, and O. jayana Ducros.

Oliva reticulata Röding, 1798

Oliva reticulata is often referred to in the literature as O. sanguinolenta (Lamarck, 1811). Tryon calls this O. sanguinolenta and gives as synonyms O. evania (Duclos) and O. pintamella (Duclos), which latter he believed to be a young specimen. Webb (1951) calls O. evania and O. sanguinolenta separate species. Webb says that they both have the same markings, but O. evania is of a lighter shade that seems to be uniform.

Johnson (1910) suggested that the name Porphyria variegata Röding be accepted for the species name; but in

1928 he chose the name O. reticulata Röding on the basis that Röding and Lamarck used the same figure of Martini.

Illustrations of this species are given by Martini (1773), Duclos (1835), Weinkauff (1878), Reeve (1850), Tryon (1883), and Habe (1966). Habe uses the name O. variegata, and Tryon uses the name O. sanguinolenta.

The typical O. reticulata shell is cylindrically oblong, with a short partly sunken spire. It is cream color or light olive, and is covered with numerous minute close zigzag chocolate lines and reticulations. Often there are a subsutural and median bands. The interior of the aperture is fleshy white and the columella and fasciole are richly colored with orange-red. The length is from 45 mm. to 55 mm. in mature shells.

Burch and Burch (1967) consider O. pintamella a valid and distinct species. Weinkauff (1878) calls O. pintamella a variety of O. sanguinolenta. Burch and Burch probably should be followed until more evidence concerning this problem becomes available.

Several color forms of O. reticulata have been described. One color form that was available in this study is what is known in the literatures as "O. evania." This color form has every shell feature of O. reticulata, except that it is consistently lighter in color. Colonies of this lighter color form have been found. An examination in the present study of the anatomy of several specimens of "*O. evania*" revealed no distinguishing characters that would separate this from typical *O. reticulata*.

O. azona Dautzenberg (1927) is a color form that is distinguished by an absence of transverse bands. *O. pallida* is a color form in which the pattern covers less of the background, giving a lighter aspect to the entire coloration. *O. zigzag* Perry (1811) is a color form which has a pattern of longitudinal lines that are isolated from each other and are disposed in zigzags.

Oliva annulata Gmelin, 1791

Oliva annulata has been called *O. cruenta* (Solander), *O. emicator* Meuschen (1787), *O. gutatta* Lamarck (1811), and *O. leucophaea* Lamarck (1811). This species is known from the figure of Martini (1773) and that of Lister (1685). The shell is illustrated in works by Tryon (1883), Kira (1962), and Webb (1951).

Several color forms have been given specific names. *O. amethysina* Röding (1798) is decorated with round purple maculations that are regularly spaced on a clear flesh colored background. *O. alba* (Sowerby, 1825) is entirely white both inside and out. *O. carnicolor* (Dautzenberg, 1927) has a yellowish white background without spots and the dorsal region of the last whorl is reddish pink. *O. intricata*

(Dautzenberg, 1927) is colored with compact brownish lines with black dots sprinkled throughout; a white background appears between the meshes of the lines in the shape of little triangular gaps. O. mantichora (Duclos, 1835) has a pronounced angle at the top of the whorl. It closely resembles the coloration of O. intricata, but there are examples where the background is more open. O. nebulosa (Dautzenberg, 1927) has spots that have the character of scattered triangular blotches, and the background is of a ruddy tinge.

The shell of O. annulata is cream to flesh color, with bluish ash-colored spots of variable size, which sometimes range to chestnut color. The suture and fasciole are spotted or streaked with chocolate or violet. The interior of the aperture is red-orange. The length of the mature shells varies from 35 mm. to 55 mm.

Oliva spicata Röding, 1798

Oliva spicata is one of the most variable of the West American olives. It is common and is found from the northern end of the Gulf of California to Panama. An average mature specimen measures approximately 45 mm. in length and 23 mm. in diameter. The basic buff olive color is flecked with small irregular dots of brown. Generally the spire is fairly high.

There are many synonyms for this species: O. venulata and O. ustulata (Lamarck, 1811); O. oriola, and O. pindarina (Duclos, 1833); O. subangulata (Philippi, 1848); O. melchersi (Menka, 1851); O. intertincta (Carpenter, 1857); O. fuscata and O. violacea (Marrat in Sowerby, 1870); O. hemphilli and O. perfecta (Johnson, 1911).

Within these synonyms, it is probable that many are color forms. For example, O. cumingi has a plain colored shell with two or three wide brown bands, O. fuscata is an almost uniformly colored dark brown with v-shaped markings showing faintly through the glaze.

According to Keen (1960), all of these color forms can be found in large colonies and are therefore not worthy of sub-specific rank. She feels however, O. polpasta and O. julieta are more plausible subspecies, the former being short and rather bulbous, the latter being large and more lightly colored.

BASIC ANATOMY OF OLIVA MINIACEA

Alimentary Tract

The mouth (fig. 13, M), which is in the form of a verticle slit, occupies the tip of the pleurembolic proboscis (PR). When invaginated, the proboscis lies in the proboscis sheath (PS), a cylindrical fold of the body wall. The invaginated proboscis and its sheath lie directly posterior to the external opening. The retractor muscles of the proboscis insert on the ventral body wall. They have their origin as branching bundles on the proboscis sheath and on the basal portion of the proboscis. The mouth leads into a short tubular buccal cavity. This enlarges into the pharynx, which at the posterior end gives rise to two tubes (the radular sac and the esophagus) lying one directly over the other. The narrow tubular radular sac, which ends blindly, extends posteriorly from the buccal cavity and ventral to the esophagus. The radular ribbon is contained in the radular sac. The radula is very small, 4 mm. at its longest and 0.4 mm. wide. The rhachidian teeth are tricuspidate, comprising two lateral cusps and one median cusp. These teeth are flanked by lateral plates that are broad at the base, tapered toward the tip, and slightly curved with tips pointing medially. No consistent variation in the radulae was found among the different species examined in this study.

Extending posteriorly from the pharyngeal cavity is the esophagus, a tube lying dorsal to the radular sac.

The accessory salivary gland (ASG) is a bulbous structure that lies ventral to the paired salivary glands (SG) and the proboscis sheath (PS). The duct of the accessory salivary gland lies exterior to the proboscis sheath beside the esophagus (E), anterior aorta, and paired ducts of the paired salivary glands (SGD). It extends into the posterior proboscis and passes under the radular mass to open mid-ventrally into the buccal cavity.

The main salivary glands form a white mass surrounding the esophagus. They extend from the nerve ring to approach the posterior of the gland of Leiblein (GL). The salivary glands and the proboscis produce a rod-like bulge in the body wall posterior to the head. The salivary gland mass cannot be recognized as two definite lobes when examined macroscopically; however, two salivary gland ducts (SGD) are apparent. One leaves the gland mass dorsally and to the left of the esophagus. The other duct emanates from a lower position on the right side of the esophagus. Both travel anteriorly, flanking the esophagus along the proboscis sheath (PS). The portion of each duct that lies on the proboscis sheath is convoluted. This is not the case in all species of Oliva. These paired ducts enter the proboscis anteriorly and empty into the sides of the buccal cavity posterior to the point of entrance of the accessory gland.

The esophagus exists from the posterior end of the proboscis and curves anteriorly along the outside of the proboscis sheath along approximately three-quarters of the length of the sheath. The esophagus then turns ventro-posteriorly where it expands into the pyriform esophageal bulb (EB). This bulb is also called pyriform organ, crop, jabot, and pharynx of Leiblein. The apex of the bulb points posteriorly and ventrally because of the ventrally located nerve ring (NR) through which the esophagus passes. Posterior to the esophageal bulb, the esophagus narrows, passes through the nerve ring and curves slightly to the left side of the median axis.

Immediately behind the nerve ring, a duct leaves the esophagus and runs to the large, lobulated, brown gland of Leiblein (GL), which is a single mass lying immediately behind and dorsal to the salivary gland mass and overlapping the esophagus. The gland of Leiblein has a white portion lying on its median side and connecting with it anteriorly. The white mass extends anteriorly and surrounds a common duct. This white portion of the gland is not prominent in all species of Oliva.

The esophagus continues posteriorly immediately beneath the body wall. It curves to the left, dorsal to the bulbous arteriosus, then turns posteriorly, parallel to the bulbous arteriosus, along the edge of the pericardium; finally it turns ventrally and to the right of the animal, entering the ventral basal portion of the visceral mass.

The stomach (ST) lies in the right ventral side of the visceral mass. In most cases the stomach is not visible from surface view because it is covered by the digestive gland, kidney, and parts of the reproductive systems.

The stomach is "U" shaped with the esophagus entering medially and the intestine (I) leaving anteriorly. The stomach is an elongate white sacciform structure, bulbous at the posterior end. Musculature is not evident as some specimens have thin, collapsible stomach walls. The shape varies considerably among individuals of the same species. The time of preservation in relation to the death of the animal may have some effect on the condition of the stomach. Autolysis may have partially destroyed the stomach walls, especially in animals that had recently been feeding. The duct (D) from the digestive gland enters the stomach opposite the esophageal opening. The duct appears to be a continuation of the stomach epithelium branching into the digestive gland.

The digestive gland constitutes the greater part of the visceral mass. It interdigitates with the gonad, kidney, the stomach and parts of the reproductive systems. The visceral mass is positioned posteriorly and is coiled dextrally. The digestive gland varies in color from brownish to dark green. This color variation might be partially due to the effects of preservation. In some cases the digestive gland had minute white spots distributed over the surface. The origin of the spots was not determined in this study.

The intestine (I) leaves the stomach at a position anterior to the entrance of the esophagus. The intestine proceeds anteriorly for a few millimeters and makes an abrupt turn to the left at the edge of the digestive gland. It runs along the inner edge of the digestive gland and passes along the pericardium. The intestine continues along the digestive gland, past the kidney, to the anus (A), which is situated near the posterior edge of the free mantle. There are isolated maculations on the rectum in some individuals. It was not determined in this study whether these maculations are the anal glands or pigmentations.

Circulatory System

The heart lies within the pericardial cavity located near the left ventral posterior portion of the mantle cavity, near the anterior visceral mass. It consists of a muscular ventricle and a smaller, thin-walled auricle, attached dorso-anteriorly to the ventricle. The ventricle gives rise to an aortic trunk, dorso-posteriorly and expands into the bulbous arteriosus, which in turn divides into an anterior aorta and a posterior aorta.

The anterior aorta runs a short distance anteriorly and then dorsally, beneath the esophagus.It lies immediately under the body wall and has small branches emanating from it. It follows parallel to the esophagus to a point near the gland of Leiblein and moves laterally from the esophagus. The anterior aorta goes through a fold of the gland of Leiblein into the salivary gland and runs anteriorly through the nerve ring beside the esophagus. It continues along the esophagus, onto the proboscis sheath and into the proboscis. It finally enters anterior to the radular mass.

The posterior aorta passes posteriorly into the visceral mass, supplying the digestive gland, stomach, gonad and adjacent parts of the digestive and reproductive systems. An efferent branchial vein runs along the posterior edge of the ctenidium and continues posteriorly to the auricle. The afferent branchial vein lies on the anterior edge of the gill, opposite the osphradium.

The circulatory systems of the other species studied revealed no variations to this pattern, therefore this system was not considered to be of value in the taxonomy of this genus.

Renal Organ

The kidney is a dorso-ventrally flattened sac located above the pericardial sac, on the visceral whorl. It is posterior to the mantle cavity and continuous with the mantle, forming part of the roof of the mantle cavity. The female pallial oviducal glands lie to the right of the kidney. No organs lie to the right of the kidney in males. The renal aperture is on the ventral wall, on the side of the kidney which faces the pallial cavity.

The inside of the kidney consists of numerous brown flecked tubular projections that make a series of lamellae extending the length of the kidney.

Respiration

The ctenidium is enclosed in the mantle cavity and attached ventrally to the mantle. It is fan-shaped and consists of a succession of lamellae attached to a longitudinal septum. The afferent vein is contained within the septum. The osphradium begins at the base of the siphon and runs separately along the entire outer edge of the ctenidium. The osphradium has the appearance of a narrow, bulbous ctenidium with a septum running medially. The ctenidium and osphradium show little variation among the individuals of this species. A comparison of these structures in this study has yielded no tangible differences.

BASIC MALE GENITAL ANATOMY

The male reproductive system consists of five regions; the testis, the seminal vesicle (fig. 1, SV), a sac-like pouch (SLP), the vas deferens (VD), and the spermiduct (S). Marcus and Marcus (1959) distinguish three regions in the spermiduct: the renal spermiduct; the pallial spermiduct, which begins as a pouch-like dilation; and a penial spermiduct. Since the different regions appear to have different functions, they will be referred to by different names. The duct from the seminal vesicle to the pouch-like dilation is called the renal vas deferens (RVD), and the duct within the penis is referred to as the spermiduct (S).

The testis lies on the visceral mass. The size varies considerably, depending upon the season. In the atrophied state, the testis is found at the posterior portion of the visceral mass. In the breeding season, the testis hypertrophies anteriorly over the surface of the digestive gland, from which it is easily distinguished by color.

The seminal vesicle (SV) varies considerably within the same species and among species; however it generally retains the same basic form. It consists of a tube with variable musculature and size. It is generally spotted brown and sheathed in connective tissue. Often it consists of a finely convoluted tube that lies on the base of the digestive gland. The shape of the convolutions and the size of the convoluting duct vary considerably among different species and might possibly be useful in distinguishing species.

The renal vas deferens (RVD) is a fine duct that leads from the seminal vesicle to a pouch-like dilation. Its only function appears to be the transport of sperm to the pouch. It is small, nonmuscular, and embedded in connective tissue. There is little variation among species.

The dilated pouch (SLP) is thin walled and has little musculature. It appears to be glandular in nature and may have a prostatic function. The glandular appearing tissue completely disintegrates in paraffin sections. This may be due to preservation effects.

The vas deferens (VD) varies considerably among species, but varies little intraspecifically. The thickness, the position, and the amount of convolutions in the vas deferens are species specific. In all cases the vas deferens is very muscular, having principally circular muscles. It travels from beneath the kidney to the penis, which is situated behind the right tentacle.

The spermiduct travels from the base to the apex of the penis and has the same general structure as the vas deferens. The characteristics of the spermiduct and the penis are species specific. The spermiduct may be highly convoluted or nearly straight. It is highly muscular and could possibly act as an ejaculatory duct. The terminus of the spermiduct might extend and attenuate during copulation and function as the intromittant organ per se.

The penis (P) is an extension of the body wall that contains a spermiduct (S). Each species of this genus has a penis that is characteristic in form. It is a muscular organ with numerous circular, longitudinal, transverse, and diagonal muscles. This type of musculature would suggest a great intrinsic manipulative capacity.

Sperm can be seen lying in small masses in the vas deferens near the pouch. However they seem to coalesce into increasingly larger aggregations as they approach the penis. Packets begin to form around the aggregations of the sperm in the penis. The spermiduct has numerous glands in it, with the probable purpose of secreting and lubricating these packets. The incomplete and complete spermatophores are moved down the spermiduct through the action of cilia and the intrinsic musculature. The spermatophores do not reach full development until immediately before the terminus of the duct. Spermatophores lie close together and many may be released during a single copulation.

COMPARATIVE MALE GENITAL ANATOMY

<u>Oliva miniacea</u> (Fig. 3)

The penis (P) is dorso-ventrally flattened and is somewhat shaped like an oar. In most cases it is smooth. It lies flat in the mantle cavity with the apex placed ventrad to the kidney. The penis varies somewhat in shape, but the general form is retained. The largest variation is in the width and the curvature of the basal portion. No consistent differences were found in structure, shape, or form of the penes of individuals of the same species from different localities. A slender spermiduct (S) opens at the apex of the penis and runs basally a short distance. It then becomes larger and proceeds in convolutions that range more than half the width of the penis. It remains nearer the left side of the penis. The convolutions diminish in size and number near the base, as the penis itself diminishes in size.

The vas deferens (VD), which is about the same diameter as the spermiduct, travels a relatively straight path posteriorly from the base of the penis to a position ventrad to the kidney, generally with two rather loose convolutions near the median portion. The sharpness of the convolutions varies slightly in individuals. The vas deferens is directly under the body wall and is relatively smaller and less prominent than those of some other species. From its position beneath the kidney it turns left, then emerges from beneath the body wall and continues as an enlarged nonmuscular duct. This pouch-like duct (SLP) is attached to the kidney by connective tissue. The duct diminishes in size and goes onto the surface of the digestive gland as the renal vas deferens (RVD).

The renal vas deferens then expands into a flattened duct vermiculation that makes a single layer of convolutions running along the base of the digestive gland. This is the seminal vesicle (SV). The convolutions become numerous and the ducts smaller as they approach the testis. The testis lies at the most posterior portion of the digestive gland.

<u>Oliva acuminata</u> (Figs. 5, 11)

The penis (P) of this species is distinct and can easily be used to separate this species from other species examined in this study. It is relatively thin and generally has two slight curves. The base of the penis is posterior to the right tentacle adjacent to the invaginated proboscis. The apical portion of the penis is usually placed ventral to the kidney, generally with the apex facing to the right. The distinctive feature of the penis of this species is the numerous transverse ridges along its length. They are caused by convolutions of the large, muscular spermiduct (S).

The vas deferens (VD), which is about one-third the size of the penis, emerges from the base of the penis. It causes the body wall to project markedly outward along its path. The vas deferens meanders posteriorly to a point ventral to the kidney. It now changes direction and moves slightly anterior and to the left toward the pericardium. About 5 mm. after the turn, the size of the muscular vas deferens diminishes and it becomes the renal vas deferens (RVD), which continues as a thin delicate duct past the pericardial cavity and into the digestive gland.

The renal vas deferens then widens and becomes a flat process lying at the base of the digestive gland and forming the seminal vesicle (SV). The seminal vesicle is a nonconvoluted structure, generally subtriangular in shape, with the base of the triangle facing the terminal whorl of the visceral mass. An extension from the triangle travels to the testis, situated on the posterior edge of the visceral mass.

<u>Oliva mustellina</u> (Figs. 4, 10)

The penis (P) of this species is wide, dorso-ventrally flattened, and usually curving to the right. The apical portion tapers abruptly so that it is not much larger than the contained spermiduct. The length of the apex varies considerably among individuals, probably because of preservation effects. It is possible that the length of the apex may be regulated to facilitate copulation. The spermiduct (S) is small when compared to other species. It extends directly basal from the apex near the ventral surface of the penis and is embedded in the heavy musculature of the penis, lying near the left side. It travels in short convolutions to the base of the penis.

At the base of the penis there is an enlargement containing the numerous convolutions of the vas deferens. This enlargement is adjacent to the proboscis and lateral to the gland of Leiblein. From the enlargement, the vas deferens (VD) travels posteriorly in a meandering and a highly convoluted manner. It then straightens for a short distance and turns to the left. Underneath the kidney, it emerges from under the body wall to form an elongate pouch, held in place by connective tissue. Near the pericardial cavity, it narrows considerably to form the renal vas deferens (RVD), which travels to the inner surface of the digestive gland. The duct then expands into an elongate, highly convoluted muscular tube which runs along the base of the digestive gland. This is the seminal vesicle (SV); it terminates apically in the testis. The testis is located along the outer edge of the digestive gland.

Oliva reticulata (Figs. 6, 12)

The penis (P) of this species is slightly variable, but its general form is constant. The penis is dorso-ventrally flattened and is smooth in most cases; in some however, a series of transverse ridges can be seen rising above the surface. These ridges are caused by the convolutions of the spermiduct (S). The penis may lie straight or curve slightly to the left. With the exception of one otherwise typical specimen that had a short stumpy penis, the penes were generally long, extending more than half the length of the body. The terminal portion exhibits much variation, mainly in the amount of curvatures, from slightly curved to a full circle. The curvature is generally to the right. The spermiduct originates at the apex of the penis and meanders down the curved portion where it expands into a thick looping duct. Near the base of the penis, the spermiduct becomes smaller and travels in deep convolutions.

The vas deferens (VD) is often as large as the spermiduct. It proceeds in a nearly straight line posteriorly, without convolutions for about 6 mm., then diminishes in size and continues posteriorly to a point ventral to the kidney. It turns to the left and travels a short distance before enlarging into a pouch-like duct (SLP). This pouch continues toward the digestive gland and diminishes to a small duct, the renal vas deferens (RVD). It enters the inner basal surface of the digestive gland, traveling along the surface in convolutions, and at this point becomes larger and highly convoluted. It extends to the edge of the digestive gland. The testis stretches out apical to this, covering varying amounts of the visceral mass.

Oliva annulata (Figs. 1, 7)

The penis (P) in this species is variable in both size and position. In some animals the penis lies straight back on the long axis while in others it curves to the left, parallel to the esophagus. On the average, the penis is equivalent to half the length of the body. The penes of this species may vary in thickness, but all are dorso-ventrally flattened. They can be easily distinguished from the penes of others by the presence of a triangularly shaped muscular extension near the base. As in the other species, vascular spaces are numerous throughout the penis; and between these spaces run muscle fibers, which are in association with a thick coat of muscles beneath the outer epithelium.

A "flagellum," which varies in length, extends from the apex of the penis. The greater mass of this "flagellum" is spermiduct (S), which extends the length of the penis in a convoluted fashion. The spermiduct is largest near the center of the penis and is composed of a heavy layer of circular muscles. Near the basal portion of the penis, its diameter decreases and the convolutions increase. The size increases again at the base of the penis and the conduit leaves as the vas deferens (VD). The vas deferens is large in diameter, and approximately half of it extends above the surface of the body wall. It is extremely convoluted as it moves posteriorly to the anterior edge of the kidney. It turns sharply to the left and after a short distance it often enlarges into a nonmuscular pouch-like dilation (SLP). Near the pericardial cavity the pouch becomes the small, delicate renal vas deferens (RVD), which run onto the inner surface of the digestive gland. This duct then becomes the larger, brown, maculated, highly convoluted seminal vesicle (SV), which extends half the length of the digestive gland. A small duct emerges from the large convolutions and forms an even more highly convoluted mass that lies on the inner surface of the apical whorl of the digestive gland. A still smaller duct emerges from the fine convolutions and leads to the testis, which lies on the outer edge of the digestive gland.

<u>Oliva spicata</u> (Figs. 2, 8)

The penis (P) of this species is shaped somewhat like that of <u>O. acuminata</u>, being thin and having the apex curve to the right. However, it does not have the length nor the transverse ridges of _O. acuminata_. The penis in freshly killed specimens is white, as is most of the rest of the anatomy. The spermiduct (S) is without convolutions. It follows essentially a median path down the penis and is embedded in the musculature. Near the base of the penis the spermiduct takes a gentle wavy course. Developing and fully formed spermatophores were found in the spermiduct in freshly killed specimens of this species.

At the base of the penis the large muscular vas deferens (VD) goes into convolutions that are nearly as broad as the penis and accompany the penis nearly half its length. This portion of the vas deferens makes a considerable bulge in the body wall, since it protrudes nearly as high as the penis. It is located to the right of and posterior to the invaginated proboscis. Apical to the convoluted portion, the vas deferens continues posteriorly, but it also moves diagonally to the left making two deep loops. Near the kidney the muscular vas deferens loops to the left and forms the nonmuscular, elongated saccular portion (SLP) that travels along the edge of the kidney towards the pericardial cavity. Near the pericardial cavity this saccular portion diminishes considerably in size and forms a slender, delicate renal vas deferens (RVD) that is embedded in connective tissue. The duct penetrates the digestive gland as it enlarges to become the seminal vesicle (SV).

The seminal vesicle lies on the inside base of the digestive gland. It is almost round in shape and consists of tube which is so highly convoluted that it appears to be a lobular structure. At the end of this large convoluted duct, another fine, tightly convoluted, brown flecked duct appears. This is sheathed in connective tissue and extends to the testis. The testis occupies the most posterior portion of the digestive gland and can be recognized as a differently colored band.

BASIC FEMALE ANATOMY

The ovary lies in the posterior portion of the visceral mass in the same relative position as does the testis in the male individual. The ovarian duct is white or brown flecked and is sheathed in connective tissue. It runs from the ovary down to and parallel with the digestive gland adjacent to the intestine. The duct runs ventral to the bulbous, thin-walled bursal vesicle and enlarges into the glandular capsule gland. The bursal vesicle is filled with a granular substance, which is reported to be sperm, and an eosinophilous secretion (Marcus and Marcus 1959). The capsule gland acts as a duct leading to the small, muscular vagina. The vagina is adjacent to the rectum and is situated directly ventral to the mantle edge on the right side of the body. When the foot is extended the vagina is located in a posterior position, just inside the shell aperture.

Tissue sections of the female reproductive system were not made, and therefore some parts were difficult to distinguish. According to Marcus and Marcus (1959) the albumen and capsule glands stain differently, but are not separable in gross dissection. They were not found to be distinguishable in the present study. The receptaculum seminis, sometimes called the "ingesting gland," is reported to be located next to the albumen gland, which it enters. However in the present study it was not possible to distinguish the receptaculum seminis, in which sperm are stored and nourished.

Further work needs to be done on the female reproductive system; there is much confusion concerning its structure. Only in the reproductive tract of O. annulata are specific differences observable. This species has a prominent bursal canal that runs along the anterior surface of the bursal vesicle.

The female reproductive structures of all species examined apparently vary considerably with the season. They may be greatly atrophied or hypertrophied. With future histological studies, it may be possible to separate the species on the basis of the female reproductive system.

COPULATION

As far as can be determined, copulation has not been described in the literature for the genus Oliva. Copulation has been described, however, in the structurally similar Olivella (Marcus and Marcus, 1959; Edwards, 1968). The process is assumed to be similar in the two genera. Since the structure of a system can imply the nature of its function, it has been assumed that the anatomy of the reproductive system of Olivella suggests strongly the specific mechanism of copulation described below.

Courting procedures of Oliva are unknown. In copulation the male positions himself behind the receptive female, brings his head very close to the spire of the female and extends the penis from beneath the mantle cavity and out the shell aperture. On the basis of histological sections, it would appear that because of the exceedingly complex musculature of the penis, this structure probably extends in almost serpentine fashion. Since the base of the penis is behind the right tentacle, the full length of the penis may be extended forward. The male places the penis into the posterior section of the shell aperture of the female. The vagina is situated beneath the edge of the mantle in this section of the aperture. Marcus and Marcus (1959) found some female *Oliva* with the vagina "mightily" distended. This would suggest that a portion of the penis is inserted into the vagina. The apex of the penis is flagelliform, i.e., it is very slender and attenuated (e.g. *O. annulata*) and would easily allow this. However, the vagina is not large enough to accept a wide penis such as found in *O. miniacea*. The vagina consists of a long chamber and an orifice surrounded by a powerful circular muscle mass, which is probably a retentor muscle. A structure of this type could easily be distended and could grasp the penis, holding it in place during copulation. All the specimens examined that did not have a flagelliform penis, had the spermiduct protruding slightly from the tip. In this type of penis, it appears that either the spermiduct is evaginated and extended, or the tip of the penis is retracted to expose the spermiduct. The small, muscular, protruding spermiduct could then easily be inserted in the vagina.

Upon proper stimulation, the very muscular spermiduct doubtless acts as an ejaculatory duct, discharging the spermatophores into the seminal receptacle.

At the close of copulation, the male withdraws the penis and tucks it under the mantle cavity into the resting position where it is normally found upon dissection.

CONCLUSIONS

There is much color variation among the species of the prosobranch gastropod genus Oliva. A single species may show color forms in different localities, such as being more lightly colored in one locality than another. It has been found that some species of this genus have varying color forms in the same locality. When a great number of shells of one species are compared, it can be seen that the color forms intergrade. Many authors have given these different color forms species rank. Much synonomy has resulted and the taxonomy of the genus is therefore confused and confusing.

The different species of this genus may be distinguished by the male genitalia. No tangible differences were found in the female reproductive system. Specimens of the same species collected from different localities revealed no significant differences in the genitalia or other aspects of their anatomy; and conversely, the anatomy of specimens of any one species of Oliva was found to be consistent for all localities.

It is suggested that present taxa, established and ranked on the basis of the color and form of the shell, be revised on the basis of the comparative anatomy of the male genitalia. Further study of the female reproductive system should be made; if species differences can be found, specific identification would be reinforced. The genital anatomy and color forms of the species not discussed in this study must be described before there can be a real understanding of phylogenetic relationships and of what constitutes a species in the genus *Oliva*.

APPENDIX

NUMBER OF SPECIMENS EXAMINED AND THEIR LOCALITIES WHERE COLLECTED

LOCATION	NUMBER OF MALES	FEMALES
Oliva miniacea		
Isabella	1	0
Marintoc Movo, Masbate	0	2
Leyte	3	1
Villa Carmen, Bataan	1	1
Little Balateros Cove, Mindoro	2	1
Oliva acuminata		
Samar	13	12
Oliva mustellina		
Western Quezon	5	4
Sorsogon	3	3
Oliva reticulata		
Batangas	7	9
Bohol	8	12
Oliva annulata		
Marinduque	5	7
Cagayan	2	6
Oliva spicata		
Cholla Bay, Sonora, Mexico	6	6
Total specimens examined	56	64

Figure 1. Male Reproductive System of *Oliva annulata*.

Figure 2. Male Reproductive System of *Oliva spicata*.

Figure 3. Male Reproductive System of *Oliva miniacea*.

Figure 4. Male Reproductive System of *Oliva mustellina*.

Figure 5. Male Reproductive System of *Oliva acuminata*.

Figure 6. Male Reproductive System of *Oliva intricata*.

Explanation of Figures.

P -- penis

SLP -- sac-like pouch

SV -- seminal vesicle

VD -- vas deferens

RVD -- renal vas deferens

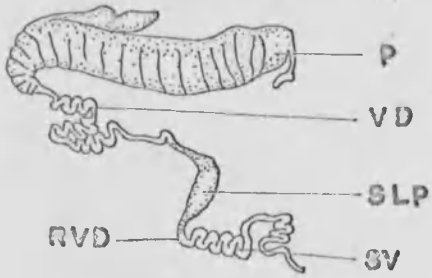

Fig. 1

— =5 mm.

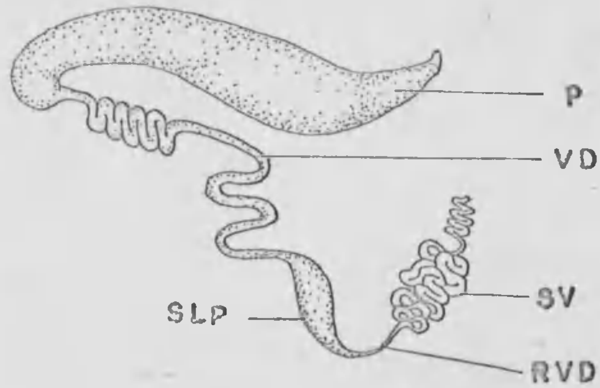

Fig. 2

— =5 mm.

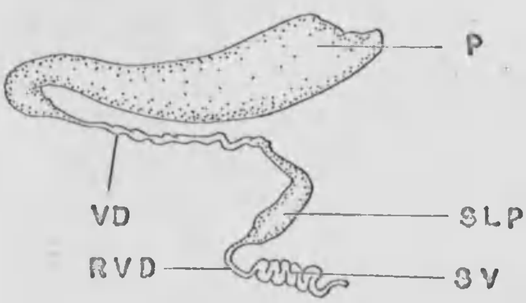

Fig. 3

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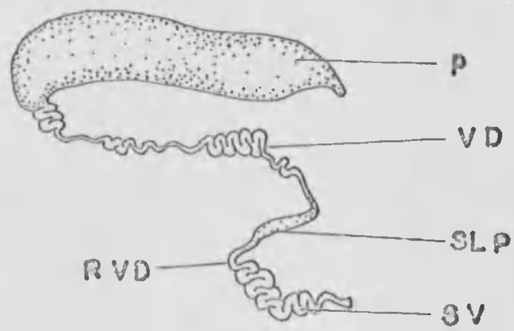

Fig. 4

— =5 mm.

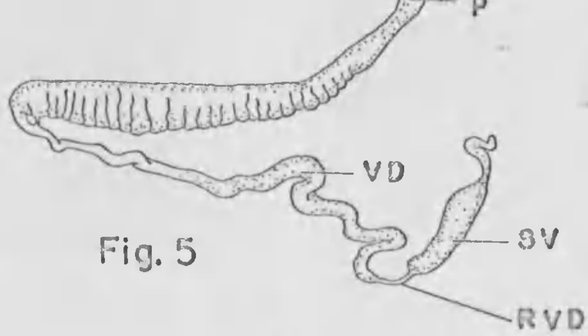

Fig. 5

— =5 mm.

Fig. 6

— =5 mm

Figure 7. Internal Penial Anatomy of _Oliva annulata_.

Figure 8. Internal Penial Anatomy of _Oliva spicata_.

Figure 9. Internal Penial Anatomy of _Oliva miniacea_.

Figure 10. Internal Penial Anatomy of _Oliva mustellina_.

Figure 11. Internal Penial Anatomy of _Oliva acuminata_.

Figure 12. Internal Penial Anatomy of _Oliva intricata_.

Explanation of Figure.

S -- spermiduct

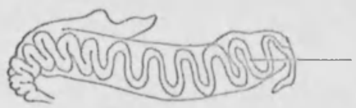

Fig. 7

—— = 5 mm.

Fig. 8

—— = 5 mm.

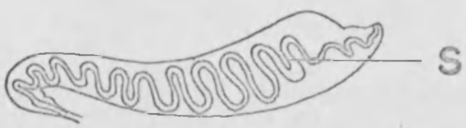

Fig. 9

—— = 5 mm.

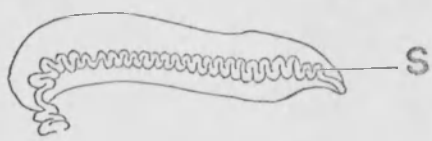

Fig. 10

—— = 5 mm.

Fig. 11

—— = 5 mm.

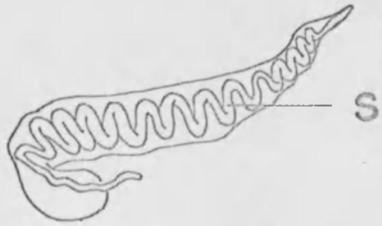

Fig. 12

—— = 5 mm.

Figure 13. Basic alimentary tract of the genus *Oliva*.

Explanation of figures.

A -- anus

ASG -- accessory salivary gland

D -- ducts of digestive gland

E -- esophagus

EB -- esophageal bulb

GL -- gland

I -- intestine

M -- mouth

NR -- nerve ring

OA -- opening of accessory salivary gland

OS -- opening of paired salivary glands

PR -- proboscis

PS -- proboscis sheath

SG -- paired salivary gland

SGD -- paired salivary gland duct

ST -- stomach

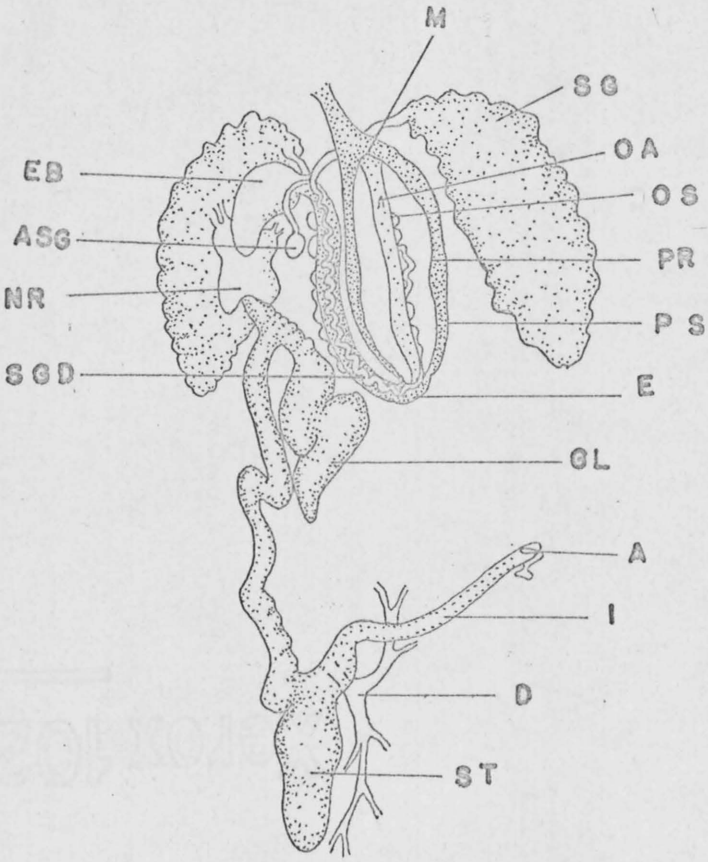

Fig. 13

Fig. 14. Color Variation Within Oliva annulata. X 1

Nearly all species of Oliva show a similar wide degree of color variation. (Photographs by Stuart Gordon and John Willard).

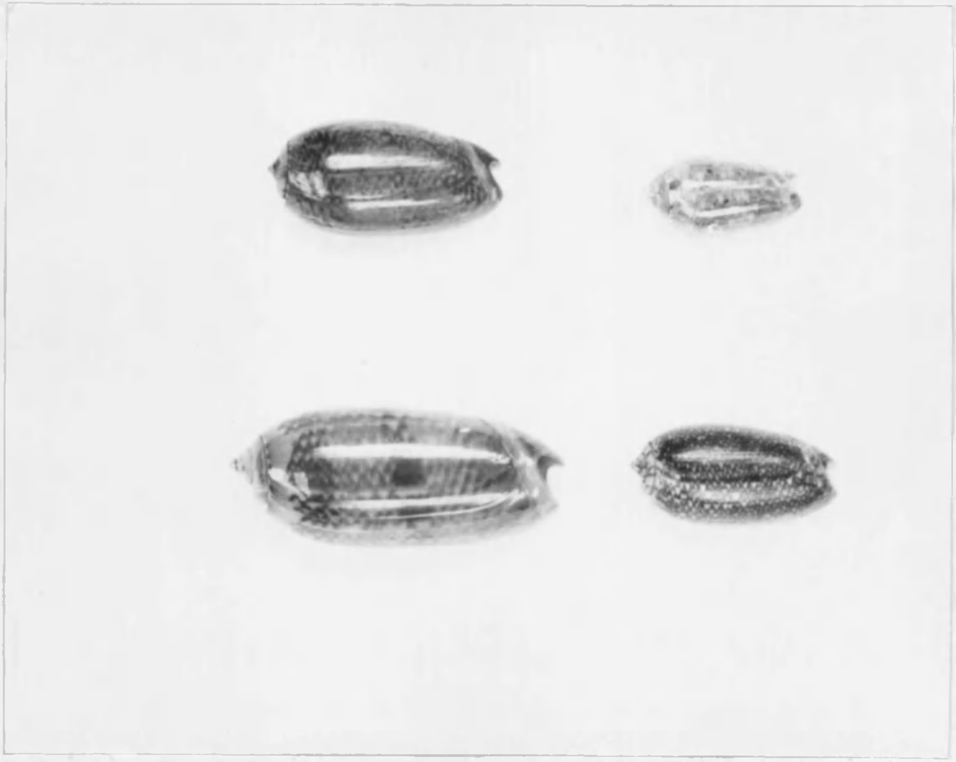

Fig. 15. Common color varieties of _Oliva_ _reticulata_, _O_. _acuminata_, _O_. _spicata_, and _O_. _mustellina_. X 7/8

Fig. 16. Common color variety of Oliva miniacea. X 7/8

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