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Oreohelix strigosa depressa (Cockerell)

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INTRODUCTION

A survey of the previous mention of this snail provides a practical background for this essentially morphological study. The literature applicable to *Oreohelix strigosa depressa* (Cockerell) in Utah may be summarized by reference to the following articles in the bibliography: directions for preparing and preserving, Chamberlin and Jones (1929); histological methods, Jones (1932); technique of sectioning the shell, Jones (1935, on tiger snail); locality records, Chamberlin and Jones (1929), Chamberlin and Berry (1929), Berry (1930), Berry (1931), Woodbury (1933), Jones (1935, on Weber Canyon mollusks), and Pilsbry (1939); comparative anatomy of genitalia with reference to taxonomy, Pilsbry (1916) (1917) (1933) and (1939); comparative histology of the supramarginal ridge, Jones (1938); and physiology (burrowing reactions), Jones (1935, Nautilus).

The preserved snails used in this article have been secured from Dry Canyon and other neighboring canyons near Salt Lake City. Specimens to be used in the study of anatomy were "pulled" and the soft parts preserved in 85% alcohol. It is estimated that about 100 specimens were used out of the four or five hundred available. Figures 7 and 8 were drawn from single specimens. In the neighborhood of forty specimens each were required for the dissections in figures 9 and 10. I have had available and studied seventy-five slides on the histology of this species, about one-half of which were made by Harry Hata, the other half by myself. These include a few shell sections, but do not include the many temporary mounts of radulae, jaws, and shell sections that were discarded after study. The work on this species has been nearly equally divided between the Zoology laboratories of Indiana University and the University of Utah. The quantitative analyses of the shell were made in the Chemical laboratories of Indiana University.

THE SHELL

The shell of *Oreohelix* is brownish to chalk white, usually the former. It may be either plain or it may possess reddish brown color bands. These latter vary from the large-sized, broad-banded "form *major*" of Pine View Lodge (Ogden Canyon) through incredible variation in the width, coloration, definiteness (sharp-line, smears, interrupted-splotching) of the color bands to the plain pattern. These variations of color patterns, together with a similar widely varying of

sculpture of transverse ribs, spiral ridges, carinae, and combinations of the preceding, still form the chief characteristics setting off such "species" as are separable. Our present knowledge of the appearance, localities, and variation of these "species" are charted adequately by Pilsbry (1939).

The genus *Oreohelix*, of which *depressa* with its various and varying "forms" is one of the most widespread "species," has long resisted satisfactory classification. W. G. Binney, in 1869, while the species were yet in the genus *Helix*, started "splitting" it. By 1885, he and various others were willing to undo most of their work and "lump" many of the divisions they had made on shell characteristics, radulae, and jaws. Pilsbry, then a young man, split off many very definite "species" on characteristics of the genitalia. Throughout a lifetime, he has seen the sharpness of many of these categories diminish as more information as to the variation within each species has increased. In 1939 he practically admits the futility of the present classification but favors "freezing" the present status, based chiefly on shell differences, rather than "lumping" and subsequently "splitting" again. Those of us who have seen the variability of this genus in the field cannot become as enthusiastic about its separation into species on any one characteristic or even on a group of several characteristics, as can casual collectors working on a few selected museum sets. It appears that regardless of the number of characteristics taken, e. g. shell, radulae, jaws, histological characteristics of mantle or foot, the variation within many of the delimited "species" exceeds the differences between the "species," which, of course, renders the classification useless. Colonies sharply delimited in one locality may show distinctive "species characteristics," while silimar colonies a few miles distant may blend the characteristics with those of quite different "species." Utah collectors are familiar with the occurrence of "*haydeni*" individuals, on the margins of an otherwise *depressa* colony. This strongly suggests mutation, but such has never been proven.

Junius Henderson and others have suggested that in *Oreohelix* we have a vast "protean" species or a network of life where in many places there are no natural boundaries between the species. I am not so certain of this. It seems to me that some of the variation is due to environment; other, to heredity. When someone has the time, the patience, and the facilities for carrying on experiments under natural conditions here in Utah, the effects of heredity and of environment, as on color bands or on shell sculpture, may be separable. In such experiments adequate "controls" under some designated "standard condition" would have to be tabulated, together with the experimental material. Records would have to be kept patiently, accurately, and continuously, which would necessitate a residence of the investigator for several years near the contrasting habitats. In a series of experiments, elimination in turn of all of the numerous factors influencing shell variation except one, would

bring out much information on that one. For example, that one factor, in successive experiments might be "alkali" dust (in Utah mostly carbonates), the inheritance of hereditary patterns, the possibility of hybridization, or the frequency of mutations. The fact that *Oreohelix*, is probably cross fertilized, even though hermaphroditic, might complicate the problem.

It seems highly desirable if possible to find a basis for separation of species in shell characteristics rather than in the soft parts, as the latter are not available in many cases in review of museum types or in paleontological research. While the lack of present information on the influence of genetic, physical, and chemical factors on the shell is to be deplored, data on the chemical composition of the shell is ready. A chemical analysis of "form *carnea*", the *depressa* stock most common in the vicinity of Salt Lake City, stands as follows:

	Per Cent
SiO_2	0.17
SO_3	0.07
Al_2O_3 and Fe_2O_3	0.35
CO_2 and volatile (organic)	46.09
MgO	.07
CaO	52.23
P_2O_5	.98
Total	99.96

Other values for the same material stand as follows:

	Per Cent
MnO_2	0.00
Organic (calculated	5.09
CO_2 (calculated)	41.00
Fe (colorimetric)	0.03
Fe_2O_3 (calculated)	0.05

More refined analyses should establish whether or not the iron in the shell is associated with the red color bands that were present in some specimens of the material.

As the above analysis shows, the shell is composed mostly of calcium carbonate in the form of aragonite. The percentage of calcium carbonate is obtained by adding the CaO to the CO_2. As the analysis was made at the same time and place as the analysis of the shell of the tiger snail (Jones, 1935, tiger snail article, p. 548 and p. 562), a comparison between the two sets of figures should involve few errors. This comparison shows but little variation in the percentage of the constituents, except for the SiO_2 which amounts to over 2% in the tiger snail, but which is an insignificant fraction of 1% in the Utah snail. The

lack of so much SiO_2 in *Oreohelix* was counterbalanced by a nearly corresponding increase in CaO. As the Indiana tiger snail has an unusually hard resistant shell, the SiO_2 figure for *Oreohelix* is probably nearer the average for SiO_2 for American large land snails in general. Only 35 shells of *Oreohelix* made approximately as much powder for analysis as did 182 shells of *Anguispira alternata* (Say), the tiger snail.

The names of the parts of the shell are indicated on figure 1, except the umbilicus, which is the opening into the center of the basal portion of the shell, and the columella, which is that twisted shelly part surrounding the umbilicus. Strange to say, the spiral shell of a snail starts as a small symmetrical plate, secreted by an embryonic shell gland. To this the mantle of the growing snail later adds unsymmetrical additions throughout life. In embryonic life these additions are smooth and regular, but in *depressa* after the young are born (in certain other land snail genera, hatched) these additions become coarser and more irregular. During growth, that part of the mantle underneath the shell is adding slightly to the thickness of the shell by secreting a nacreous lining. A series of sketches showing the growth of the shell of a Utah fresh water snail, *Stagnicola kingi*, is shown in plates II and III of Lowrance's (1934) article. No such series has been made for *depressa*.

Most of our land snails coil dextrally (clockwise when viewed apically). A sinistrally coiled specimen of *depressa* would be regarded as a freak. However, some tropical snails are known in which some individuals coil dextrally, others sinistrally. Moreover, the exact embryonic stage, in which this direction of coiling is determined, has been found. A review of the rather extensive literature giving both embryonic and genetic explanations is found in T. H. Morgan's "Experimental embryology" (1927, pp. 255-263). E. B. Wilson (1928, p. 992) also reproduces a diagram by Conklin on the development of dextrality and sinistrality in the aquatic snails, *Lymnaea* and *Physa*, both of which genera are found in Utah.

A study in *depressa* of the symmetrical apical plate (sometimes called the shell "nucleus") in uneroded spires of adult shells, shows not only the point where dextrality was established, but also exactly how much of the spire was formed before birth, also the potentialities of variation as to both transverse riblets and as to spiral ridges. Both are present on the embryonic whorls of *depressa*, but become obsolete in the adult whorls of the shell; but in *idahoensis*, the transverse ribs persist onto the adult whorls; in *haydeni*, it is the spiral ridges that persists onto the adult whorls; and in *corrugata*, both persist.

In a ground cross section of a whorl the shell of *depressa* appears as in figure 5b. At first glance the shell appears to have a middle prismatic layer and two more homogeneous layers, somewhat as in fresh water mussels. Such, however, is not the case, for if the shell is sectioned at right angles to this plane, as in figure 5c, there appears to be an upper and a lower layer that resemble the prismatic layer of mussels and a middle layer that is homogeneous or nearly so.

Flossner (Jones, 1935, tiger snail, p. 559 and figs. 8a, 8b, and 5) interprets such a condition as due to the rhomboidal form of the aragonite crystals involved. He suggests that these rhomboidal crystals, lying all in the same direction in any one layer, but at right angles to those in the next layer, produce fracture patterns, as shown above. Thus in figure 5b in the middle layer, the cut ends of the crystals produce a block-like fracture pattern, while the same layer in figure 5c, having fewer crystals fractured, appears almost homogeneous, though the comparatively few crystals disturbed may produce fine fractures that show as X-shaped markings due to the oblique ends of the rhomboidal crystals. A Flossner diagram of *depressa* would differ only in minor respects from that of the tiger snail.

The periostracum on the mature whorls of this species is often scant or absent. Whether this is due to erosion, or whether the supramarginal ridge that secretes it becomes non functional as suggested (Jones, 1937) is not definitely known. In *tooelensis* the periostracum apparently is absent. The calcareous lining, secreted by those thin parts of the mantle beneath the shell, is extremely thin in *depressa*. *Oreohelix strigosa depressa* as a shell builder is a poor "splicer." In land snails additions to the shell are not made continuously. Many times because of dryness, diurnal fluctuations, escape from enemies, mechanical vibrations, and for various other reasons, the mantle margin is retracted from the shell margin, where construction is under way, and is withdrawn far within the shell. When favorable environment, or shall we say "industrious inclination," again prevails, the mantle again moves forward to resume the unfinished job, but at this point a splice has to be made. Most land snails are very adept at making this splice inconspicuous, but *depressa* is apparently very "awkward" or "careless" as figure 5a will show. The layers are for the most part discontinuous. Such splices are one factor in the irregularity of the lines of growth on the surface.

Color bands for the most part lie in the middle calcareous layer, usually "diffusing" into upper and lower calcareous layers. Longitudinal color bands, such as occur in this species, each must be produced by a single narrow region in the outer margin of the mantle. No mantle mechanism at this point has as yet been reported. In finding such a mechanism, the histological technique would have to be varied from standard procedures which bleach out the reddish brown color in the mantle (Jones, 1935, tiger snail article, p. 553).

THE MANTLE

The mantle of this land snail consists of a thickened mantle collar, continuous centrally with the epithelium of the body, and continuous peripherally, or rather backward under the shell, with the thin shell-secreting portion of the mantle which is transparent (figs. 7 and 8). Through this portion can be seen the chief blood vessels of the pul-

monary wall. At the edge of the mantle collar, close to the pulmonary and marginal veins (figure 7) is a black spot, apparently of pigment, which has been remarkably constant in the specimens examined. Its function and histology are as yet unknown.

The general features and functioning of the mantle can best be studied in a section of the mantle collar (fig. 4). Functionally the mantle collar can be divided in two parts, the shell-secreting part and the slime-secreting part. The former consists of the supramarginal ridge, the supramarginal groove, and the epithelium under the shell, which is continuous with the thin portion of the mantle.

The periostracum is secreted by the supramarginal ridge, but is secreted into the supramarginal groove. There is a possibility (Jones, 1938, supramarginal ridge article, pp. 127-128) that under certain conditions this periostracum-secreting supramarginal ridge may involute with maturity. This would be more apt to happpen in alkaline habitats where *Oreohelix*, e. g. *tooelensis* H. and D., and the Stansbury mountain variety of *depressa*, has very little or no periostracum. Dall (1896) has already noted the effect of alkaline dust on shells of the Galapagos Islands.

The morphology of the supramarginal ridge presents certain features in *Oreohelix*, such as the division of the ridge in flap-like groups of cells, that resemble the eastern *Mesomphix* supra-marginal ridge. The ridge of *Polygyra* and *Anguispira* have no tendencies in this direction. No publication to date has done justice to the variation found in any one genus or species, or even in any one specimen, with reference to the change in shape of cross section of the supramarginal ridge in different locations around the aperture. The inner lip of the mantle collar of *Oreohelix* in cross section has the ridge reduced to a small triangular peg-like finger, which in the third dimension would appear as a sharp ridge. The outer lip approximates the ridge as shown in fig. 4.

In *Oreohelix depressa* many sections show large mucous glands apparently opening into the supramarginal groove. As there are usually several large unicellular mucus glands immediately beneath the groove, the possibility of artifacts was considered. Under certain conditions, e. g. immersion in warm water (Jones, 1935, tiger snail article, pp. 549-550) the mucus swells as a vesicle. When the cover glass is placed thereon this vesicle is flattened and overlaps neighboring structures. However, not all these cases seem to be artifacts. As mucus has nothing to do with any phase of shell secretion, but rather is a constituent of the slime, it certainly is exceptional to have it poured into the supramarginal groove. Perhaps this happens only when involution has progressed to the point where no periostracum is being secreted into the groove.

The calcareous layers of the shell are evidently secreted by the epithelium of the mantle collar behind the supramarginal ridge (fig. 4), probably back to the thin-walled part. The general principles, out-

lined and discussed by Jones (1935, tiger snail article), need not be repeated here. However to these principles should be added the following considerations: (1) While the material for the secretion of the calcium carbonate layers is traced through the mantle structures and into the shell itself, no attempt has been made to explain why the three layers crystallize out alternately at right angles to each other. If it depends on the configuration pattern of the shell material previously laid down, how far back toward the apical whorl can these three layers be traced, and how did they start? If scratches on a beaker facilitate the precipitation of crystals from a supersaturated solution, it seems only reasonable to suppose that the configuration of previously deposited shell material should affect the pattern of crystallization and the deposition of new shell material. (2) In the article cited above, resorption (perhaps of water by the mantle) as a factor that might initiate crystallization of shell material from the liquid mass is neglected. Much of the literature of resorption will be found in connection with researches on kidney tubules.

In considering the deposition of the crystalline layers of calcium carbonate which form the bulk of the shell, many other problems arise. The roughness of the surface of the shell in *depressa* has been shown to arise not only from the interruption of periostracum secretion, but also from irregularity in "beveling-on" the calcareous layers (fig. 5A) with no attempt to join corresponding layers. This roughness is not to be confused with the formation of riblets which is entirely different.

The time interval during which the mantle collar is in contact with the shell is obviously a factor in determining the size of the shell. In favorable conditions secretion and deposition proceeds at a rapid rate; in unfavorable, they are interrupted by withdrawal of the snail (including the mantle collar) into the shell. The snail can retreat just within the shell without retracting the mantle collar, but if it withdraws far within the shell the mantle collar must be detached and the secretion of the crystalline layers interrupted. If this interference lasts over a long period of time the shell is definitely smaller. Late emergence together with early hibernation in the colder regions of higher elevation would tend to "depauperize" a species. Preliminary experiments on the tiger snail (Jones, 1938, pp. 116, 118, and 119) show a tendency toward emergence and shell secretion, which is affected much by temperature, the optimal temperature being 11 degrees Centigrade for that species. Humidity is also an important factor, 100% relative humidity being optimal. Barometric pressure seems to have little effect, though unpublished calculations recently made from these data by Max Woodbury indicate a slight tendency that lessened barometric pressures tend toward lessened shell secretion. If these tendencies are finally verified and proven to be real factors, operative not only in *Anguispira*, but in other land snails, they might aid in explaining high-altitude depauperization as is found in *Oreohelix eurekensis and* associated Oreohelices

at Eureka, Utah, also the *maxima* form of Yellowstone National Park. A summary of the tendencies as they appear at present may be stated as follows: Lessened humidity of high wind-swept altitudes, the lessened barometric pressures and colder temperatures of the same, all tend to keep the animal retracted in its shell for longer periods of time, thus decreasing secretion time, hence causing the shell to be smaller.

In the formation of the calcareous layers the amount of limestone in the region must not be overlooked. *Oreohelix* in the intermountain area is widespread in range but confined in distribution to those localities where it has enough moisture, lime, and leaf mould to survive. Colonies in this region are to be found chiefly in or near limestone debris at the base of shady cliffs. In Ogden and Provo Canyons where limestone slides are common, *Oreohelix* thrives, growing very large in the moist side canyons as at Pine View. On the other hand, in Little Cottonwood Canyon near Salt Lake City, a granite canyon with very little lime, *Oreohelix* has difficulty even to exist. Thin-shelled forms, as *fragilis* from the red sandstone regions of Idaho, are evidently a result of deficient lime in those regions.

From the foregoing, it would appear that the shell differences, the outstanding, though admittedly-inadequate taxonomic characteristics, are all directly a result of mantle activity. Because of this, a study of mantle functioning at different ages, under different environmental conditions, and in different genetic strains, would seem to be of prime importance in untangling the confused systematics of this genus.

The last portion of the mantle to be considered in shell secretion is the thin-walled portion. It secretes the innermost layer (c of fig. 5), a thin mother-of-pearl lining beneath the crystalline calcareous layers. The potentialities of this portion of the mantle in secreting replacement material in shell repair has been investigated for tiger snail (Jones, 1938, experimental article, pp. 114-117), but not for *Oreohelix*.

Slime secretion results from the activity of the mantle collar and of the foot. Mantle slime is apparently for lubricating the mantle collar where the body of the snail in emerging and withdrawing has to rub against it (Jones, 1937, p. 9). Foot slime on the other hand is for laying down a mucous roadway on which the snail can travel without injury to the delicate pedal epithelium. At this point we shall consider only the mantle slime.

Mantle slime is produced by several large unicellular glands (fig. 4) which open on the front or under side of the mantle collar. Descriptions given for the tiger snail (Jones, 1935, tiger snail article, and Jones, 1937) will, in regard to the derivation of these cells from the epithelium, also hold for *Oreohelix*. However, in other ways there are differences to be noted. In *Oreohelix* there are no yellow glands to contribute the extra stickiness to the slime. There are no small mucous glands in the mantle, as they are confined to the foot. Small albuminous glands are not clearly set off in the mantle from the large

albuminous glands. Albuminous glands in *Oreohelix* have been observed to contain homongeneous and granular secretions, but not vesticulate secretion. Color glands are probably absent in *Oreohelix*, though our material has not been fixed to detect them. There is, however, color secretion by the epithelium, in the cases where the two color bands are present on the shell. Color glands, however, have nothing to do with these red stripes. Their function in tiger snail is apparently to excrete excess red pigment into the slime. My statement that the color glands are probably absent in *Oreohelix*, is based on the fact that I have never observed red flecks in the slime of *Oreohelix*. The slime of *Oreohelix* is clear, watery, and not very sticky.

The mantle collar of *Oreohelix* is characterized by many large mucous glands, large albuminous glands, and numerous neutral glands, which are interspersed with vertically-extending muscular or tendinous strands that become strikingly attenuate. They appear almost like nerves except for the abrupt bulge produced by the nucleus near the middle of their length. Neutral glands, so called because they remain unstained when acidic and basic stains are applied, may serve for the secretion of the watery element of the slime. Digitations of the mantle (fig. 4) which have the same structure as the front of the mantle on which they occur, are rather uncommon in *Oreohelix*.

Histologically mantle structure presents many problems. Occasionally there are open spaces (as in fig. 12), in which large nuclei occur with meager cytoplasmic fragments. Neutral glands in such a situation would show definite structure though unstained. Their cytoplasms would fill the spaces. These, however, present practically empty spaces. They may be regarded as large wandering cells in natural lymphatic spaces, or again they may be remnants of another type of gland, the cytoplasm of which, like fats, has been mostly dissolved by standard procedures. I favor the latter hypothesis. There are no amoeboid pigment cells in the mantle of *Oreohelix*, as are found in certain other snail mantles.

ORGANS IN SITU

No description of the organs "in situ" need supplement the figures (figs. 7 and 8). However, a study of the relations of the organs during successive events of retraction and expansion is well worth the time. The movement of the mantle is almost independent of the movement of the body and vice versa. Therefore, if an organ is attached to the mantle or mantle collar (e. g. the kidney or excretory duct) it will move with the mantle. If, however, it has an attachment to the head or the body (e. g. the digestive system) it will move with the body. At different stages of retraction and expansion this places the location of the organs with reference to one another in very different situations. In the case of those systems that are affected by extension of the body, there is ample provision for the extreme stretch, e. g. the salivary ducts

are kinked when retracted; the digestive tract is loosely looped and "gives" considerably when the oesophagus is pulled forward in the body.

Another interesting phase of retraction is the telescoping of the body and of many organs of the body. The organ or part concerned usually actually turns inside out, e. g. watch a tentacle contract. The tip can be followed from the exterior by watching the black eye spot as it shows through the skin. The tentacle turns inside out much as one would punch in the finger of a glove. There is no tentacle when it is completely retracted, only a group of tentacle-organs loose in the body cavity and an empty tentacle sheath, showing as an invagination from the outside. Similarly the penis when retracted consists of only an empty penis sac. Even the body loses much of its identity when retracted, but the foot does not. It is curiously inrolled, as one of the initial steps of retraction. No description of its involution can even approximate observation of this act in the living animal. Retraction of the snail is accomplished by means of the columellar set of muscles. Of this, the columellar muscle proper, is largest. It is all that holds the snail to the shell. After killing the snail, the hold of this muscle can be loosened by immersing shell and animal for about fifty seconds in boiling water, which permits the snail to be "pulled." Branching from the columellar muscle are the penis retractor muscle and the retractor of the buccal pouch. These act synchronously with the columellar muscle but at different rates and in different degrees, which makes observation of the results effected quite complicated.

The snails are peculiar in that the set of muscles opposing the retractors is almost lacking. Most of the expansion is accomplished by cell-turgor and body-turgor, which simply means that the pressure of fluids, chiefly of the blood, on the inside compels expansion, much as a rubber glove with the finger-stalls pushed inward, suddenly expands and rights the fingers when the glove is placed over a running faucet, the water pressure here being substituted for the turgor. Students of mammalian histology are familiar with the appearance of the spongy tissue in the corpora cavernosa and corpus spongiosum, which, when filled with blood, renders the penis erect. In the snail, not only the penis, but the tentacles, and the whole body are thus expanded by turgor. Ellis (Jones, 1932-33, p. 244), the British author, states that when the blood pressure of the snail is utilized in copulation, the tentacles have been observed to droop, due to withdrawal of blood therefrom. The study of retraction and emergence in snails is a study of retractor muscles working against blood turgor. The blood in *Oreohelix* is of the faintly bluish type which contains haemocyanin instead of haemoglobin.

The water loss of a snail during retraction can easly be measured. From where does it come,—from the foot, from the body surface, through the kidneys, from the pulmonary cavity, or from the mouths of the neutral glands? It is reasonable to suppose that if a snail

loses water in retracting, it must have to gain water in expanding. Snails usually emerge during moist intervals, in rains or in early morning dew. While I have no experimental data on *Oreohelix*, I have tried to cause an Oregon *Monadenia* to retract so many times, that it would lose so much water, that it could not raise enough internal pressure to emerge from its shell. I succeed in forcing it back into its shell somewhat permanently, but whether this was due to water loss was doubtful. It is probable that enough water can be maintained in the body and mantle of most snails, even against the retraction-pressure of the muscles, to permit of emergence at will, though the environment be dry. There is also the possibility of internal gases as well as liquids contributing to the internal pressure.

Quite on the other aspect, is a snail's tolerance to submergence. When subjected to such conditions, the Oregon *Monadenia fidelis* is very little inconvenienced, but proceeds to crawl over the bottom of the aguarium, and out at the side if possible. It takes several hours to "waterlog" a *Monadenia*, a phase of "webfoot" adaptation heretofore overlooked in the misty Wahlamet Valley. A waterlogged snail, when taken out of the water, cannot retract within its shell for some time. Waterlogged land snails if left in the water eventually drown, but in the case of *Monadenia* it may take twenty-four hours or more, if there is free air above the water. Other land snails from drier areas drown without becoming waterlogged. No such experiments have been recorded on Utah snails.

THE DIGESTIVE SYSTEM

The digestive system of *Oreohelix* (fig. 9) varies but little from that of the tiger snail (Jones, 1932-33, p. 248). The salivary glands are larger and whiter. Features shown in figure 9 need not be described. The lips, however, which are not shown, should be studied from a living specimen of medium size on a plate of glass (a microscopic slide will do). By providing a cool moist-chamber the snail may be induced to emerge from its shell and crawl on the glass. If paste or other food material has been smeared thereon, it may start eating. Examination from the underside of the glass plate with hand lens or binocular discloses the movements of the lips, the jaw, and the radula, which are surprisingly different in certain genera.

The buccal pouch of land snails contains a jaw (fig. 3) and a radula (figs. 2 and 11). The buccal pouch of many mollusks contains two jaws, e. g. the squid has two jaws that much resemble the beak of a parrot. C. C. Nutting often used the pearly *Nautilus* as an illustration, stating that its jaws were strong enough to snap off the leg of a chicken. Land snails, however, have only one jaw, which, of course cannot be used for biting, nor even much for scraping. It is situated above and in front of the radula. Hegner (p. 338) has a very useable diagram of these structures. The radula is a lingual ribbon, beset with many rows of file-

like teeth. It is moved forward and backward by radular muscles with a rasping action, over an odontophore, which in *Oreohelix* is composed of connective tissue. The jaw in the land snail is so situated, that when lowered, it presses the piece of dead leaf against the rasping organ. It has relatively little range in its movements or in its power to manipulate food material. The radula, however, is very moveable. By moving the odontophore on which it rests, the snail can thrust the radula forward almost out of the mouth. On the other hand it can be retracted into a radular sac, the lining of which in *Oreohelix* is composed of tall cells.

Radulae are easily prepared as permanent mounts. The heads of several preserved snails are cut off, care being taken to leave the radulae undisturbed in the head. These are placed in strong caustic solution for several days, after which the radulae are washed from the disintegrating tissues with water. A minimum amount of dissection with needles is preferable, as it is difficult to avoid tearing the radular ribbons. These radulae are for temporary mounts simply mounted in water under a coverglass. For permanent mounts this procedure is modified by the usual alcoholic dehydration and clearing before mounting in Canada balsam.

The teeth in the central row of the radula of *Oreohelix* (fig. 2) are symmetrical. They consist of a base and an exposed portion, which is reflected to form a cusp. Secondary cusps are not present in the central teeth of *Oreohelix* but they appear on the lateral teeth and marginal teeth as one proceeds from the center. These secondary cusps appear on the lateral side of the main cusp in *depressa*. Students desiring further study on snail dentition should familiarize themselves with the nomenclature of the cusps—ectocones, mesocones, etc. The number of teeth in a transverse row on each side of the central tooth is variable in *depressa*. There were thirty on each side in the specimen drawn (fig 2). The number, shape, and size of the radular teeth have been used in separating species, where their variation is not so excessive as to invalidate their taxonomic value.

The food of most land snails is of decaying plant material, occasionally green vegetation and green algae. Most of our land snails will become omnivorous if deprived of their natural diet. The genus *Haplotrema*, with one representative species in the central states and two or three species in the Pacific Northwest, is naturally carnivorous. The food, after being rasped into bits, is mixed with the secretion of the salivary glands (see fig. 9 for anatomy, but fig. 16h for histology, after which it proceeds through the oesophagus (the histology of which is shown in fig. 16c), into the stomach (fig. 16b). In some land snails the stomach contents are still identifiable, but after the hepatic (actually more like pancreatic) juices are emptied thereon, it disintegrates rapidly. The hepatic cells that secrete this powerful digestive juice, have numerous golden yellow granules in their cytoplasm (fig. 15), which

sometimes collect as yellow concretions in large cavities among the hepatic cells. The hepatic ducts (fig. 16A) conduct this fluid into the stomach, opening at the acute flexure of that organ (fig. 9). Demarcation between the stomach and intestine in this species is gradual and not well marked. The intestinal wall is of the same simple structure as the previous portions of the digestive tract, though the rectum wall may be thinner. The rectum in section is difficult to identify with certainty unless filled with faecal matter. In this species there has as yet been found no evidence of typhlosolar structures or of crystalline style in the intestine.

In the digestive system, the buccal pouch, the oesophagus, and part of the stomach lie freely in the coelom. The apical portion of the stomach and most of the intestine are rather loosely imbedded in or between the apical and lower lobes of the liver (figs. 7 and 8). The liver is divided into lobules, which anatomically are not evident in this species. The gonads also lie imbedded in the liver. The rectum, however, is free, but is in close relation to the wall of the transparent pulmonary cavity. Absorption evidently takes place chiefly in the intestine. The anal opening is located on the front of the mantle, close to the respiratory pore, the excretory opening, and the genital aperture. In some snails the front of the mantle is ciliated in this region.

The question may arise as to how the digestive tract becomes so intricately looped. Berry (1929, p. 105) has a diagram showing how it develops in a mollusk having a veliger larva, which *Oreohelix* does not possess. However, *Oreohelix* embryos have a visceral hump which would develop similarly. The digestive tract is straight before the visceral hump develops. By relative growth, the digestive tube is pulled up into the visceral hump, thus taking on the shape of an inverted "U". Eventually (Berry claims gravity to be a possible factor), the hump rotates through 180 degrees, twisting the digestive tract, the nervous system, and various other organs. Hegner (1933, p. 339) shows the effects of this torsion on the nervous system. Other developmental factors are obviously involved in the looping of the digestive system.

THE REPRODUCTIVE SYSTEM

The reproductive system of *Oreohelix strigosa depressa* (fig. 10B) is much more complicated than that of the tiger snail (Jones, 1932-33, p. 248). The former gives birth to young, each with approximately two or two-and-a-half whorls of the shell already formed, while the latter lays eggs. Both are hermaphroditic.

The ovotestis lobes are embedded in or between the liver lobules. In *depressa* it is difficult to separate them, even in histological sections, from the liver lobules. Eggs and sperms mature in neighboring, though separate, compartments, and at different seasons. All our work on *Oreohelix* has been done in the spring (April and May). At this season the eggs in the ovary compartments are large, and the spermatozoa in the

spermaries are immature (fig. 15). Mature sperms are found in the spermatheca and in the duct thereof (fig. 16d). The time of egg laying is unknown. Likewise copulation has never been observed in this species. For several years in the spring we have dug specimens out of hibernation and have continued observations until the summer season, with no data thereon. It is possible, but not very probable, that development may be parthenogenic. On the other hand, copulation may occur in late summer or fall, at which time the spermatheca would be filled. There is also the possibility that copulation may occur after they have burrowed into the ground for the winter. Any data on these points will be appreciated.

The ovary compartments, unlike those of the tiger snail, contain usually more than one developing ovum. These compartments may or may not be in conjunction with the spermary or testis compartments (fig. 15). Pilsbry's dissections (1939) show the ovotestis compartments more densely clustered in tufts than do our drawings. Our sections through the ovotestis duct (fig. 16g) and through the hermaphroditic duct (fig. 16f) should be verified, as it is very difficult to differentiate these tubules from hepatic ducts (fig. 16a).

The hermaphroditic duct, also called the spermoviduct or the ovispermduct, consists of a non-coiled and a coiled portion. The coiled portion is much more kinked than is the similar structure in tiger snail. The albumen gland of *depressa* is much shorter than that of the tiger snail. In comparing it with that of other Oreohelices, Pilsbry (1933) states that it varies from moderately large to quite small, depending upon the stage of the reproductive cycle. Near the junction of the hermaphroditic duct and the albumen gland with the uterus is the talon, very different from the vestigial spherical accessory gland in the tiger snail. In *depressa* it is a long coiled tube, enlarged and blind at the end. The enlarged distal portion is intensely black in this species. Pilsbry reports this to be the case in all the northern races of *Oreohelix*, in contrast to brown, in the southern group.

The uterus as an anatomical mass, can be separated into two portions (fig. 10b): the uterus proper and a glandular mass. The former, in section shows evidence of two ducts, which are usually regarded as the splitting of the hermaphroditic duct into an oviduct and a sperm duct. Our slides will not permit a tracing of the full course of these in the uterus. The two ducts, however, continue separate courses after leaving the uterus, as shown in figure 10b, in which figure the vas deferens is displaced. It either coils around the vagina or under and around that organ and finally enters the penis sac in the epiphallus region. The oviduct, after leaving the uterus, enlarges. In figure 10B it is not labelled, but can easily be located as the large tube leading from the uterus into the vagina.

In the uterus histologically, from off the intrauterine oviduct are several uterine compartments into which the contiguous uterine glands

empty, apparently by more than one duct. The structure of the much-folded wall of these uterine compartments and of the contiguous uterine glands is shown in figure 16e. Similarly situated to the trophozoites (probably of certain sporozoon parasites) in the uterine compartments of the tiger snail (Jones 1932-33, p. 249, fig. 10, x), are glistening refractive cysts parasitizing the walls of the uterine compartments of *depressa* (fig. 16e, p. 41). The former, however, were intercellular, while the latter are intracellular, parasitizing the cytoplasms. The uterine compartments in *depressa* are capable of distending to accommodate numbers of foetal snails with embryonic shells of more than two whorls. In one specimen the uterus contained 16 embryonic snails, in another the number was 22.

The vagina in *depressa* is a very variable organ, especially that part between the spermathecal duct and the junction with the oviduct. It may be as well developed as in figure 10B, or on the other hand it may be lacking, in which case the spermathecal duct and the oviduct unite to enter the vagina. The spermathecal duct is long and usually lies alongside of the uterus. Its structure is shown in figure 16D. It terminates distally in the subspherical spermatheca, which in the spring is full of sperm from the other snail.

The spermatozoa are of the usual shape, a dense ovoid head with concentrated nuclear material, and a long flagellar tail, which in sections, as in figure 16d, is usually partially cut off. There is only one kind of spermatozoon in *Oreohelix*. In *Pauldina* and allied genera of fresh water snails, in addition to the regular type (or eupyrene) spermatozoa, there are peculiar worm-like (or oligopyrene) sperms. In the marine snail or conch shell, *Strombus*, there occasionally occur enormously large (or apyrene) sperms, due to failure of normal functioning of the maturation divisions in spermatogenesis. All types of abnormal sperm are thought to be non-functional (Wilson, 1928, pp. 300-303).

Opening into the genital pore in common with the vagina is the penis sac. It is a long hollow tube, bent in U-shape, tapering distally. The penis-retractor muscle is inserted into the side of the penis sac, Pilsbry states that in rare cases it is inserted terminally, also that rarely it may be split at the insertion. In our dissections we did not find examples of these exceptional cases.

The vas deferens enters the penis sac near its blind tip (fig. 10e). The free end of the penis sac represents a vestigial flagellum. The vas deferens proceeds proximally inside of the penis sac, but separate from the lumen of the sac. This part of the penis sac having in cross section two ducts (fig. 10, uppermost section) is known as the epiphallus. Cavities of the epiphallus and vas deferens in *depressa* may remain separate for a very short distance, according to Pilsbry. After the vas deferens unites with the cavity of the epiphallus, the structure is called the penis sac proper. The cavity of this part of the penis sac

may be ribbed (as shown in cross section in the two lowest sections of fig. 10a) or papillose. Relation of these parts, e.g. the vestigiality of the flagellum, cannot easily be determined, even from a great number of dissections of one species. Such relationships show up only in a long series of dissections of various species, such as Pilsbry has made.

Classification of this genus was attempted by Pilsbry and co-workers, as previously stated, on characteristics of the genitalia in general, and of the penis sac in particular, e.g. as to whether the latter showed a ribbed or papillose duct, the relative extent of these modified portions, the relative lengths of the epiphallus or of the flagellum, the point of insertion of the penis-retractor muscle, the obliquity of insertion of the vas deferens in the epiphallus, and various other features.

In description it is common to refer carelessly to the penis sac as the penis. This, however, is not the case. With figure 10b before you, let us try to comprehend the relation between the two. The penis (also called the verge or the phallus) results from the turning-inside-out of the penis sac, beginning with the flagellum, if that were of normal length in this species. Consider progressively this telescoping of the flagellum, the epiphallus, and finally the penis sac proper continuing until the entire organ has emerged through the genital aperture. Then the formerly-slack vas deferens will be the tube inside the penis. Where will the ribs and papillae be? Where will the epiphallus be? The vas deferens in the epiphallus will be located where? Attempt to visualize now the relation of the penis-retractor muscle to neighboring parts.

Insemination at copulation time is mutual between mating snails, the spermatheca of each being filled with the sperms from the other snail. After copulation ceases the sperms may mature for a considerable time in the spermatheca. Since the young of *Oreohelix depressa* develop in the brood pouches of the uterus, and even at that level have received the albuminous coats from the albumen gland, it would seem that the sperms ejected from the spermatheca would have to pass down the spermathecal duct, then up the oviduct, through the uterus, and at least into the hermaphroditic duct, much as mammalian sperms do, to fertilize the descending eggs before they are coated. If this occurs in such a manner, the fertilized egg would then proceed down the hermaphroditic duct, receiving the first albuminous coat from the albumen gland, following which it would pass down the oviduct into the uterine pouches where it would be retained for some time, while the nuclear whorl and the first few apical whorls of the shell are being formed. During this period an outer transparent coat may be added by the uterine glands. Hatching within the uterine pouches would be accomplished by the rupturing of the egg membranes after most of the contents of the enveloping layers had been used for nutrition. After further development in the pouches the snails would be born. This sequence of events is probably not much different than in an oviparous snail, as *Physa*, except that the embryo in *Physa* is not retained in the uterine pouches for any considerable time, but is laid as a developing

egg, with an active embryo inside, enveloped by transparent coverings from which it hatches. The latter case is very much more convenient for class observation.

Some land snails, as *Helix* (Hegner, 1933, p. 340) have even a more complicated reproductive system than *Oreohelix*. In these a dart sac and its complicated mucous gland are present. The former opens into the vagina near the genital aperture. The dart sac secretes an arrow-like dart, which prior to copulation is shot into the mate. Its piercing the flesh of the mate produces an excitatory effect, which is regarded by malacologists as one of the initial stimulating stages in copulation. The *Helix* snails possessing this mechanism are native of Europe, but also thrive, as introduced species, in and around the cities of southern California. Some of our Utah genera probably have darts and dart sacs, especially our endodont family, e.g. *Gonyodiscus*, but all our species are quite small for observation.

CIRCULATORY, NERVOUS, AND OTHER SYSTEMS

From the circulatory and respiratory systems, which are intimately related in land snails, comes the name of the order, Pulmonata, which refers to the "lung" or respiratory cavity. The pulmonary cavity is continuous with the mantle cavity through the respiratory aperture. It is lined with thin squamous epithelium (fig. 16i, p.e.). Small papillae (fig. 16i, p.a.) occur thereon, which may be but tangential sections of folded epithelium. In the roof of this pulmonary cavity, blood vessels are suspended, either in a layer (fig. 4) or by mesenteries. The blood vessels are the chief factor in the aeration of the bluish-tinged blood, which contains the respiratory pigment haemocyanin instead of haemoglobin. These blood vessels are either tributaries of the pulmonary or marginal veins or constitute these structures themselves.

In tracing the circulation, let us start with the pulmonary vein. The pulmonary vein leads into the single atrium of the heart (fig. 8), which in turn leads into the ventricle. This simple heart lies in a pericardial cavity. The ventricle leads into an aorta. This is said to fork into an anterior branch leading to the head and foot, and into a posterior branch leading to the rest of the viscera. The blood passes along into successively smaller arteries, finally attaining the arterial capillaries, from which it passes into large visceral sinuses. The venous capillaries drain these, from whence by veins of increasing diameter, the blood finally enters either the tributaries of the marginal or pulmonary veins or these veins themselves. The marginal vein appears to bend sharply in the previously mentioned "black spot" (fig. 7) and to continue as the pulmonary vein. However, this point needs verification. Recent investigation makes it appear increasingly more probable that the blood sinuses are lined with some sort of thin endothelium. If this is the case, the blood does not bathe the tissue directly, hence the snail would have a "closed" rather than an "open" system.

In many thin-shelled land snails the heart-beat is observable. In such cases the rate can be timed at different temperatures. Adult *depressa* has, in most instances, a shell that is too opaque to permit this. Irregular heart-beat rhythms are characteristic of certain land snails. Others maintain very regular rhythms at a given temperature.

The excretory system consists of a kidney which lies close to the heart, but in intimate physiological relation with the highly vascular roof of the pulmonary or respiratory cavity (fig. 8). Its highly-folded walls are composed of easily vacuolated cells (fig. 16j), an indication of turgidity in these cells during life. The excretory duct (fig. 7) drains the kidney, then turns abruptly, courses in close relation to the marginal vein and the rectum to open at the excretory aperture in the front of the mantle near the anus.

A dissection of the nervous system is shown in figure 6. Most of these ganglia lie back of the buccal pouch, the connectives, two on a side, completing a couple of rings around the oesophagus. Coalescence of ganglia render identifications difficult, as there is much variation in different snails (Hegner, 1933, p. 339). Complete verification would have to include a study of the distribution of nerves from each ganglion. The pairs of ganglia barely suggest metamerism, which is generally considered to be absent in mollusks. The nervous system resembles the ladder-type of nervous system of worms and arthropods, but is much modified. Details of a ganglion are shown in figure 17.

Mollusks have a highly developed series of eyes, the cephaloped eye (Hegner, 1933, 352) standing near the top in complexity. In this series the peculiar development of the optic vesicles, results in the rods and cones pointing toward the source of light, rather than away from the source of light as in the vertebrate retina. The eyes of *Oreohelix* (fig. 14) and other land snails would place somewhere near the middle of the molluscan series in complexity. Snails have tactile and olfactory senses well developed, but little is known of the underlying morphology. Statocysts and statoliths, organs of equilibrium, are known. They usually occur near the supraoesophageal ganglia. One of our slides of *Oreohelix* shows a structure somewhat resembling one of these. Nothing concerning taste is known in snails. Some have claimed a sense of barometric pressure in certain snails, as evidenced by behavior preceding thundershowers. *Oreohelix*, however, has never been considered in the suspected group.

The locomotor system is concerned with the foot, the pedal gland of which (fig. 13) secretes mucus. Its function has been discussed (see under mantle) in contrasting pedal slime with mantle slime. In the foot of *Oreohelix* there are small albumen glands intermingled with many small mucous glands. In some genera of snails both these types of glands appear in the mantle, but in *Oreohelix* they are confined to the foot. The secretion is carried from the pedal gland by a large ciliated duct that opens on the anterior portion of the sole, not far back of the

mouth opening. The musculature of the foot is an intricate cross work of muscles, many of them almost of tendinous structure. Snails move by undulating contractions of the foot muscles which produce peculiar anteriorly-moving waves on the sole, which are very interesting to time at certain temperatures. The method of observing these is the same as that given for observation of the movements of the lip and radula. The extent of pedal waves on the sole of *Oreohelix depressa* comprises the entire width, no marginal zones being present. The foot is also used for burrowing (Jones, 1935, Nautilus).

DISTRIBUTION

The genus *Oreohelix* ranges from the Rocky Mountains of southern Canada into northern Mexico, being primarily a Great Basin genus. That its range was at one time wider, is suggested by the scattered present occurrence in the Puget Sound region, by an isolated species on Catalina Island, and by a loess-fossil species in Iowa. *Oreohelix* is found living today in the Black Hills of South Dakota.

The genus can be divided into two great groups: the northern and the southern, roughly separated by the Grand Canyon, suggesting the possibly that the two groups may have differentiated since the Colorado River started cutting the canyon. Utah Oreohelices are for the most part of the northern group, though *eurekensis* represents an isolated branch of the southern group that evidently invaded Utah via Nevada and established itself among the northern group species found also in the same locality. The northern stock in general is much more confluent as to its species-differentiation, even though at present colonies may be isolated. It would appear that the species of the southern stock have been isolated for a much longer period of time. Charts, maps, and definite locality records of the species and groups have recently been published in Pilsbry's monograph (1939), cataloging our present knowledge, not only of recent, but also of fossil Oreohelices.

The Helicid stock from which Oreohelices originally differentiated, if such were the case, is obscure. The present-day genera *Ashmunella*, and to a lesser extent, *Sonorella*, the former in Arizona and New Mexico, the latter from the U. S.-Mexican border into South America, have the most similar morphological characteristics. *Oreohelix* is quite different from the Helicids of the genus *Polygyra* which bound its range on the eastern and northern borders, in some places, e. g. northern Idaho, overlapping. *Oreohelix* has no resemblance to the oriental-appearing Helicid genera of the Pacific coast, *Helminthoglyptae Micrarionta*, and *Monadenia*, the second of which overlaps the Arizona and California range of *Oreohelix*, the third of which overlaps in the Pacific Northwest. Some malacologists claim that the present distribution suggests migration of parental stock from South America through Mexico; others, using the same data, insist on a theory that *Orcohelix* is indigenous to the Great Basin. The latter theory, while less spectacular, has much indirect paleontological evidence to back it.

Habits of a snail are oftentimes to an interesting degree correlated with its distribution, e.g. our Utah midgets (*Vallonia*) and many of our barrel snails (Family Pupillidae), when retiring within the shell, seal the shell onto a dead leaf. Windstorms scatter these far and wide. Many perish, but others may be found, if conditions are at all favorable, in the most unexpected places, as in the midst of deserts, on salt flats, in dust areas, or even on high wind-swept cedar-tipped peaks. In some such localities they fight a losing fight, hence the colony is temporary, but in other unfavorable situations they become an established, though isolated, colony.

Oreohelix is just the opposite. It does not spread easily, and apparently is not carried from place to place. The colonies are found chiefly on the shady side of canyons, near quite steep rock slides, where leaf coverage is ample. From these colonies emigrations occur, as from Red Butte and Emigration Canyons up to the intervening peak. This peak, on the crest of which is the "big airplane beacon," is directly east of the University of Utah. On its slopes are a series of whitened or "dead" shells, extending completely up to the beacon light. The slopes of this peak are in many places gradual. Let a damp season occur, and the snails from the canyons, progressing a few yards each day, will climb the mountain, each day starting from the point reached at the end of the preceding day. All goes well while the damp season lasts, but with the return of clear weather, the emigrants die of exposure, leaving their bleached shells to mark the degree of success of their attempt. Only those living near high cliffs are unsuccessful climbers. They climb up the face of the cliff each morning, but in the afternoon, even though they attempt to seal their shells to the rock, they usually fall back to the starting point below. This is repeated each favorable day with the same fruitless result. But when clear weather comes, instead of perishing from exposure, they are yet in the shelter and shade of the cliff, where they perpetuate the colony. After many observations, I have come to believe that this negative geotropism of the animal, frustrated by the force of gravity, is the reason why we so generally find thriving *Oreohelix* colonies in Utah at the base of cliffs. Colonies established in other favorable localities may persist for a few years, but the dry years usually are too much for them. In another place (under "Mantle") the necessity of lime in shell-building has already been discussed.

The "clustering" habits of certain eastern snails (Jones, 1935, the burrowing of snails) may explain why their range extends farther north than that of *Oreohelix* which does not "cluster." Snails, like most invertebrates, become sluggish as the temperature gets colder, yet they are rarely found frozen on the surface of the ground. This apparent anomaly, led to the above investigation, in which another brief period of extreme activity was discovered, usually just above the Centigrade zero, but in *Oreohelix*, extending slightly below that mark. A land snail has to "dig in" while the temperature is dropping these three or four degrees. In *Oreohelix* young and old each dig for themselves. In some

species of *Polygyra* and in *Anguispira* "clustering" occurs at these temperatures, the young gather in clumps around and on the older individuals, which of course can, with the larger and stronger foot, "wedge in" and disappear faster, but the young go down the same hole on top of them. Considering how quickly and how severely cold snaps can occur as one approaches the Canadian border, it is evident that the northern range of a species may depend on how quickly the young can get below the freezing line. In such cases the snails that "cluster" have the distinct advantage in attaining the possibility of "becoming Canadians."

Key to Figures of

Oreohelix strigosa depressa

FIG. 1. LATERAL VIEW OF SHELL

a. apex

sp. spire

b. body whorl

c. callus

l. lip

ap. aperture

col. columella

u. umbilicus

r. riblet of growth

c. b color band

s. suture

FIG. 2. RADULAR TEETH

r. reflection

b. base

c. cusp

Cen. central tooth

Arabic numbers indicate the number of teeth (up to 30)

Figure drawn by Calvin Richins

FIG. 3. JAW

st. striations

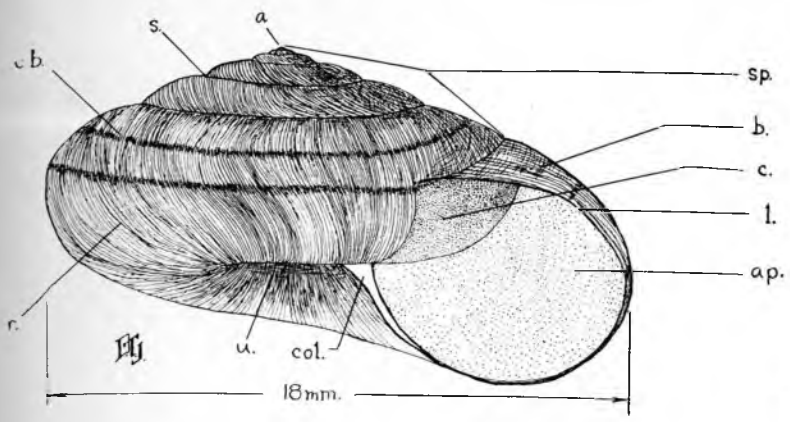
a. s. anterior surface

p. s. posterior shelf

e. p. end plate

m. muscle

Figure drawn by Arthur Ellis



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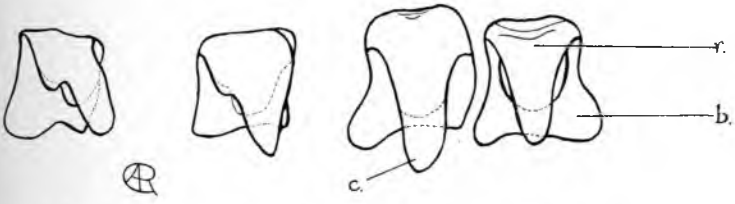

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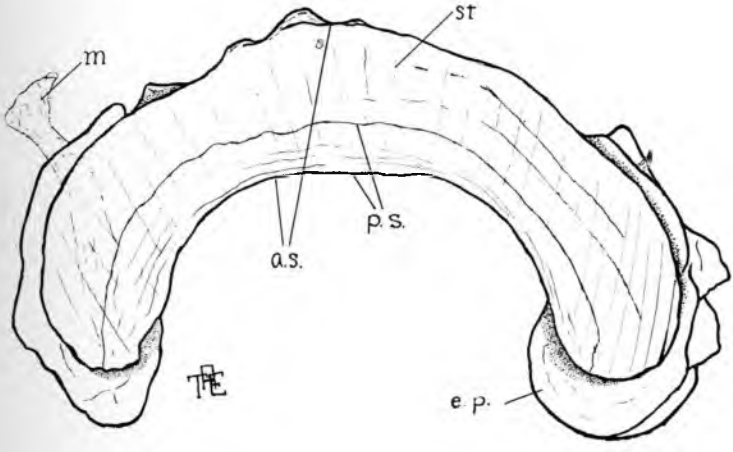


3.

FIG. 4. LONGITUDINAL SECTION OF THE MANTLE COLLAR

p. c. pulmonary cavity

n. nerve

b. v. blood vessels

a. p. air passage

t. thin shell-secreting epithelium

s. r. supramarginal ridge

s. g. supramarginal groove

f. front of mantle

dig. digitation

tend. tendinous muscle fiber

a. g. albuminous gland

n. g. neutral gland

l. m. g. large mucous gland

dor. dorsal epithelium of the body of the snail.

m. muscle

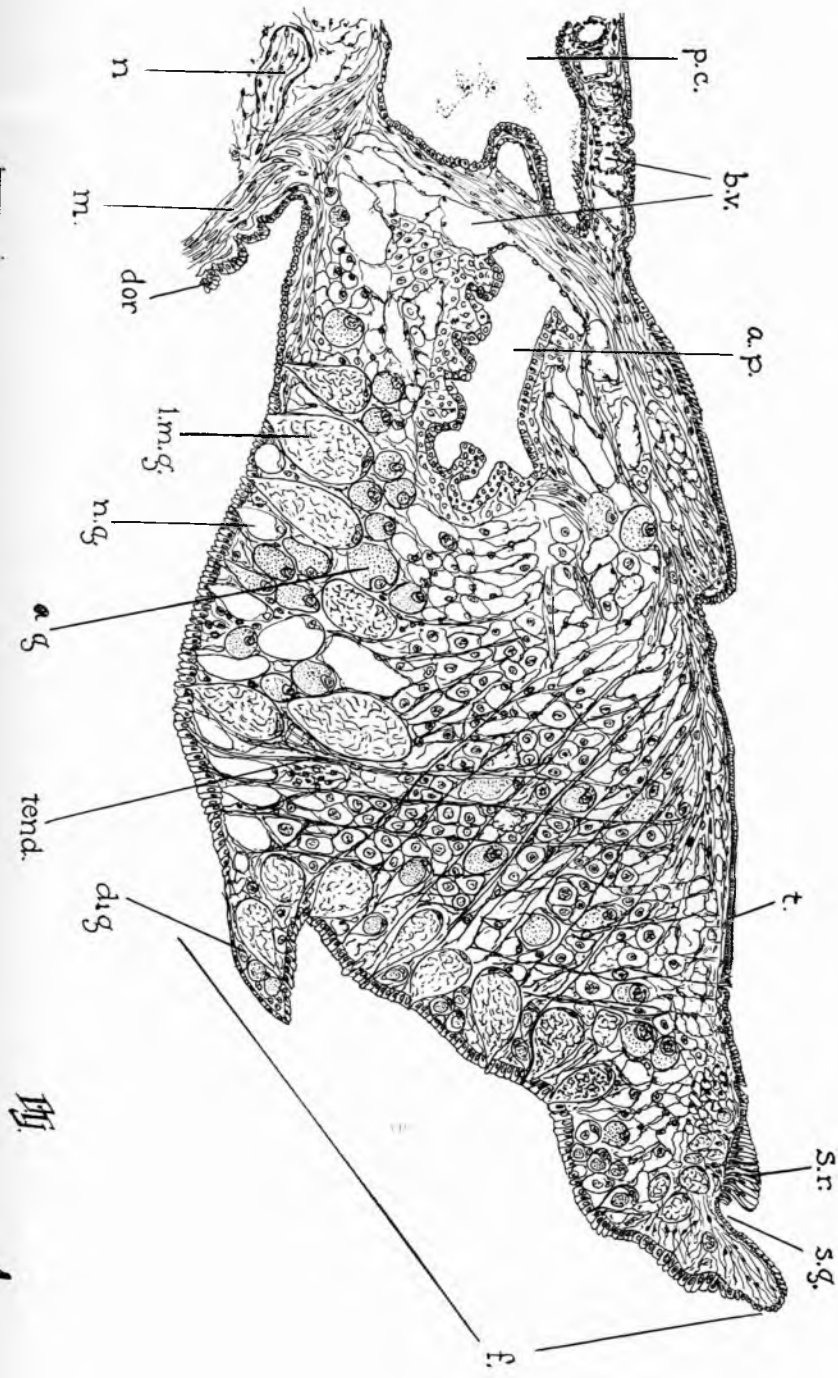


Fig. 4.

FIG. 5. FIGURES AS LISTED BELOW

A. cross section of shell

B. cross section of shell, as above, enlarged

C. longitudinal section of shell

p. periostracum

s. splice, showing interruption in shell secretion

o. outer of the crystalline calcareous layers

m. middle of the crystalline calcareous layers

i. inner of the crystalline calcareous layers

c. calcareous lining of the shell

c. b. color band in section

FIG. 6. DORSAL VIEW OF GANGLIONIC MASS

b. g. buccal ganglion

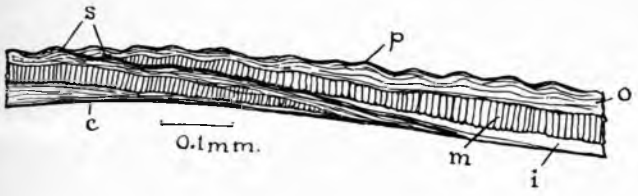
opt. optic nerve

s. o. supraoesophageal ganglion

ant. anterior connective

post. posterior connective

inf. infraoesophageal ganglionic mass



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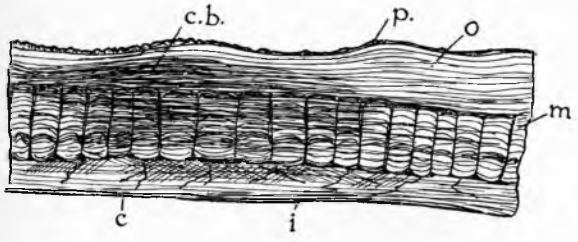

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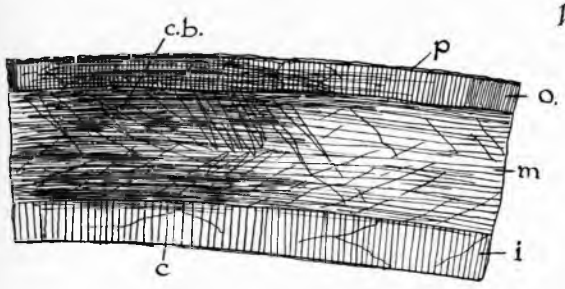

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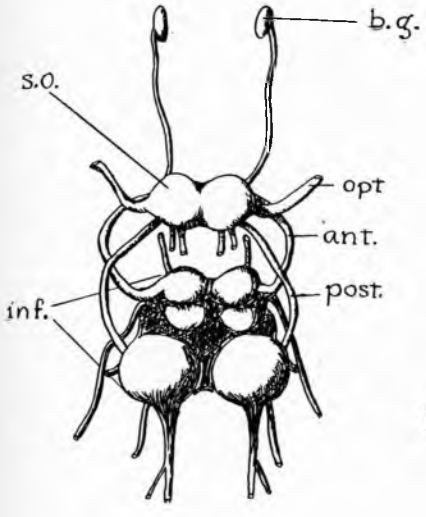


6.

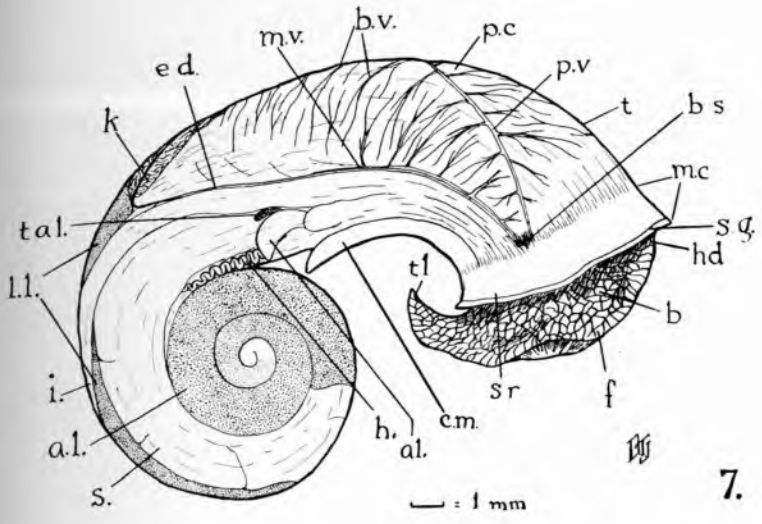
FIG. 7. ORGANS IN SITU, APICAL VIEW.

p. v. pulmonary vein
b. v. blood vessels
m. v. marginal vein
m. c. mantle collar
e. d. excretory duct
k. kidney
tal. talon
l. l. lower lobe of the liver
a. l. apical lobe of the liver
i. intestine
s. stomach
h. hermaphroditic duct
al. albumen gland
c. m. columellar muscle
f. foot
b. body of the snail
t. thin shell-secreting portion of the mantle
tl. tail
hd. head
s. g. supramarginal groove
s. r. location of the supramarginal ridge
b. s. black spot
p. c. roof of the pulmonary cavity

FIG. 8. ORGANS IN SITU, UMBILICAL OR BASAL VIEW.

(For labels see under Fig. 7, except as below.)

s. o. sole of the foot
sp. spermatheca
m. f. muscle fibers
ao. aorta
v. ventricle of the heart
at. atrium of the heart
p. pericardial cavity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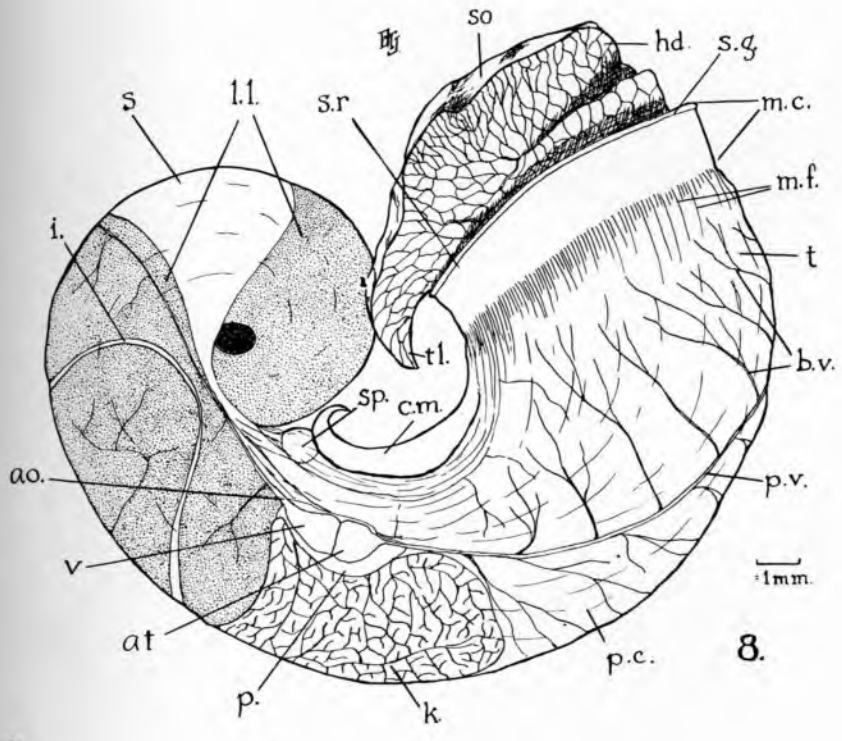
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8.

FIG. 9. ANATOMY OF THE DIGESTIVE SYSTEM, DISSECTED

m. mouth

b. p. buccal pouch

ra. radula (within)

s. d. salivary duct

s. g. salivary gland

oes. oesophagus

s. stomach

i. intestine

h. d. junction of hepatic ducts with stomach

r. rectum

an. anus

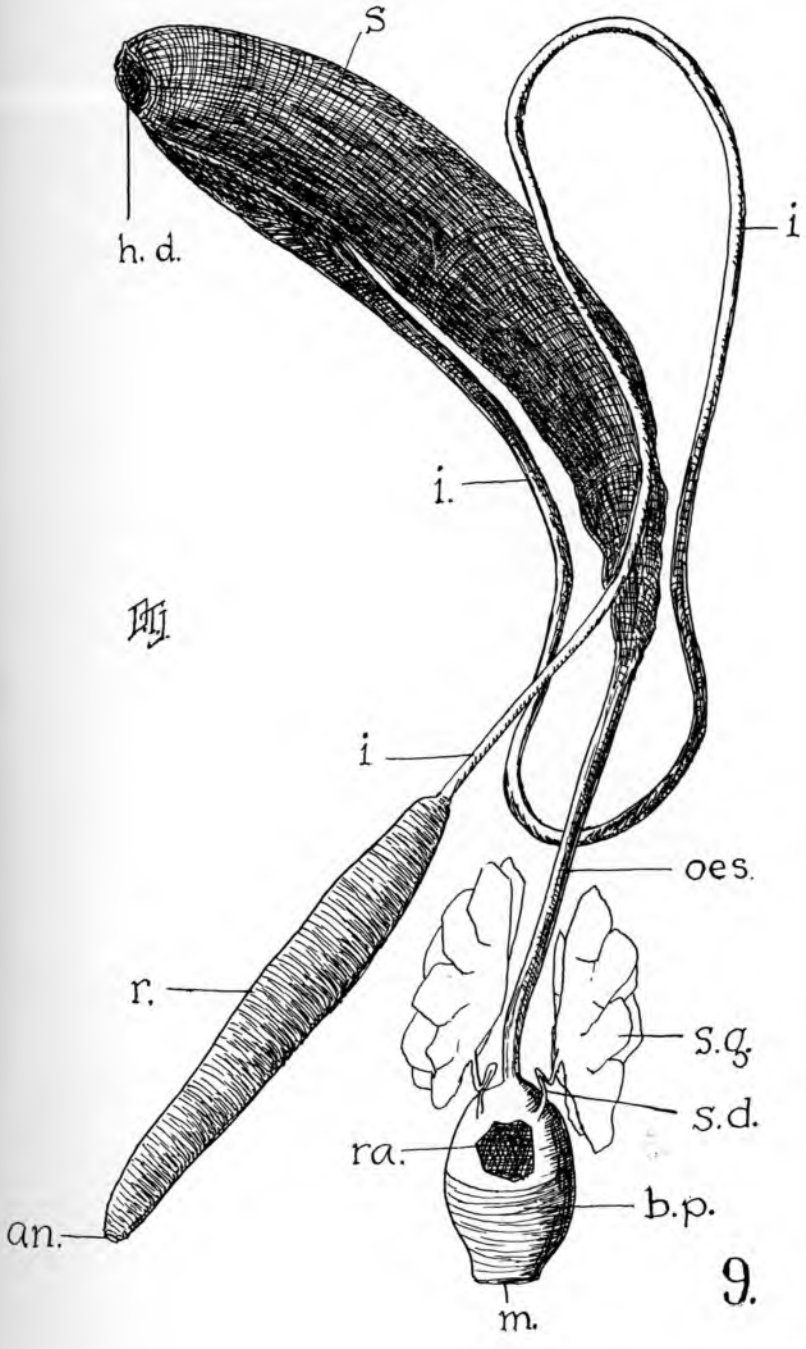
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FIG. 10. ANATOMY OF THE REPRODUCTIVE SYSTEM.

A. diagrammatic sections (after Pilsbry, 1933) of the epiphallus, the distal penis sac, and the proximal penis sac respectively, showing the union of the cavity of the epiphallus with that of the vas deferens.

B. dissection of the reproductive system.

v. d. vas deferens

d. ep. duct of the epiphallus

ep. epiphallus

c. p. s. cavity of the penis sac

p. s. penis sac or verge sac

fl. flagellum (vestigial)

v. vagina

ot. ovotestis

ot. t. ovotestis tubule

h. hermaphroditic duct

tal. talon

al. albumen gland

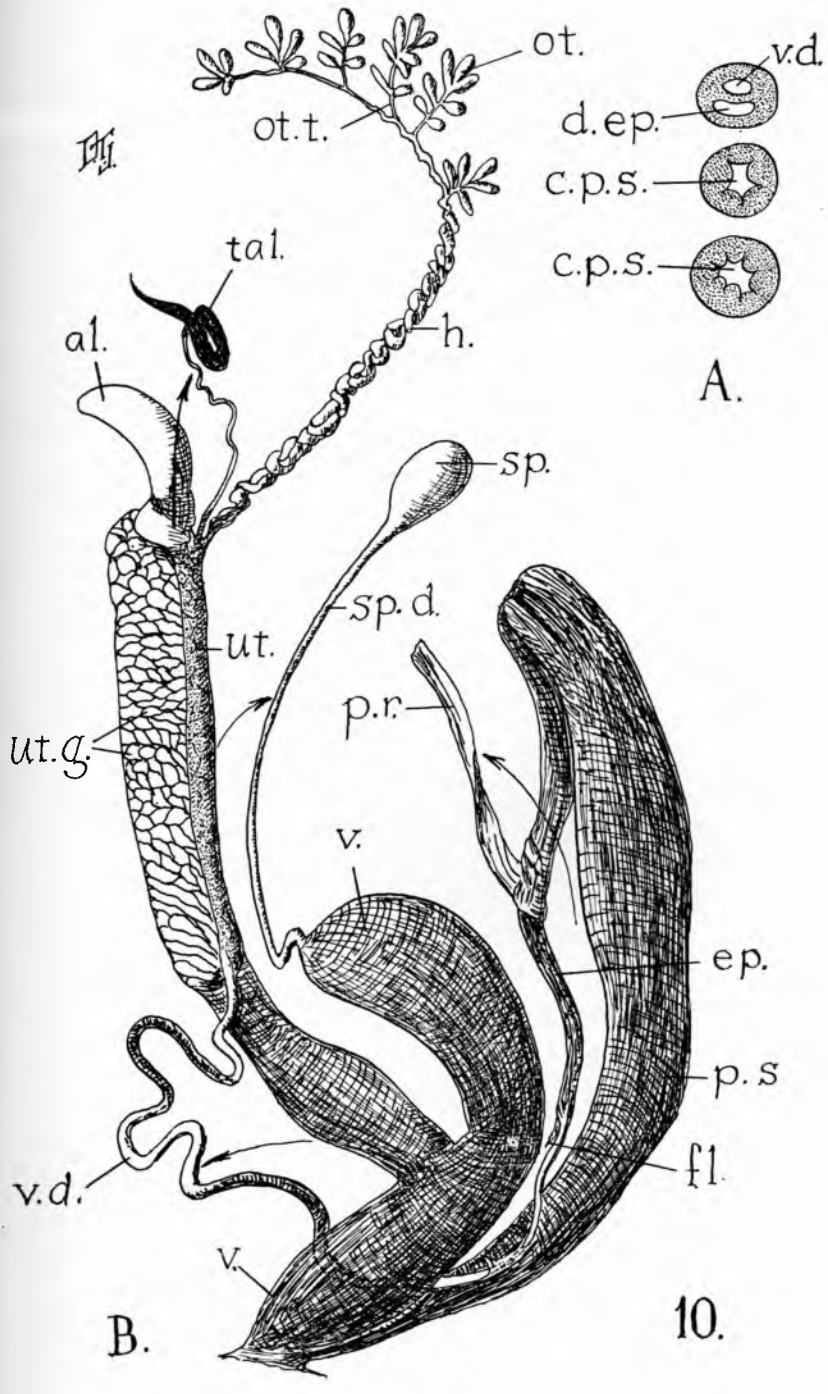
ut. uterus

ut. g. uterine glands

sp. spermatheca

sp. d. spermathecal duct

p. r. penis retractor muscle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10.

FIG. 11. SECTION THROUGH THE RADULA AND ADJACENT STRUCTURES

b. c. buccal cavity

o. odontophore

m. muscle

r. t. radular teeth

FIG. 12. DETAIL OF OPEN WORK IN THE CONNECTIVE TISSUE FROM THE BACK PART OF A MANTLE COLLAR

e. epithelium that secretes the crystalline calcareous layers of the shell

s. m. small muscles beneath epithelium

b. small blood vessels beneath epithelium

b. v. larger blood vessel

c. t. n. connective tissue nucleus

l. n. large nucleus

m. muscle

n. m. nucleus of muscle cell.

FIG. 13. SECTION OF THE SLIME GLAND OF THE FOOT

s. m. g. small mucous gland

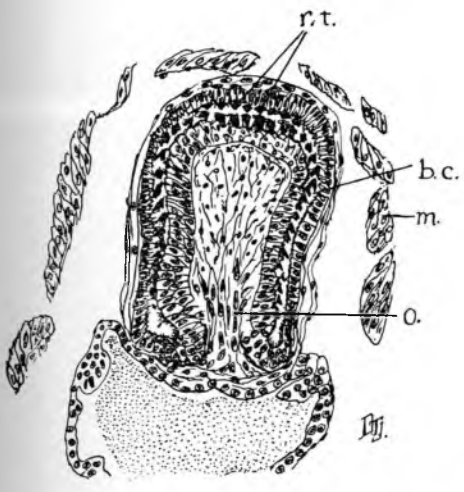
n. network of muscles and connective tissue

m. muscle

mes. mesentery-like support

s. a. g. small albuminous gland

d. duct of the slime gland



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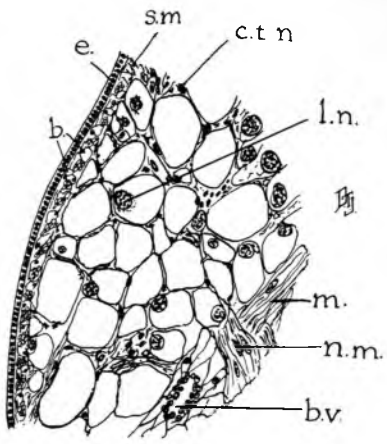

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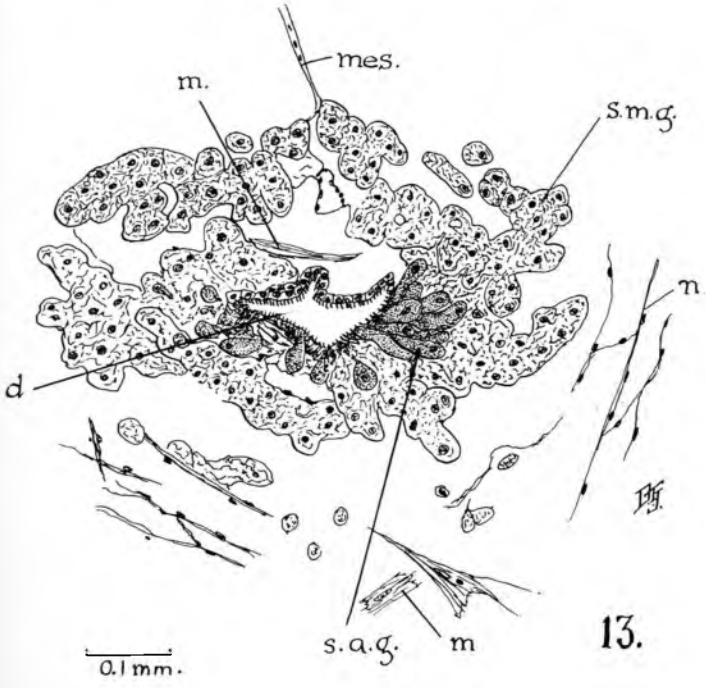


13.

FIG. 14. SECTION THROUGH TENTACLE SHOWING EYE

e. eye
p. pigment
g. ganglion
b. v. blood vessels
m. muscle
n. nerve

FIG. 15. DETAIL OF LIVER AND OVOTESTIS

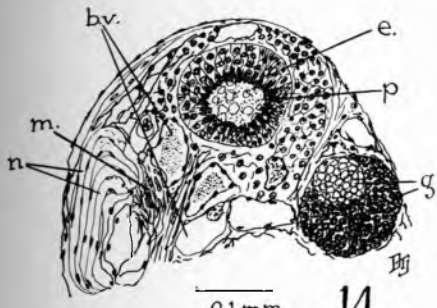
h. l. lumen of the hepatic lobule
t. thin shell-secreting portion of the mantle covering the liver
e. egg or ovum
s. immature spermatozoa
h. hepatic cell
y. yellow granules

FIG. 16. VARIOUS EPITHELIA

A. epithelium of the hepatic ducts
B. stomach epithelium and underlying layers
C. section through the oesophagus
D. wall of the spermathecal duct
s. spermotozoon
E. section of small portion of the uterus
ut. g. small albuminous uterine gland
ut. e. uterine epithelium
p. parasitic cyst
F. section through straight portion of hermaphroditic duct
G. section of an ovotestis tubule
H. section of a portion of the salivary gland
lo. small mucous lobule
d. duct
I. section through the wall of the lung
p. a. papilla
p. e. pulmonary epithelium
J. section through the wall of the kidney

FIG. 17. GANGLION FROM THE INFRAOESOPHAGEAL GANGLIONIC MASS

f. nerve fibers
l. n. c. large nerve cell
s. n. c. small nerve cell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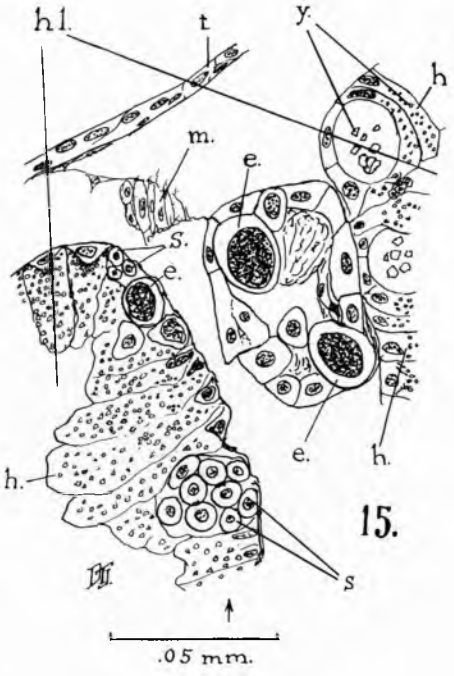
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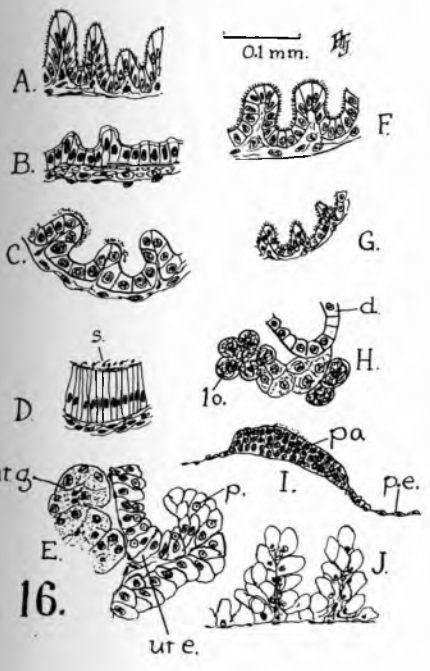
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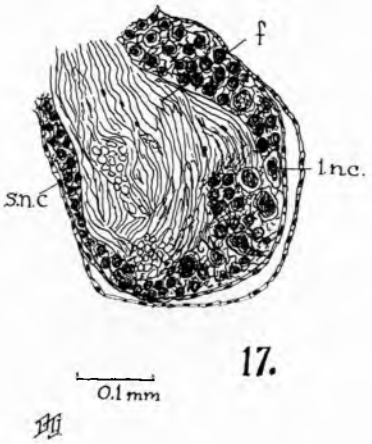
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Bibliography

Berry, Edward Wilber

1929. Paleontology. McGraw-Hill Book Co., Inc., New York. 392 pp.

Berry, Elmer

1930. Mollusca of the Henry Mountains and some neighboring points in Utah. Bull. Univ. Utah, Vol 21, No. 2 (Biol. Ser., Col. 1, No. 3), pp. 1-7

Berry, Elmer

1931. Mollusca of Lamb's Canyon, Utah. Naut. Vol. 44, No. 4, pp. 113-114.

Chamberlin, Ralph V. *and* Berry, Elmer

1929. Notes on the mollusca of southeastern Utah. Naut., Vol. 42, pp. 123-125.

Chamberlin, Ralph V. and Jones, David T.

1929. A descriptive catalog of the mollusca of Utah. Bull. Univ. Utah, Vol. 19, No. 4 (Biol. Ser., Vol. 1, No. 1), pp. 1-203. With map and 86 text figs.

Dall, W. H.

1896. Insular land shell faunas, especially as illustrated by data obtained by Dr. G. Baur in the Galapagos Islands. P. A. N. S. Phila., 1896, pp. 395-459.

Ellis, Arthur Erskine

1926. British snails. Oxford at the Clarendon Press. 275 pp. and 14 plates.

Hegner, Robert W.

1933. Invertebrate Zoology. The Macmillan Co., New York. 570 pp.

Jones, David T.

1932 (1933). Some anatomical features of the tiger snail, *Anguispira alternata* (Say). Proc. Ind. Acad. Sci., Vol. 42, pp. 243-250. With 2 plates.

Jones, David T.

1935. Mollusks from Weber Canyon, Utah. Utah Acad. Sci., Arts, and Letters, Vol. 12, pp. 227-228. With one map.

Jones, David T.

1935. Burrowing of snails. Naut., Vol. 48, No. 4, pp. 1-3.

Jones, David T

1935. The formation of shell in the tiger snail. J. Morph., Vol. 57, No. 2, pp. 547-569, including 2 plates and 2 text figs.

Jones, David T.

1937. A comparative study of certain goblet cells. Bull. Univ. of Utah, Vol. 27, No. 7 (Biol. Ser., Vol. 3, No. 6), pp. 3-15. With 2 plates.

JONES, DAVID T.

1938. Some preliminary experiments on the snail, *Discus alternatus* (Say). Proc. Utah. Acad. Sci., Arts, and Letters, Vol. 15, pp. 111-120. With 3 charts and 3 plates.

JONES, DAVID T.

1938. The supramarginal ridge in certain American snails. Ohio J. Sci., Vol. 38, No. 3, pp. 125-135. With 21 text figs.

LOWRANCE, EDWARD

1934. On the early development of *Stagnicola kingi* (Meek), the Utah ribbed snail. Bull. Univ. of Utah, Vol. 24, No. 5 (Biol. Ser., Vol. 2, No. 5), pp. 1-22, including 38 figs.

MORGAN, THOMAS HUNT

1927. Experimental embryology. Columbia University Press. New York. 766 pp.

PILSBRY, HENRY A.

1905. Mollusca of the southwestern states I. Urocoptidae, Helicidae of Arizona and New Mexico. P. A. N. S. Phila., Vol. 57, pp. 211-290, Plates 11 to 27, inclusive.

PILSBRY, HENRY A.

1916. Notes on the anatomy of *Oreohelix*, with a catalog of the new species. P. A. N. S. Phila. Vol. 68, pp. 340-359.

PILSBRY, HENRY A.

1917. Notes on the anatomy of *Oreohelix* II. P. A. N. S. Phila., Vol. 69, pp. 42-46.

PILSBRY, HENRY A.

1933. Notes on the anatomy of *Oreohelix* III, with descriptions of new species and subspecies. P. A. N. S. Phila., Vol. 85, pp. 383-410.

PILSBRY, HENRY A.

1939. Land mollusca of North America (north of Mexico), Monograph No. 3 of the A. N. S. of Phila., Vol. 1, Part 1, Philadelphia. 573 pp. and 377 figs.

WILSON, EDMUND B.

1928. The cell in development and heredity. Third Edition. The Macmillan Co., New York, 1232 pp.

WOODBURY, A. M.

1933. Biotic relationships of Zion Canyon, Utah, with specific reference to succession. Ecol. Mon., Vol. 3, No. 2, pp. 150-245.