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Title The Morphology of the Reproductive Tracts of the Pacific Northwest Pulmonates

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The morphology and taxonomic use of the reproductive tracts of some of the Pacific Northwest Pulmonates were studied. The snails examined were, Monadenia fidelis (Gray), Vespericola columbiana (Lea), Allogona townsendiana (Lea), Haplotrema sportella (Gould), and Haplotrema vancouverense (Lea).

The length of the reproductive tracts of nine or more individuals of each species were measured in millimeters and these measurements were used as a quantitative means for identifying each species. Each snail not only varies in the length of specific structures, but also was seen to differ from others by the presence or absence and the position of certain structures. Some of the structures used to separate the species were: The muscular collar on the vagina in Haplotrema sportella and Haplotrema vancouverense, along with the size and shape of the talon; the presence or absence of a stimulator, verge, flagellum

and epiphallus in Allogona townsendiana and Vespericola columbiana; and the presence of a dart, mucus gland, and mucus ejector in Monadenia fidelis.

The use of reproductive tract data in taxonomy appears to provide a more accurate means of identifying species. It does not have the problems that are prevalent in shell characters, nor does it require the skill necessary in preparing and reading radula mounts. Combined with the other taxonomic characters it probably provides a better phylogenetic diagnosis of the various species.

THE MORPHOLOGY OF THE REPRODUCTIVE TRACTS OF THE PACIFIC NORTHWEST PULMONATES

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

The snails discussed in this paper are members of the class Gastropoda, order pulmonata and they represent three major families: Polygyridae (Allogona townsendiana Lea and Vespericola columbiana Lea); Helminthoglyptidae (Monadenia fidelis Gray); and Haplotrematidae (Haplotrema sportella Gould and Haplotrema vancouverense Lea).

In the literature Haplotrema vancouverense was first described by Lea (16, p. 87) as Helix vancouverense. There are several synonyms for this species. Pilsbry in 1908 (21, p. XI) described the genus Circinaria in which he included Haplotrema vancouverense as Circinaria vancouverense. Baker in 1930 (4, p. 416) described and erected the genus Haplotrema, in which he included Haplotrema vancouverense. All of the above classifications were based on shell and radula characteristics and little emphasis was placed on internal anatomy.

Haplotrema sportella was first described by Gould in 1846 (13, p. 167) as Helix sportella. Baker (4, p. 418) included it under Haplotrema.

According to Pilsbry (23, V. I, pt. 2, p. 32) the genus Monadenia was first described by Albers in 1850 as Aglaja to include Helix ghiesbreghti. He further stated that "the group was enlarged by Von Martens in 1860 as Aglaia." Pilsbry (20, p. 198) substituted Monadenia for

Von Marten's Aglaia. The species fidelis had been described by Gould as Helix fidelis (13, p. 169) and Pilsbry transferred it into the genus Monadenia.

Allogona townsendiana was first described by Lea in 1837 (16, p. 99) as Helix townsendiana. Gould described a similar specimen in 1846 (13, p. 178) as Helix ruida. Pilsbry included a similar form as Polygyra townsendiana, in 1894 (19, p. 76) and Vanatta described a similar specimen as Polygyra townsendiana brunnea (26, p. 25). Pilsbry (23, V. I, pt. 1, p. XVII) introduced the genus Allogona under which he included Lea's Helix townsendiana.

Vespericola columbiana was first described by Lea in 1836 (16, p. 89) as Helix columbiana. Pilsbry in 1928 (22, p. 182) described a similar specimen as Polygyra columbiana, and later in his monograph on North American land snails introduced the genus Vespericola (22, V. I, pt. 1, p. XVII) which included Lea's described species.

The range of these pulmonates varies with each species. Haplotrema vancouverense and Haplotrema sportella are found in the moist wooded regions of Northwest California, and northward to the Alexander Archipelago, Alaska, between the Cascade range and the sea; Northeast Oregon and Northern Idaho.

Monadenia fidelis has been found at Sitka, Alaska, and southward into California. It occurs along the coast and inland to Seattle and along the west slope of the Cascades

in Washington and Oregon. In California it has been found in Shasta and Mariposa counties. Allogona townsendiana ranges from British Columbia to the Willamette Valley. Vespericola columbiana ranges from southern Alaska south to Monterey county, California, and is confined to a strip within a hundred miles of the Pacific Ocean.

Only a few studies have been done on the morphology of the gentalia of pulmonates. Mead (17, p. 675-719 & 18, p. 219-291) studied Ariolimax (moerck) and Achatinida and found that careful studies of the genital system revealed tangible differences between genera and species. On the basis of his findings he was able to revise the taxonomy of the west coast slugs of the genus Ariolimax (moerck). Abdel-Malek (2, p. 94-102 & 3, p. 285-296) using a study of the genitalia of some planorbid snails was able to separate two genera which had formerly been listed under one subfamily into two distinct subfamilies. Boettger (6, p. 49-64), Webb (25, p. 213-218) and Franzen (12, p. 82-95) used morphological data of the genitalia to study systematics in the family Succineidae. Watson (24, p. 6-30), Fretter (12, p. 312-351), Johansson (14, p. 337-387), and Creek (10, p. 228-240) found that the morphology of the genitalia was instrumental and necessary in studying taxonomy and evolution of prosobranchs.

Since most of the descriptions of the Pacific Northwest pulmonates are based upon shell and radula

characteristics, the purpose of this study was to attempt to provide another method for identifying these organisms. The study is not intended to replace the other methods, but to add more information that can be used in conjunction with previous methods or as an alternative to the other methods. The general morphology of the genitalia of each form will be described and histological and cytological material will be used only when it is necessary to do so.

Morphological studies of the genitalia should be useful in taxonomical and evolutionary studies. Since several of these snails are intermediate host for certain parasites additional means of identification will be useful in helping to elucidate the life cycles.

The measurements of the reproductive structures were taken to supply supplementary data in the taxonomy of the species studied. These data are not conclusive, because no measurements were taken of the height and diameter of the shells, which would be necessary in order to supply some correlation between size of snail and length of structure. However, these data are included in the appendix for reference, as length of structure may be useful in determining the difference between a structure common for two or more snails.

MATERIALS AND METHODS

The snails used were collected at Woods Creek, nine miles west of Philomath; along the banks of the Alsea river, west of the city of Alsea; Burnt Woods, Oregon and Coffin Butte, north of Corvallis. The snails were identified as Haplotrema sportella, Haplotrema vancouverense, Vespericola columbiana, Allogona townsendiana and Monadenia fidelis by Pilsbry's Key in Academy of Natural Science of Philadelphia (23, V. 1, pts. 1 & 2, V. 2, pt. 1).

The snails were brought into the laboratory and maintained in a terrarium made of plastic and filled with soil and organic debris from the snail's original habitat. The terrarium was kept in a cold room where the temperature was approximately sixty-five degrees farenheit. Some snails were kept for a period of nine months under these artificial conditions.

All of the specimens were dissected and the genitalia removed and measured in millimeters. The soft parts were carefully removed by cutting the shell along the spirals with a pair of scissors and gently teasing away the cut pieces. The genitalia were not usually harmed by removal, but the fragile ovotestis, which is embedded in the liver was usually broken into several pieces. The study of this organ was attempted in spite of this difficulty. Dissections were made only on freshly killed specimens. The

specimens were killed by drowning them in cold tap water. This method killed the snails in a relaxed state and retarded hardening and contraction of the tissues. The genitalia were preserved in seventy per-cent ethyl alcohol and Bouin's fluid.

When sections were made the structures were fixed in Bouin's, embedded in paraffin, and sectioned at eight and ten microns. The sections were stained in hematoxylin and eosin, basic fuchsin and alcian blue and neutral red.

All drawings were made free hand after measurements, and photographs were taken by Mr. Bill Reasons.

Haplotrema sportella

Refer to Figs. 3 & 6

Ovotestis consisting of five groups of alveoli. The hermaphrodite duct is short and passes to the ventral surface of the albumen gland where it joins a duct from the talon and the albumen gland (region of the carrefour). The united ducts pass into the body of the terminal end of the albumen gland and into the spermoviduct which is adjacent to the albumen gland.

The spermoviduct is a long (17-25mm) tortuous, glandular structure extending from the base of the albumen gland to the bifurcation of the vas deferens and the free oviduct.

The short vas deferens (10-21mm) passes from the terminal end of the spermoviduct and passes behind the base of the spermathecal duct following a path parallel with the penis. The vas deferens comes to lie closely appressed to the penis and the two structures appear attached to each other. The vas deferens eventually leads into the penis at its apical end.

There is a short epiphallus on the apical end of the penis which is attached to the penial retractor muscle.

The penis a short muscular structure (4-9mm) with a wide diameter, passes into the short genital atrium. The penial chamber is differentiated into apical and basal

halves; the apical region is thin walled except for a large, internal pilaster under the vas deferens; the basal region with thick rugose folds that continue into the genital atrium.

The free oviduct (2-5mm) runs from the terminal end of the spermoviduct to the point where it is joined by the spermathecal duct. The organ is straight and hollow with a relatively wide diameter.

The spermathecal duct is short (2-4mm) having a broad base and narrowing near its apex where it forms a very prominent constriction. The constriction is the line of demarcation between the spermathecal duct and the spermatheca. The spermatheca is short (1mm) having the shape of a spinning top, broad at one end and narrowing to form a blunt point at its terminal end. The spermatheca appears sacculate and somewhat glandular. It is connected to the upper portion of the spermoviduct by a thin muscle.

The vagina is short (1-7mm) and is almost entirely covered by a muscular collar. The collar is very thick on the dorsal surface, but forms only a narrow band on the ventral surface.

The genital atrium is very short (5-8mm) receiving the ducts from the penis and vagina and opens to the exterior.

Haplotrema vancouverense

See Figs. 4 & 8

Ovotestis consisting of numerous large groups of alveoli. The hermaphrodite duct passes from the ovotestis, following a tortuous route. It leads to the ventral surface of the albumen gland and receives a duct from that structure and the minute clavate talon (region of the carrefour), and these united ducts pass into the spermoviduct. The spermoviduct extends for 25-35mm towards the genital opening. At the terminal end the vas deferens branches off and follows a tortuous path toward the apical end of the penis. The vas deferens begins as a narrow tube, but increases in diameter on the lower portion. This increase in diameter reaches a maximum that is about four times the initial diameter. At the level of the muscular collar on the vagina the vas deferens turns and travels laterally for 15-20mm and then turns upward and runs parallel with the penis and eventually fuses with the penis at the junction of the penial retractor muscle. The length of the vas deferens is 47-63mm.

The point at which the vas deferens separates from the spermoviduct demarcates the starting point of the free oviduct which extends from 3-8mm and terminates at the point where the spermathecal duct joins with it.

The spermathecal duct extends from 19-36mm in length

and terminates in a large bulbous structure, the spermatheca. The spermatheca is 3-5mm long and 1-4mm wide. The spermathecal duct is swollen at the base and tapers off rapidly until it approaches a diameter of about 0.25mm for the biggest portion of its length.

The vagina is a long tube that extends for 7-13mm beginning at the junction of the free oviduct and the spermathecal duct and terminating in the genital atrium. A large muscular collar covers the vagina on about the middle of its length. The muscular collar is thick on its dorsal surface and does not form a circlet around the vagina.

The genital atrium is from 1-2mm long and receives both the vagina and the penial ducts, opening to the exterior. The atrium is not capacious, but contains a number of rugose folds.

The penis is located lateral to the vagina and is from 5-19mm in length. It is long and narrow and begins at the point where the vas deferens and penial retractor fuse with it and terminates in the genital atrium.

Vespericola columbiana(lea)

Refer to Figs. 1 & 13

The hermaphrodite duct leads from the ovotestis following a tortuous path and joins a duct from the talon, a digitiform process which contains varying numbers of diverticula, on the ventral surface of the albumen gland. These ducts, along with the duct from the albumen gland, form the carrefour and pass through the posterior part of the albumen gland and into the spermoviduct.

The spermoviduct is a long (15-28mm), winding, glandular structure with its apical end being adjacent to the albumen gland and terminating at the bifurcation of the vas deferens and the free oviduct. The male and female conduits are in close approximation with each other having become confluent in the hermaphrodite duct and can not be differentiated externally. The branching off of the vas deferens and the free oviduct clearly demarcated the terminal end of the spermoviduct.

The vas deferens runs parallel with the free oviduct across the peniovaginal crotch terminating in an epiphallus. The epiphallus which tapers at both the vas deferens and the penial end extends from 8.5-20mm terminating at the apical end of the penial chamber. The epiphallus is greater in diameter than the vas deferens.

The free oviduct extends for 4-9mm in length

terminating in the vagina. The oviduct is narrow and straight and is joined at the apical end of the vagina with the spermathecal duct. The junction of the spermathecal duct and free oviduct is the terminal point of the free oviduct.

The spermathecal duct is short and broad at the base, extending from 2.5-5mm. The base is very broad, but it narrows until it forms a prominent constriction which is the dividing line between the spermathecal duct and the spermatheca. The spermatheca is saccular and not as broad as the duct. It extends from 3-6mm in length and in some specimens is closely appressed to the spermoviduct.

The vagina is wider in diameter than either the free oviduct or the spermathecal duct and extends from 2.5-5mm in length and is smooth in the interior, terminating in a small genital atrium.

The genital atrium ranges from 0.5-2mm in length opening to the exterior of the animal and receiving both the vagina and the penis.

The penis is a long oblong structure extending from 4-11mm in length and is located inside a thin membranous penial sheath. A long verge is found inside the penial cavity and is joined at its apical end with the epiphallus.

Allogona townsendiana

Refer to Figs. 2 & 16

This genus is characterized by the possesion of a strongly developed stimulator in the penis (24, V. I., pt. 2, p. 876).

The ovotestis is located underneath the visceral hump, embedded in the liver. It is a complex structure consisting of three main branches, each being composed of many rhizoid shaped structures. The three branches unite at their basal ends forming a single conduit, the hermaphrodite duct, which follows a tortuous route that terminates in the basal portion of the talon.

The talon is a digitiform diverticular process which contains a varying number of smaller diverticula, that lie closely appressed to the ventral surface of the albumen gland. The talon can be divided into two regions, an apical region and a basal region that is simply a stalk. It receives the hermaphrodite duct and the duct from the albumen gland (region of the carrefour) and then passes into the interior of the albumen gland.

The spermoviduct is a long (20-40mm) winding, glandular structure with its apical end being adjacent to the albumen gland and terminating at the bifurcation of the vas deferens and the free oviduct. The male and the female conduits are in close approximation with each other having become confluent in the hermaphrodite duct and can not be

differentiated externally. The termination point of the spermoviduct is at the region where the vas deferens and the free oviduct branch off, each from a specific structure of the spermoviduct.

The vas deferens (18-46mm) passes anteriorly, parallel with the free oviduct, crosses the peniovaginal crotch and then runs parallel with the penis terminating in a short epiphallus. There was a swelling between the epiphallus and vas deferens which may be a remnant of the vestigal flagellum.

The epiphallus (1-3mm), a short enlarged structure which receives the vas deferens is the terminal point of the apical penis. The penial retractor muscle is attached to the epiphallus and the apex of the penis. A penial retentor muscle, which assist the retractor muscle, runs from the beginning of the epiphallus to the top of the penial sheath.

The penis is a club shaped structure (4-20mm) enclosed in a thin sheath and extends from the genital atrium to the epiphallus. The penis can be divided into two regions; the basal region which is enlarged and quite capacious, and the apical region which is narrow in diameter terminating with the epiphallus. The penis is quite muscular with a large penial chamber in which is found the stimulator. The stimulator is a complex structure originating on the dorsal lateral walls of the penis,

forming three-fourths of a circle, being interrupted only on the ventral surface and terminating as two irregular shaped fleshy, bodies hanging free in the penial cavity. The stimulator is not an intromittent organ, and probably serves as an excitatory organ during coitus.

The free oviduct is straight and appears muscular (8-16mm in length). It extends from the terminal end of the spermoviduct to the base of the spermathecal duct.

The spermathecal duct is short (4-10mm) with a broad base that tapers to a constriction, terminating as a clavate spermatheca. The spermatheca (3-8mm) is attached by a long muscle to the median portion of the spermoviduct.

The vagina is short (2-5mm) extending from the base of the spermathecal duct to the genital atrium. It has a wide diameter with a moderately capacious chamber which is lined by a number of rugose folds.

The genital atrium is short (1-3mm) and capacious receiving both the penial and vaginal ducts and opening to the exterior.

Monadenia fidelis

See Figs. 5 & 10

The hermaphrodite duct follows a tortuous route terminating in the albumen gland where it joins the basal portion of the short, unbranched talon and the duct from the albumen gland. The common duct passes into the albumen gland and makes its way to the spermoviduct.

The spermoviduct is very long (34-80mm) and extends from the albumen gland to the point where the vas deferens and free oviduct bifurcate from it.

The vas deferens passes from the terminal end of the spermoviduct and travels caudad, passing across the penio-vaginal crotch, turns dorsally and runs parallel with the penis. The vas deferens is connected by connective tissue to the base of the penis, but it is not closely appressed. The length is from 29-52mm and it terminates by joining the epiphallus at the point where the latter joins with the flagellum.

The penis is a short (5-15mm), stout, clublike structure being divided into a thin apical and a broad basal region. The basal region is adjacent to the genital atrium and has a broad diameter and a capacious chamber. The capacious chamber contains a short fleshy verge. The verge was quite striking, being very rough in appearance and having a number of rugose folds on the external surface.

The apical region of the penis is joined posteriorly by a long epiphallus (13-26mm) which is in turn joined by a lengthy flagellum at the junction where the vas deferens empties into it. Baker (personal communication) states that the epiphallus develops the body of the spermatophore with the tail developing in the flagellum.[1]

The line of demarcation between the penis and the epiphallus is not clearly defined, but the two may be separated by a small constriction.

The penial retractor muscle joins the epiphallus in its median region and attaches on the other end to the columella muscle.

The free oviduct extends for 4-10mm in length and is a straight and moderately wide tube. It terminates at the point where the spermathecal duct joins it.

The spermathecal duct is a long, narrow tube 30-75mm in length that terminates in a saccular spermatheca (4-11mm).

The point at which the spermathecal duct and the free oviduct become a common duct marks the beginning of the vagina, a rather short structure of 2-7mm. The vagina empties into the genital atrium.

The genital atrium is a large capacious structure (2-10mm) and receives the products of several independent

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[1] Baker, Horace B. Editor of Nautilus. 11 Chelten Road, Haverton, Pennsylvania.

structures. In addition to the penial and vaginal products mucus from the mucus gland and the dart from the dart sac are passed into the genital atrium.

The mucus gland is from 6-15mm in length, being oblong in shape and appears quite glandular. The mucus ejector, separated from the mucus gland by a narrow constriction, is a long narrow, muscular tube that inserts at the base of the dart sac.

The pear-shaped dart sac is located laterally to the genital atrium and opens into its right side. The dark is a double edged structure ranging from 2-6mm in length.

SUMMARY AND DISCUSSION

The anatomical facts collected have been applied to the scheme of classification of the Pacific Coast pulmonates in order to aid in identifications. Variations in the reproductive tracts of gastropods has proved to be the more accurate method in separating the lower taxa. It offers likewise a method for studying familial and evolutionary relationships. Johansson (14, p. 1-24) by studying the genital tracts of some mesogastropods was able to give an account of the origin of the pallial gonoducts and their present status in three genera. Webb in 1953 (25, p. 213-218) described two new species of Succineidae on the basis of their genitalia. Mead in 1943 (17, p. 675-719) and 1950 (18, p. 219-291) used the genital anatomy to reveal tangible differences between members of the genus Ariolimax (moerck) and some Achatinidae respectively. Mead found that not only did a careful study of the genital system reveal tangible differences between species and genera, but that the study was also valuable in arriving at an understanding of problems in phylogeny, taxonomy and even physiology. He states "to be absolutely sure of an identification of an immaculate specimen from a new locality, one must examine the genitalia." He placed a limitation on the area by stipulating a new locality, but I found in my study that positive identification of a specimen from any location is based

upon an examination of the genitalia.

Anatomy of the reproductive tracts in taxonomy is not without its problems. One that might arise has been pointed out by Franzen (11, p. 82-95), "the extent to which anatomical characters of species within a genus may be used successfully as a guide to systematic relationship is dependent upon sound knowledge of the nature and degree of variation that may exist among the members of a freely inter-breeding local population, or among a disjunct population of the same species. Without information concerning the nature and degree of individual and geographical variation within a population or in a series of populations, anatomical data can not be employed in full confidence."

Despite the reservations that one must take in using and interpreting this sort of data I am convinced that studies of this nature will help to clear up much of the chaos that exists within the taxonomic schemes of many classes. The use of reproductive tract data in taxonomy can best be summarized by Boudreaux (8, p. 145-150) "my feeling is that reproductive data are objective, and may be put to excellent use in helping to decide the relationship of arbitrary taxa whose erection was based upon subjective interpretation. Even though reproductive data are impossible to secure for many cases of dubious classificatory procedures, these data nevertheless should be used if

available because of their lack or arbitrariness."

Comparison of Described Species

In the genus Haplotrema, size would appear to be a major characteristic in distinguishing between the species H. vancouverense and H. sportella because H. vancouverense, according to Pilsbry (23, V. 2, pt. 1, p. 223), is the largest species in the genus. But one encounters a major problem when trying to distinguish between a small H. vancouverense and a mature H. sportella. I found that the shell characters are not different enough to distinguish between the two. For example the recurvature of the lip of the shell, (Fig. 3) characteristic of H. sportella was variable in my specimens. Superficially a small H. vancouverense cannot be differentiated from a typical H. sportella, therefore one must depend upon an examination of the genitalia in order to obtain an accurate identification. In both H. vancouverense and H. sportella the vagina is covered on some portion by a muscular collar and I found that the position of the collar, on the vagina is characteristic. In H. vancouverense the muscular collar was found to cover about one-eights of the median portion of the long vagina (Fig. 8): whereas in H. sportella the muscular collar covered almost the entire surface of the vagina (Fig. 6). In addition the talon in H. vancouverense was minute and clavate in comparison with

H. sportella where the talon was long with a spherical knob (Fig. 7); the vas deferens was long (47-63mm) and swollen at the base in H. vancouverense, but simple and short (10-21mm) in H. sportella; the penis was not divided into apical and basal chambers in H. vancouverense, but in H. sportella the principal penial chambers were divided into apical and basal halves. The free oviduct was longer in H. vancouverense (2-8mm) than in H. sportella (2-5mm) and the genital atrium of both species measured approximately the same: 1-2mm in H. vancouverense and 0.5-2mm in H. sportella. (Figs. 6 & 8)

As there are no species or genera closely related to Monadenia fidelis in this area one has no real problem in establishing a positive identification. For this snail shell characters were satisfactory (Fig. 5), but having a knowledge of the genitalia was also useful. Monadenia fidelis is a true helicoid with a prominent mucous gland and a two bladed dart 2-6mm long. (Figs. 10 & 12) The mucous gland was oblong in shape, 2-15mm in length. The epiphallus secretes the body of the spermatophore and was terminated in an appendix, the flagellum. There was a long spermoviduct and vas deferens, a moderately long free oviduct, a fleshy verge inside a bulbous penis and a capacious genital atrium.

Allogona townsendiana and Vespericola columbiana are both members of the family Polygyridae, which is

characterized by having the penis partially covered with a sheath adnate to the base and terminating in an epiphallus upon which the penial retractor is inserted. The epiphallus bears a very short concealed flagellum or sometimes none. A penial retentor muscle connects the epiphallus with the penis at the upper border of the sheath and the duct of the spermatheca is usually swollen (23, V. 1, pt. 2, p. 789).

The genital tract of Allogona differs from that of Vespericola in that it is larger, with longer spermoviduct, vas deferens, and spermatheca. (Figs. 13 & 16) The penis has no verge, but does have a stimulating organ. (Fig. 17) The penial chamber is capacious, the penial retentor muscle is prominent and there is a vestigial flagellum present. Vespericola has a long verge inside its penial sheath and the epiphallus is well developed, tapering at both ends. (Fig. 15)

Vespericola columbiana differs from Haplotrema sportella by having a spermatheca and spermathecal duct that are longer in length; by having a penial sheath that encloses the penis; by having a prominent verge and a long conspicuous epiphallus; and by the absence of a muscular collar covering the surface of the vagina. (Figs. 6 & 13)

Vespericola columbiana differs from Haplotrema vancouverense by having a penial sheath enclosing the

penis, epiphallus and a long prominent verge; and by the absence of a muscular collar covering a small portion of the vagina. (Figs. 8 & 13)

Monadenia fidelis differs from Vespericola columbiana by the presence of the dart and dart sac; the strongly developed mucus gland and ejector; the well developed flagellum; and the fleshy verge inside the penial chamber; however, it lacks the penial sheath enclosing the long verge. (Figs. 10 & 11)

Monadenia fidelis differs from Allogona townsendiana by the presence of the dart and dart sac; the strongly developed mucus gland and ejector; the well developed epiphallus and flagellum; and the fleshy verge inside the penial chamber. It lacks the penial retentor muscle; and the stimulating organ inside the penial chamber. (Figs. 10 & 16)

Monadenia fidelis differs from Haplotrema sportella by having the following: dart and dart sac, well developed epiphallus and flagellum, fleshy verge inside the penial chamber, prominent mucus gland and mucus ejector; and lacking a muscular collar on the surface of the vagina. (Figs. 6 & 10)

Monadenia fidelis differs from Haplotrema vancouverense by having the following: dart and dart sac; fleshy verge, well developed epiphallus and flagellum, and strongly developed mucus gland and ejector; and lacking a

muscular collar on the vagina. (Figs. 8 & 10)

Allogona townsendiana differs from Haplotrema vancouverense by having a stimulating organ inside the penial chamber, vestigial flagellum, and a penial retentor muscle; however, it lacks a muscular collar on the vagina. (Figs. 8 & 16)

Allogona townsendiana differs from Haplotrema sportella by having a stimulating organ inside the penial chamber, a vestigial flagellum, and a penial retentor muscle; however, it lacks a muscular covering of the surface of the vagina. (Figs. 6 & 16)

Key to the Terrestrial Snails Included Herein

1. Shell depressed, umbilicate; slightly thickened or narrowed; expanded peristome; upper lip margin usually somewhat straightened or curved downward 2

   Shell obtusely conical and narrowly umbilicate; white peristome is reflected and thickened; aperture rounded or nearly round 4

2. Shell dark and usually having a dark band above the periphery with pale borders above and below. Radula without side cusps or central and lateral teeth; marginal with bifid inner and usually simple outer cusp. Well developed mucous gland, and mucous ejector; two bladed dart inside a pear-shaped dart sac located laterally to the genital atrium.
   Monadenia fidelis (Figs. 5 & 10)

   Shell generally light colored without bands along the periphery; radula with relatively few, inverted chevron-shaped transverse rows. Central, vestigial or absent. Remainder of teeth aculeate; majority of teeth unicuspid and slender 3

3. Shell diameter 11-22mm.; rather sharply close striae on spire. Muscular collar covering almost all or all of vagina. Talon long with a spherical knob
   Haplotrema sportella (Figs. 3 & 6)

Shell diameter 22-33mm.; striations wrinkle-like and irregular. Muscular collar covering one eighth of the median portion of the long vagina. Talon minute and clavate ..... Haplotrema vancouverense (Figs. 4 & 8)

4. Shell with 6 whorls; diameter 15.6mm.; brown to black in color. Last whorl has weak, irregular spaced wrinkles and more or less find wrinkling and granulation. Shell covered with sparse hair. Penis with long verge (7-9mm.) inside a thin penial sheath; possessing a prominent epiphallus that tapers at both ends. ..... Vespericola columbiana (Figs. 1 & 13)

Shell with 6 whorls; diameter 25.8mm; smooth without hairs; color tawny olive to clay colored to pecan brown. Aperture nearly as high as wide. Prominent stimulator inside the penial chamber (7-10mm.); no epiphallus, but with vestigial flagellum present at terminal end of vas deferens
Allogona townsendiana (Figs. 2 & 16)

BIBLIOGRAPHY

1. Abdel-Malek, Emile T. The preputial organ of snails in the genus Helisoma (Gastropoda. Pulmonata). American Midland Naturalist 48:94-102. 1952.

2. _____. Morphological studies on the family Planorbidae (Mollusca:Pulmonata). I. Genital organs of Helisoma trivolus (Say). (Subfamily Helisomatinae F. C. Baker 1945). Transactions of the American Microscopical Society 73:103-124. 1954.

3. _____. Morphological studies of the family Planorbidae (Mollusca:Pulmonata). II. The genital organs of Biomphalaria boissyi (subfamily planorbinae, H. A. Pilsbry, 1934). Transactions of of the American Microscopical Society 73:285-296. 1954.

4. Baker, Horace Burrington. The land snail genus Haplotrema. Proceedings of the Academy of Natural Sciences of Philadelphia 82:402-425. 1930.

5. _____. Some Haplotrematidae. Nautilus 54:130-136. 1941.

6. Boettger, Von Caesar. Bemerkungen über im Deutschland vorkommenden Bernsteinschnecken (Family Succineidae). Zoologischer Anzeiger 127:49-64. 1934.

7. Boycott, A. E. The genitalia of Acanthinula aculeata. Proceedings of the Malacological Society of London 12: 221-226. 1917.

8. Boudreaux, H. Bruce. Reproductive data in classification. Symposium. The data of classification. Systematic Zoology 11:145-150. 1962.

9. Creek, Gwendoline A. The reproductive system and embryology of the snail Pomatias elegans (Muller). Proceedings of the Zoological Society 121:599-639. 1951.

10. _____. The morphology of Acme fusca (Montagu) with special reference to the genital system. Proceedings of the Malacological Society of London 29:228-240. 1953.

11. Franzen, Dorothea S. Variations in the anatomy of the Succineid gastropod Oxyloma retusa. Nautilus 76:82-95. 1963.

12. Fretter, Vera. The genital ducts of Theodoxus, Lamellaria, and Trivia and a discussion of their evolution in the prosobranchs. Journal of the Marine Biological Association 26:312-351. 1946.

13. Gould, A. A. New species of Helix. Proceedings of Boston Society of Natural History 2:167-178. 1846.

14. Johansson, John. Genital organs of two Alvania species, and a comparison with related families (Mollusca:prosobranchs). Arkiv for Zoologi 9:377-387. 1956.

15. _____. On the genital organs of some mesogastropods: Cerithium vulgatum(Brug), Triphora perversa and Melanella(Eulima) intermedia (Cantr). Contributions to the phylogeny of the pallial gonoducts of the prosobranchia. Zoologiska Bidrag fran Uppsala 30:1-24. 1956.

16. Lea, Isaac. Descriptions of new freshwater and land snails. Transactions of the American Philosophical Society 6:87-89. 1839.

17. Mead. Albert R. Revision of the giant west coast land slugs of the genus Ariolimax(Moerck). (Pulmonata: Arionidae). American Midland Naturalist 30:675-719. 1943.

18. _____. Comparative genital anatomy of some African Achatinidae(Pulmonata). Bulletin of the Museum of Comparative Zoology 105:219-291. 1950.

19. Pilsbry, Henry A. In Manual of Conchology Vol. 9, Philadelphia, Conchological Section, Academy of Natural Sciences, 1894. p. 76.

20. _____. Genus Epiphragmophora. In Manual of Conchology Vol. 9, Philadelphia, Conchological Section, Academy of Natural Sciences, 1895. p. 198.

21. _____. Family Circinaria. In Manual of Conchology Vol. 19, Philadelphia, Conchological Section, Academy of Natural Sciences, 1908. p. XI.

22. _____. Species of Polygyra from Montana, Idaho and Pacific Coast states. Proceedings of the Academy of Natural Sciences of Philadelphia 80:182. 1928.

23. _____. Land Mollusca of North America (North of Mexico). Philadelphia, 1940. 2 vols. in 4. (Academy of Natural Sciences of Philadelphia. Monograph no. 3).

24. Watson, Hugh. The affinities of Pyramidula, Patulastra, Acanthinula and Vallonia. Proceedings of the Malacological Society of London 14:6-30. 1920.

25. Webb, Glenn R. Anatomical studies on some midwestern Succineidae and two new species. Journal of the Tennesse Academy of Science 28 (3):213-218. 1953.

26. Vanatta, E. G. Description of four new American shells. Proceedings of the Academy of Natural Sciences of Philadelphia 76:25. 1924.

APPENDIX

Key to the figures

Fig. 1. Dorsal and Ventral view of *Vespericola columbiana* shell.

Fig. 2. Dorsal and ventral view of *Allogona townsendiana* shell.

Fig. 3. Dorsal and ventral view of *Haplotrema sportella* shell.

Fig. 4. Dorsal and ventral view of *Haplotrema vancouverense* shell.

Fig. 5. Dorsal and ventral view of *Monadenia fidelis* shell.

FIG 1

FIG 2

FIG 3

FIG 4

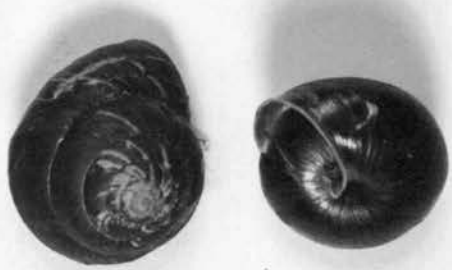

FIG 5

PLATE 1

Key to the figures of Plate 2.

HD--Hermaphrodite duct
AG--Albumen gland
SO--Spermoviduct
C --Region of carrefour
FO--Freeoviduct
VD-- Vas deferens
F --Flagellum
D --Dart
SP--Spermatheca
ME--Mucus ejector
PG--Prostate gland
VG--Vagina
GA--Genital atrium
E --Epiphallus
P --Penis
S --Stimulator
V --Verge
DS--Dart sac
SD--Spermathecal duct
MG--Mucus gland
PR--Penial retractor muscle
MC--Muscular collar

Fig. 6. Drawing of the reproductive tract of Haplotrema sportella.

Fig. 7. Drawing of talon and albumen gland of Haplotrema sportella.

Fig. 8. Drawing of reproductive tract of Haplotrema vancouverense.

Fig. 9. Drawing of albumen gland and talon of Haplotrema vancouverense.

Fig. 10. Drawing of reproductive tract of Monadenia fidelis.

Fig. 11. Drawing of verge of Monadenia fidelis.

Fig. 12. Drawing of double edged dart of Monadenia fidelis.

Fig. 13. Drawing of reproductive tract of Vespericola columbiana.

Fig. 14. Drawing of albumen gland and talon of Vespericola columbiana.

Fig. 15. Drawing of verge of Vespericola columbiana.

Fig. 16. Drawing of reproductive tract of Allogona townsendiana.

Fig. 17. Drawing of stimulator of Allogona townsendiana.

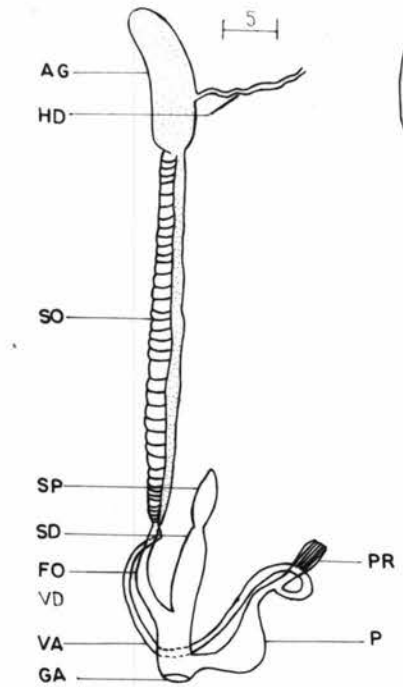

FIG 16

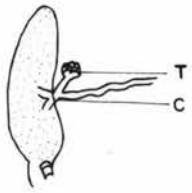

FIG 9

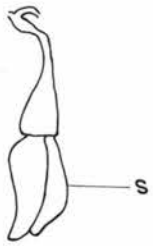

FIG 17

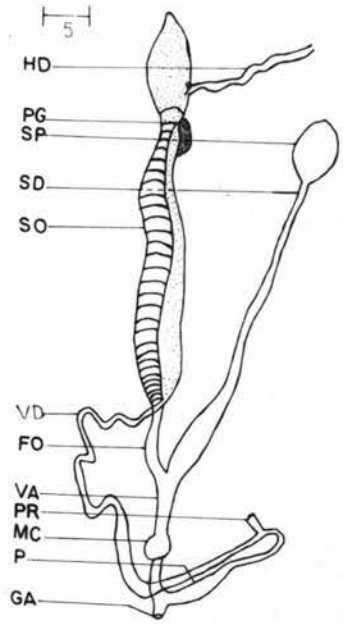

FIG 8

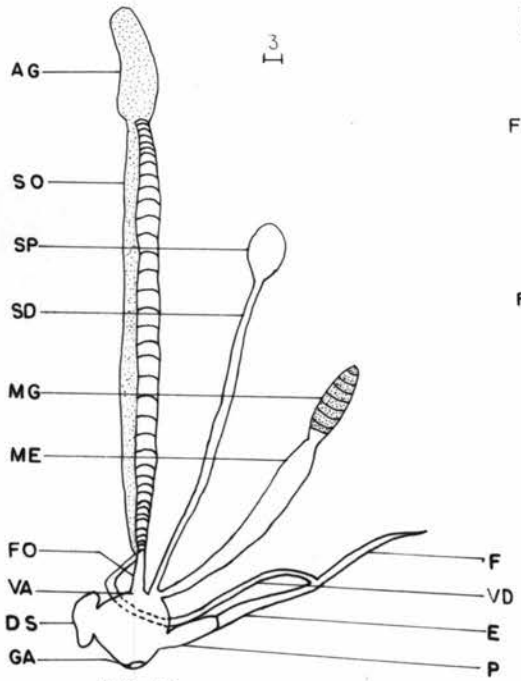

FIG 10

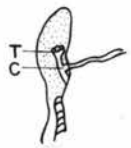

FIG 14

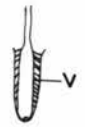

FIG 15

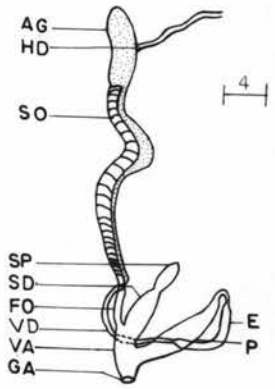

FIG 13

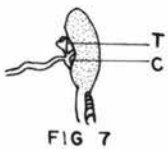

FIG 7

FIG 12

FIG 11

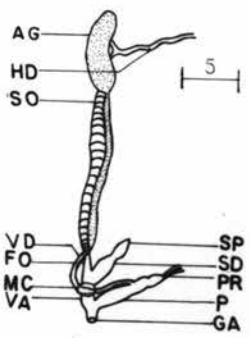

FIG 6

PLATE 2

Table 1. Measurements of Genitalia in mm of Haplotrema sportellis

Spermathecal duct	--	4	3	3	--	--	2	--
Spermatheca	--	--	1	1	--	--	1	--
Free oviduct	--	2	3	3	2	5	3	4
Sperm oviduct	--	--	25	22	--	--	17	17
Vagina	7	1	2	2	3	3	1	1.5
Vas deferens	--	--	21	12	--	21	--	10
Penis	4	4	9	6	4	9	5	6
Genital atrium	2	0.5	0.5	--	1	1	0.5	1
Epiphallus	--	--	2	--	--	--	1	--

Table 2. Measurements of Genitalia in mm. Haplotrema vancouverense

Spermathecal duct	25	--	--	24	24	--	35	27	--	--	29	25	22	30	21	28	26
Spermatheca	--	--	--	3	--	--	4	5	--	--	3.1	3	4.5	4	--	4.5	4
Free oviduct	8	8	4	3	2	3	4	6	4	3	7	6	5	5	4	5	4
Sperm oviduct	--	--	--	--	25	--	--	30	20	30	36	35	33	33	--	26	--
Vagina	12	7	10	11	10	9	9	11	9	9	13	11	10	12	9	11	8
Vas deferens	55	45	--	56	50	--	--	--	47	63	--	--	--	--	--	--	--
Penis	13	5	11	12	12	11	11	12	12	16	19	16	15	15	10	13	9
Genital atrium	1	--	1	--	1	1	--	2	1	1.5	--	1	--	1.5	1	1	--

Table 3. Measurements of Genitalia in mm. Vespericola columbiana

Spermathecal duct	3	3	3	3	3	2	3	6	7	3	3	3	4	6	4	2	2	3	3	3
Spermatheca	3	3	3	3	4	3	4	4	3	3	3	3	3	5	3	4	5	4	4	5
Oviduct	5	5	5	6	6	5	5	6	5	4	7	6	5	7	5	9	6	7	7	4
Sperm oviduct	15	15	15	20	15	20	25	--	23	22	--	23	20	27	22	23	--	22	--	28
Vagina	3	3	3	3	3	2	2	3	3	3	3	2	4.5	4	4	4	4	4	3	3
Vas deferens	14	23	22	--	--	--	--	--	19	22	22	--	16	18	12	15	20	21	14	20
Penis	5	4	4	4	4	11	6	9	9	10	11	9	5	10	9	10	8	7	6	9
Genital atrium	1	1	1	--	--	1	--	--	1.5	2	2	2	2	1	--	0.5	--	1	1	1
Epiphallus	3.5	12	12	--	13	14	--	--	12	15	14	9	10	20	12	19	14	13	10	12
Verge	--	--	--	--	--	7	--	--	8	8	--	--	--	9	--	--	--	--	--	--

Table 4. Measurements of Genitalia in mm. Allogona townsendiana.

Spermathecal duct	6	6	4	10	7	9	10	7	6	3	6	6	5	5	6	6	6	4	6	4
Spermatheca	3	3	5	7	3	8	7	5	6	3	4	5	3	4	3	3	6	4	4	8
Free oviduct	8	12	6	13	12	16	16	12	17	14	13	14	15	13	12	8	12	15	12	14
Sperm oviduct	40	30	35	32	30	20	30	30	40	33	37	30	20	20	30	--	25	25	25	35
Vagina	3	3	5	5	3	4	5	3	3	4	5	3	--	3	3	2	3	3	3	3
Vas deferens	21	36	28	--	42	18	41	30	46	50	46	34	40	34	40	43	45	40	--	42
Penis	8	8	7	14	15	20	14	10	9	8	10	8	8	7	4	8	4	9	7	9
Genital atrium	2	2	3	2	1.5	3	3	3	2	2	1	2	2	1	--	1	1	1.5	--	1
Epiphallus	3	--	--	--	1	--	--	1	--	1	1	--	2	--	--	--	--	--	--	--
Stimulators	--	9	7	8	10	11	10	9	11	10	8	--	8	6.5	8	12	10	11	10	10

Table 5. Measurements of Genitalia in mm. Monodenia fidelis

Spermathecal duct	--	53	30	33	70	34	52	60	42	48	55	45	41	60	70	64	--	55	60	70
Spermatheca	--	7	--	8	7	4	5	9	6	6	5	6	4	6	8	6.5	7	5	8	11
Free oviduct	--	4	7	5	4	8	6	10	6	6	7	6	4	8	9	8	6	7	6	5
Sperm oviduct	--	80	45	--	60	70	55	70	60	52	60	46	34	65	82	77	65	70	80	60
Vagina	--	6	2	4	6	6	6	6	4	4	6	4	3	5	5	6	6	5	7	7
Vas deferens	47	43	32	--	47	40	30	28	40	40	47	46	--	--	55	53	--	--	29	43
Penis	9	5	5	6	10	12	13	12	10	10	12	8	10	9	10	12	15	--	12	10
Genital atrium	--	2	--	4	6	--	--	7	--	4	--	2	--	--	10	7	3	5	6	10
Epiphallus	10	15	12	17	22	20	10	22	13	18	18	19	15	23	24	17	30	20	20	17
Flagellum	27	15	9	18	17	17	20	21	16	18	20	14	17	21	21	16	15	20	21	13
Dart sac	8	4	4	4	5	4	7	8	6	6	6.5	6.5	4.5	6	6	6	8	9	6	9
Dart	4	2	--	5	5	3	3	6	--	4	5	3	3	4.5	4	4	4	--	5	--
Mucus ejector	--	34	--	36	30	37	38	35	--	--	28	25	14	34	38	30	40	40	40	37
Mucus gland	--	2	--	11	15	12	15	15	--	--	10	12	7	12	12	12	15	15	13	12
Verge	3	3	6	--	3	4	--	3	3.5	3	3	3.8	3	3	2.5	3.5	3.7	3	3	3