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STUDIES ON THE ANATOMY OF LYMNAEA HUMILIS SAY[1]

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Abstract

The topographic anatomy of *Lymnaea humilis* is described, giving the relative positions of the various internal organs. A description of the anatomy of the cephalic hemocoele is also given. Like *Lymnaea stagnalis* the central nervous system of *L. humilis* consists of the paired cerebral, buccal, pedal, pleural, and parietal ganglia and the unpaired abdominal ganglion. The nerves arising from the central nervous system are described and particular attention was devoted to the nerves arising from the pedal ganglia and innervating the foot; fourteen new nerves are named or described. The reproductive system of *L. humilis* is divided into: (*a*) the ovotestis and its duct, (*b*) the female system, and (*c*) the male system. In reproductively active snails, the female system is the largest of the three portions, and consists of the uterus, oothecal gland, vagina, and seminal receptacle. An accessory structure, the albumen gland, is very large in *L. humilis*. The male system consists of the upper and lower prostate, vas deferens, and male copulatory organ. The connections between the hermaphrodite duct and the male and female systems show considerable structural consolidation compared to these connections in *L. stagnalis*. The muciparous gland is not a distinct entity in *L. humilis*.

Introduction

In recent years, the anatomy of gastropods has received increased attention because certain of the internal structures are important in understanding the systematics of this group of molluscs. In his critical study of the Lymnaeidae, Hubendick (18) based much of his revision of this family on the size and shape of parts of the reproductive system. However, there is still evident need for comparative anatomical studies upon many of the Lymnaeidae, as well as other Pulmonata. Moreover, a knowledge of snail morphology is essential in studying trematode life cycles, as it forms an important basis in the interpretation of the developmental stages of flukes.

An excellent bibliography on snail anatomy is contained in the paper by Carriker (12) and only the more pertinent works will be mentioned here. The topographic anatomy of *Lymnaea stagnalis appressa* has been described by Carriker (12), who made an exhaustive study on the structure of the alimentary canal of this snail. The work of Carriker and Bilstad (13) on the histology of the digestive system of *L. stagnalis* is an extensive one.

The nervous system of the Lymnaeidae has been studied by Lacaze Duthiers (21), Baker (5, 6), Bargmann (10), Elo (15), and most recently Carriker (12). One of the most thorough investigations into the nervous system of any pulmonate is that done by Schmalz (22) on *Helix pomatia*. Lacaze Duthiers' paper (21) was the first extensive work dealing with the nervous system of the Lymnaeidae alone. He described the principal ganglia and nerve trunks of *Lymnaea pereger* and *L. stagnalis*. Elo (15) dealt particularly with the

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ramifications of the main nerve trunks, especially those serving the penis, mantle, and intestine of *L. stagnalis*. He also attempted to homologize some of the principal nerves of *L. stagnalis* and *H. pomatia*. Although Carriker (12) was concerned primarily with the innervation of the alimentary canal of *L. stagnalis*, he also studied most of the remaining principal nerves. In general, the findings of these two authors agree reasonably well. However, Carriker (12) clarified the nomenclature of the central nervous system of *L. stagnalis*, basing as much as possible on the names used by former investigators. Carriker's (12) system of nomenclature is used in the present study, except where new nerves are described.

The gross morphology of the reproductive tract of *Lymnaea* has been studied by Baudelot (11) and Crabb (14), who also briefly mentioned the histology as did Klotz (20). The first accurate description of the reproductive system of *L. stagnalis* was given by Crabb (14). More recently, Holm (17), in his detailed histological studies, elaborated and clarified many of the functional aspects. The ovotestis (hermaphrodite gland) of *L. stagnalis* has been investigated by Archie (4) and the embryology of the reproductive system as a whole by Fraser (16).

The reproductive system of members of the Planorbidae has been investigated by Baker (8), Hubendick (19), and also by Abdel-Malek (2, 3), who gave a brief but thorough coverage of the literature on these structures in other groups of Gastropoda.

Some aspects of lymnaeid systematics, and, in particular, the position of *Lymnaea humilis* Say deserve special comment. Recently, Hubendick (18) questioned the extensive use of some morphological features in the taxonomy of the family Lymnaeidae. One of these is the shell, which shows great intraspecific variation. This variation is well exemplified in his biometric analysis of the shell *Lymnaea peregra*. Shell size and thickness, as well as zebrine coloration and the position of growth lines, do not possess taxonomic value because they are less dependent upon hereditary conditions than upon environmental factors. Another is the radula, the use of which as a key character is limited by the fact that divergences in its structure are generally so small that reliable observations are difficult to make. This is further complicated by the smallness of the radula itself. Previously, considerable importance has been attached to variations in the shell and radula (6, 7). However, the findings of Hubendick (18) indicate that extreme care is necessary in using these characters in the systematics of the Lymnaeidae. As a result of critical study, the following species recognized by Baker (6) have been linked by Hubendick (18) to *Lymnaea humilis* Say: *doddsi* Baker, *umbilicata* Adams, *cyclostoma* Walker, *parva* Lea, *parva sterki* Baker, *owascoensis* Baker, *pilsbryi* Hemphill, *ferruginea* Haldeman, *humilis modicella* Say, *humilis rustica* Lea, *obrussa* Say, *obrussa peninsulae* Walker, *obrussa exigua* Lea, *obrussa decampi* Streng, *galbana* Say, and *petoskeyensis* Walker. Hubendick (18) was hesitant to link *caperata* Say with *Lymnaea humilis*. *L. caperata* is recognized as a pond or woodland pool inhabitant.

Material for the present study was collected in the region of Ann Arbor, Michigan, principally from two localities. Both were on the Raisin River. One was located 3 miles southeast of Clinton, at Newburg, in Lenawee County; the other 1 mile northwest of Clinton, in Washtenaw County.

Materials and Methods

For both gross anatomy and histological studies it was necessary to relax snails prior to preservation or fixation. Menthol crystals were found to be satisfactory for relaxation (1). Living snails were placed in a stender dish and powdered menthol crystals were spread over the surface of the water. Best results were obtained by then refrigerating the menthol-treated snails for 18 to 24 hours. At room temperature sufficient relaxation occurred in 2 to 4 hours. However, at room temperature some menthol-treated snails occasionally died and the resultant degenerative changes made tissues unsatisfactory for sectioning. As soon as the snails failed to contract when placed in preservative or fixative they were judged to be sufficiently relaxed.

A 10% aqueous solution of formaldehyde was the fixative used most frequently. Gilsons and Bouins were also used. The relaxed snails were placed directly into the fixative and transferred after 24 hours to 70% alcohol. The alcohol was changed again after 24 hours to obtain a more complete removal of formaldehyde.

A Petri dish, partially filled with wax, served as a dissection tray. 'Minuten-nadeln', jeweller's forceps, and standard laboratory equipment were used as dissecting instruments. Tiny scalpels were made from the 'minuten-nadeln' by grinding them down on a fine grade of stone. Both the needles and the scalpels were inserted into balsawood handles. Equal parts of glycerin and 70% alcohol were used as a dissecting fluid for relaxed and preserved snails. This solution kept the tissues soft and easy to work. Relaxed living snails were also dissected. A few of these snails were raised in the laboratory; however, most were field specimens. These field snails were remarkably free of parasites.

Serial sections of both the entire animal and individual organs were made to confirm the identification of dissected structures. Acid alcohol was used for the removal of the shell, and gas trapped under the mantle cavity was removed by vacuum pump. If the gas were not removed, inadequate infiltration of wax resulted. Sections 8 or 10 to 50 μ were made and these were stained with Harris's hematoxylin and orange G and mounted in Canada balsam.

Topographic Anatomy

The description of the topographic anatomy of *L. humilis* (Figs. 1 to 6) is based upon that of a relaxed snail with the following shell dimensions: length 10.2 mm.; greatest width 5.5 mm.; length of aperture 5.7 mm.; width of aperture 5.1 mm. *L. humilis* of these dimensions has about five whorls and may be described as an 'average' size for a snail which has overwintered in the region of Ann Arbor, Michigan, and is 8 or 9 months old.

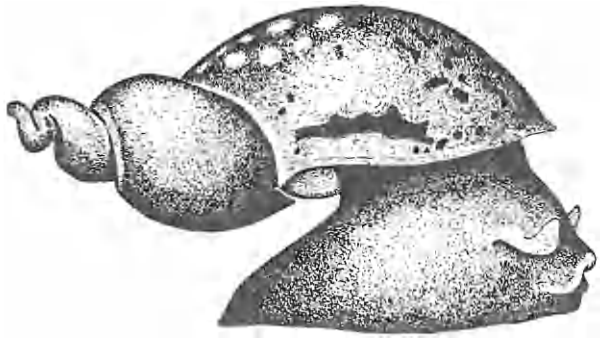
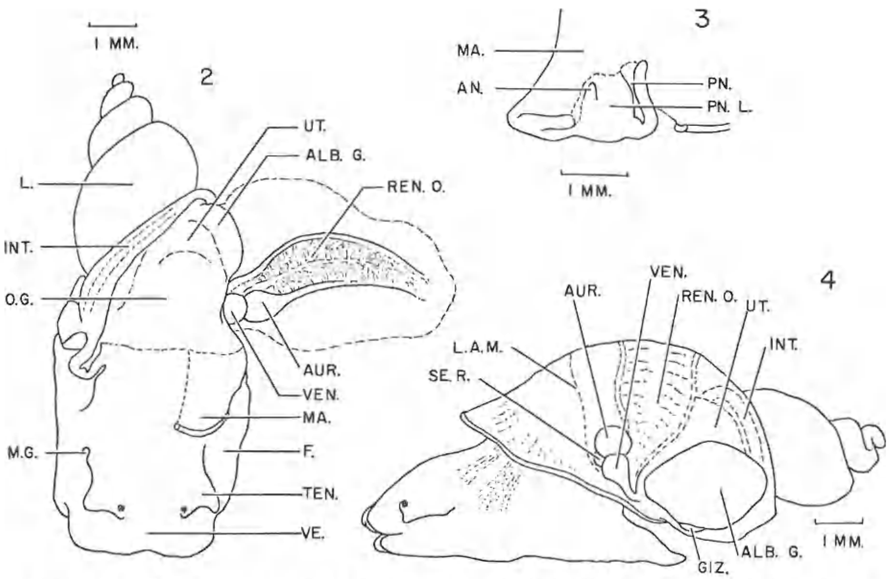


FIG. 1. *L. humilis* with the shell removed to show mantle pigmentation. Note the conspicuous bar of pigment parallel to the edge of the mantle.



FIGS. 2–4. Topographic features of *L. humilis* after removal of the shell. FIG. 2. Dorsal view with mantle cut. FIG. 3. Mantle partly cut to show anal and mantle cavity openings. FIG. 4. Lateral view of *L. humilis*.

A.—first portion of the hermaphrodite gland duct
AB.G.—abdominal ganglion
ALB.G.—albumen gland
ALB.G.D.—albumen gland duct
AN.—anus
AO.N.—aortic nerve
A.P.N.—anterior pedal nerve
A.PL.N.—anterior pallial nerve
AUR.—auricle
A.V.N.—anterior velar nerve
B.—second portion of the hermaphrodite gland duct
BC.C.—buccocerebral connective
B.G.—buccal ganglion
B.M.—buccal mass
B.R.M.—buccal retractor muscle
C.—third portion of the hermaphrodite gland duct
C.L.—commissural lobule
CO.N.—columellar nerve
C.P.N.—central pedal nerve
DB.N.—dorsobuccal nerve
DL.N.—dorsolabial nerve
D.M.—dorsal mandible
E.—eye
E.P.N.—external pedal nerve
F.—foot
F.A.C.P.—first anterocentral pedal nerve
F.G.P.—female genital pore
F.L.P.P.N.—first lateroposterior pedal nerve
F.N.—frontal nerve
GIZ.—gizzard
G.N.—gastric nerve

In a living *L. humilis* the color of the foot (F.) and body normally exposed beyond the rim of the aperture varies from light to dark gray. Occasionally the dorsum of the body is almost black. In a relaxed animal the length of the foot from the tip of the velum (VE.) to the most posterior part is 7.2 mm.; the greatest width at the anterior end is 4.2 mm. The velum (Fig. 2) of *L. humilis* is prominent and the longitudinal mouth as well as part of the dorsal mandible (Fig. 6, D.M.) are on the mid-ventral surface of the velum.

The eyes are located at the base of the triangular tentacles in the anterior angle, and measure about 100 μ in diameter (Figs. 2 and 4). The height from the base of the tentacle to its apex is approximately 0.85 mm. The length of the entire base is 1.9 mm. and the distance between the eyes is about the same.

The male genital pore (Fig. 2, M.G.), situated at the base of the right tentacle in the posterior angle, is a longitudinal slit about 200 μ long.

When the shell is removed, the mantle over the entire body whorl is found to be heavily pigmented but is windowed by circular areas where pigmentation is absent (Fig. 1). These areas vary in size but are generally smaller posteriorly. Through these, the outlines of the organs beneath the mantle may be partly seen (Fig. 4). In the region of the pneumatopore, about 1.70 mm.

H.D.B.—second portion of the hermaphrodite duct
H.D.C.—third portion of the hermaphrodite duct
IN.C.N.—inferior cervical nerve
IN.L.N.—inferior labial nerve
INT.—intestine
I.P.N.—internal pedal nerve
I.PL.N.—internal pallial nerve
L.—liver
L.A.M.—line of attachment of mantle to body
LB.N.—laterobuccal nerve
L.IN.C.N.—lateral inferior cervical nerve
L.L.—lateral lobule
L.M.—longitudinal muscle
L.P.G.—lower prostate gland
L.PL.N.—left pallial nerve
L.R.CO.N.—lateral ramus of the columellar nerve
L.S.C.N.—lateral superior cervical nerve
L.V.N.—lateral velar nerve
MA.—mantle
M.G.—male genital pore
M.IN.C.N.—medial inferior cervical nerve
M.PL.N.—median pallial nerve
M.S.C.N.—medial superior cervical nerve
M.V.N.—medial velar nerve
OE.—esophagus
O.G.—öothecal gland
OP.N.—optic nerve
OT.N.—optotentacular nerve
PE.G.—pedal ganglion
PE.N.—penial nerve
PE.S.—penis sheath
P.G.—parietal ganglion
PL.G.—pleural ganglion
PN.—pneumatopore
PN.L.—pneumatopore lip
P.P.N.—posterior pedal nerve
PRE.—preputium
PRO.M.—protractor muscle of buccal mass
P.V.N.—posterior velar nerve
REN.O.—renal organ
R.M.PRE.—retractor muscle of the preputium
R.M.P.S.—retractor muscle of the penis sheath
R.PL.N.—right pallial nerve
R.P.P.N.—right posterior pedal nerve
S.A.C.P.—second anterocentral pedal nerve
S.C.N.—superior cervical nerve
S.D.—salivary duct
SE.R.—seminal receptacle (Fig. 4)
S.G.—salivary gland
S.L.N.—superior labial nerve
S.L.P.P.N.—second lateroposterior pedal nerve
S.N.—salivary nerve
SPL.N.—splanchnic nerve
S.R.—seminal receptacle (Figs. 10, 13)
S.R.D.—duct of the seminal receptacle
TEN.—tentacle
TE.N.—tentacular nerve
U.P.G.—upper prostate gland
UT.—uterus
VA.—vagina
VB.N.—ventrobuccal nerve
V.D.—vas deferens
VE.—velum
VEN.—ventricle
VL.N.—ventrolabial nerve
VPL.N.—ventropallial nerve

above the edge of the mantle, is a bar of pigment, a constant feature in *L. humilis* found in the region of Ann Arbor (Fig. 1). This bar of pigment runs approximately parallel to the edge of the mantle and is about 2.75 mm. long and 0.75 mm. wide.

The pneumatoporal (or pneumostomal) lip (PN.L.) is under the mantle at the right posterior edge near the tip of the aperture of the shell (Fig. 3). On its lateral surface is the pneumatopore (PN.), the more or less vertical (to the edge of the mantle) opening of the lung; the anus (AN.) is posterior to it. The length of the pneumatoporal lip at its base is 1.5 mm. The pneumatopore is the only opening into the mantle cavity.

The female genital pore (F.G.P.) is a longitudinal slit about 400 μ long under the lip of the pneumatopore (Fig. 12). It is borne on a distinct oval mound of tissue. Occasionally, in sufficiently cleared specimens, the vas deferens is visible as a narrow tube running through the hemocoele wall between the male and female pores.

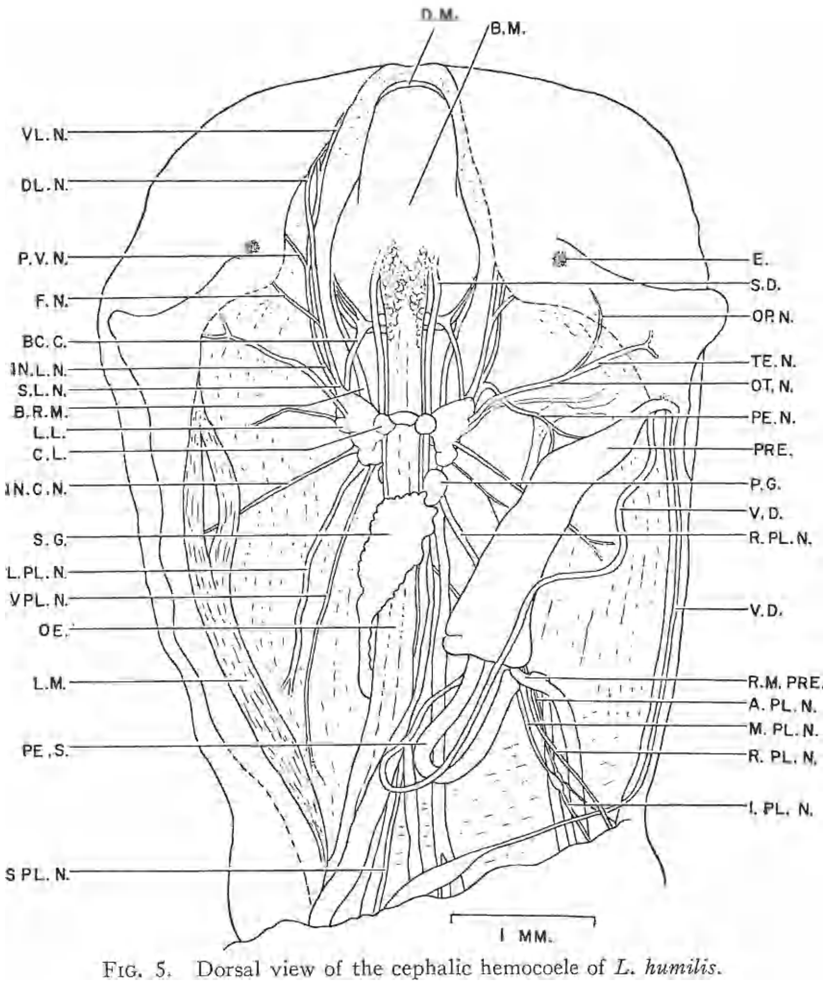


FIG. 5. Dorsal view of the cephalic hemocoele of *L. humilis*.

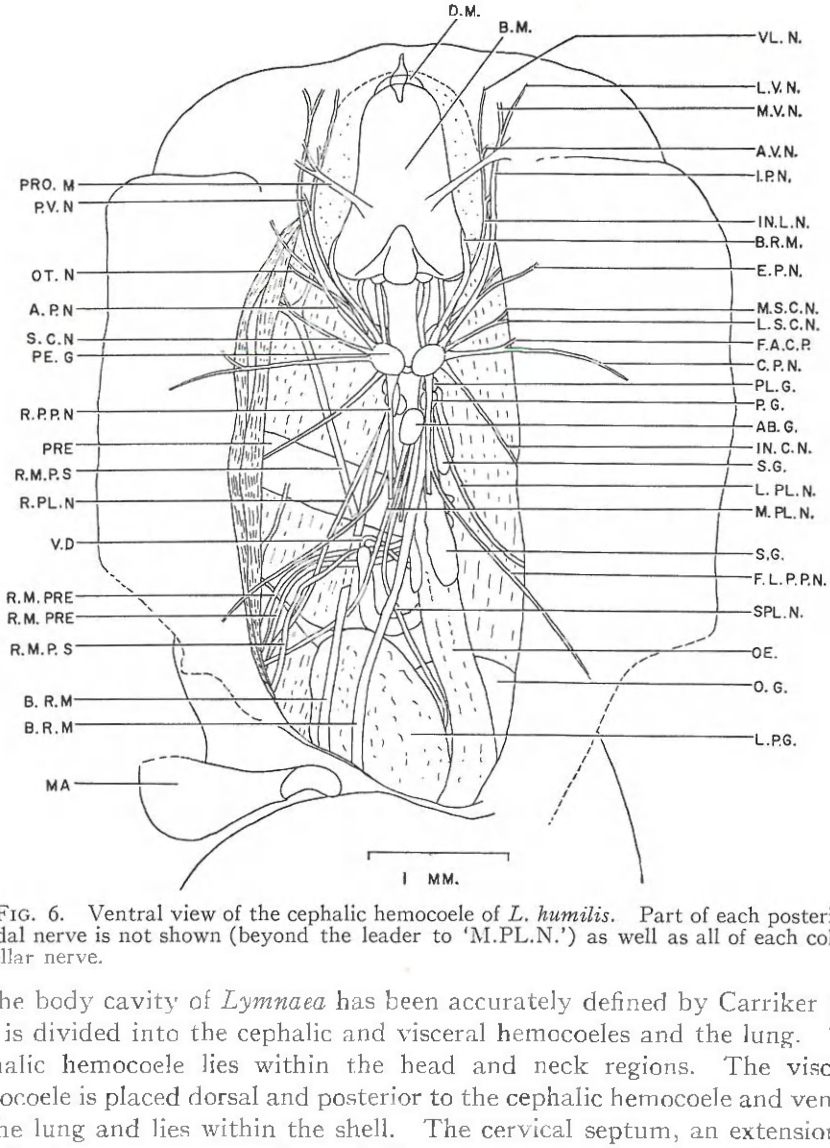


FIG. 6. Ventral view of the cephalic hemocoele of *L. humilis*. Part of each posterior pedal nerve is not shown (beyond the leader to 'M.PL.N.') as well as all of each columellar nerve.

The body cavity of *Lymnaea* has been accurately defined by Carriker (12) and is divided into the cephalic and visceral hemocoeles and the lung. The cephalic hemocoele lies within the head and neck regions. The visceral hemocoele is placed dorsal and posterior to the cephalic hemocoele and ventral to the lung and lies within the shell. The cervical septum, an extension of the diaphragm, separates the cephalic and visceral hemocoeles (12).

Beneath the mantle on the left side the outlines of several organs may be seen (Fig. 4). The distinctness of these outlines varies with the degree of mantle pigmentation. The ventricle (VEN.) and auricle (AUR.) of the heart are usually easily discernible as is the seminal receptacle (SE.R.) which lies mostly under the heart. The seminal receptacle is bright orange in the living snail. The broad, flat, creamy-white kidney or renal organ (REN.O.), posterior to the heart, is attached to and crosses the mantle transversely to the pneumatopore. Its general outline is visible through the mantle. A small extension of the kidney reaches ventrad between the ventricle and the voluminous albumen gland (ALB.G.). The kidney is exceedingly friable in the living snail, disintegrating into flocculi if manipulated roughly. Dorsal to the albumen gland the outline of part of the uterus (UT.) can be seen. The lung lies dorsal to the uterus and is devoid of accessory respiratory structures as in *Lymnaea stagnalis* (Carriker (12)).

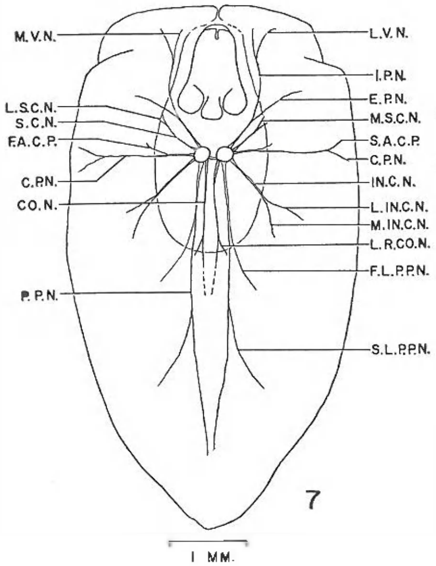
The principal features of the cephalic hemocoele are shown in Figs. 5 and 6. The greatest length of the cephalic hemocoele is approximately 4.5 mm. The floor of the hemocoele is gently rounded from side to side and the posterior portion of the floor narrows and slopes in a posterodorsal direction towards the cervical septum making an angle of about 60 degrees with the ventral surface of the foot. Strong longitudinal muscles (L.M.), which converge posteriorly under the lower prostate (L.P.G.) and öothecal glands (O.G.) to form the columellar muscle, define the walls of this cavity. These muscles extend to both sides of the buccal mass. The expansive arched roof of the cephalic hemocoele extends anteriorly from the line of attachment of the mantle to the body wall. The muscles of the roof arise as a common sheet but soon separate into six broad, flat bands, three on either side of the middorsal line. The posterior pair pass lateroventrad and become continuous with one another on the floor of the cephalic hemocoele where they lie transversely. The central pair extend anterolaterad, and the anterior pair extend anteriad, lateral to the buccal mass. These muscles line the roof of the cephalic hemocoele internally and pass internal to the longitudinal muscles which form the walls of the cephalic hemocoele. Only in well-cleared animals are they visible externally.

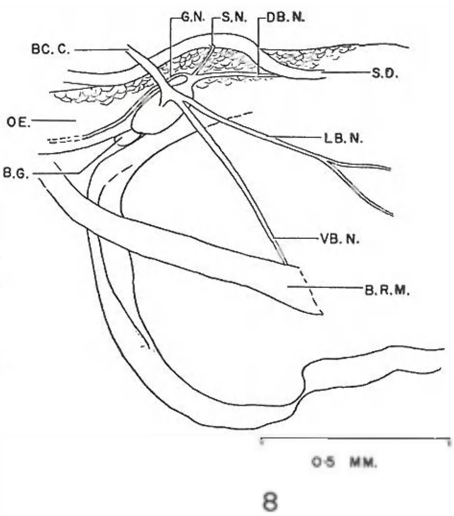
The anterior part of the cephalic hemocoele is occupied by the pear-shaped buccal mass (B.M.). It is a light orange-red in the living snail. The prominent buccal retractors (B.R.M.), which arise in the columellar muscle, insert on the lateral surfaces of the buccal mass. The delicate capitocerebral membrane, which is peppered with pigment, surrounds the buccal mass as it does in *Lymnaea stagnalis* (12), screening this organ from the rest of the cephalic hemocoele. The large preputium (PRE.) occupies the right central portion of the cephalic hemocoele.

Posterior to the ganglia of the central nervous system are the salivary glands (S.G.), which mostly flank the esophagus (OE.) on either side. Two thick salivary ducts (S.D.) lead from the glands into the dorsum of the buccal mass. The esophagus bends slightly to the left in the cephalic hemocoele, penetrates the cervical septum, and turns ventrad, passing beneath the albumen gland. The esophagus is fairly heavily pigmented, especially in its posterior part. It is followed by the crop and the bright, orange-red, bilobed gizzard (Fig. 4, GIZ.), both of which are ventral to the albumen gland. The pylorus, leading from the gizzard, turns anteriad around the right lobe of the gizzard. The alimentary canal continues as the intestine (Figs. 2 and 4, INT.), which turns sharply posteriad, ventral to the esophagus and crop, and follows a course along the left ventral margin of the albumen gland. It then angles sharply to the right and makes a gradual loop upon itself in the liver (Fig. 2, L.) where it passes superficially into the liver tissue and becomes less distinctly outlined. It continues towards the right along the edge of the mantle beneath the suture of the body whorl. The intestine merges into the short rectum which terminates in the anus (Fig. 3, AN.).

The Nervous System

The central nervous system of *L. humilis* consists of the paired cerebral (C.G.), buccal (B.G.), pedal (PE.G.), pleural (PL.G.), and parietal ganglia (P.G.) and the unpaired abdominal ganglion (AB.G.) (Figs. 5 to 9). The cerebral ganglia lie dorsolateral to the esophagus and are joined by a stout connective; the pedal and parietal ganglia and the abdominal ganglion are ventral to the esophagus. The pleural ganglia are lateral and the buccal ganglia are nestled under the esophagus at its junction with the buccal mass. The buccal ganglia are obscured from view dorsally by the thick salivary ducts but are partially visible from the ventral aspect (Figs. 6 and 8). With exception of the pedal connective, which is delicate and seen only with difficulty, the connectives between the remaining ganglia are stout and conspicuous. The width of the cerebral ganglia and connective, measured from the dorsal aspect, is about one millimeter. The greatest length of a cerebral ganglion is approximately 400 μ and of the abdominal ganglion, 300 μ. The pedal ganglia and the right parietal ganglion, which is markedly larger than the left, are about equal in length to the abdominal ganglion. The remaining ganglia are smaller; the smallest are the buccal ganglia which are about 200 μ in length.





FIGS. 7 and 8. Nerves of the foot and buccal mass of *L. humilis*. FIG. 7. The principal nerves arising from the pedal ganglia and innervating the foot of *L. humilis*. FIG. 8. Lateral view of the main nerves supplying the buccal mass and alimentary canal of *L. humilis*.

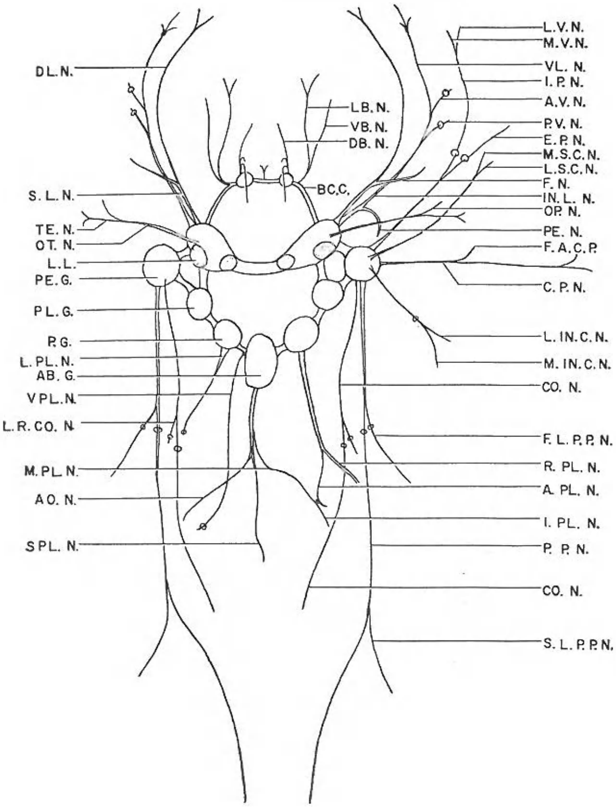


FIG. 9. Diagram of a dorsal view of the nerves arising from the ganglia of the centra nervous system of *L. humilis*. The pedal ganglia are separated and the complete number of pedal nerves is shown for the right pedal ganglion only.

Each cerebral ganglion has two lobules projecting from its surface, the commissural lobule (C.L.) and the lateral lobule (L.L.) (Fig. 5). The lateral lobule is similar to the 'lobule de la sensibilité spéciale' of Lacaze Duthiers (21), which he described for *Lymnaea pereger* and *L. stagnalis*. The superior lobule which Lacaze Duthiers (21) figured for the same two species is not a distinct entity in *L. humilis*. The capitocerebral membrane which envelops the buccal mass surrounds the ganglia of the central nervous system. The nerve trunks passing from them are covered proximally. In *L. humilis* this membrane also surrounds the ganglia internally, as well as externally, separating them from direct contact with the esophagus.

The ganglia of the central nervous system circle the esophagus loosely so that when the buccal mass is retracted by the buccal retractors, the esophagus is able to accommodate accordingly in a posterior direction.

Cerebral Ganglia (Figs. 5, 6, 9)

In *L. humilis* the optic (OP.N.) and tentacular nerves (TE.N.) are branches of a long common trunk, here named the optotentacular nerve (OT.N.). In *L. stagnalis* this common trunk is short (12). The optotentacular nerve arises close to the lateral lobule of each cerebral ganglion and divides into the delicate optic nerve and the posterior, thicker tentacular nerve. The optic nerve can be traced to the eye with relative ease. It passes into the anterior muscles of the roof of the cephalic hemocoele. As it enters the base of the tentacle, the tentacular nerve divides into anterior and posterior branches. Occasionally the anterior branch sends off a small nerve near the point of division of the two main branches.

The superior labial nerve (S.L.N.) arises dorsal to the inferior labial nerve (IN.L.N.) and gives rise to the frontal nerve (F.N.) and then passes superficially into the hemocoele wall lateral to the buccal mass as the dorsolabial nerve (DL.N.), which divides into two branches terminally. The inferior labial nerve gives rise to the anterior and posterior velar nerves (A.V.N., P.V.N.) and continues as the ventrolabial (VL.N.), which terminates ventrolateral to the dorsal mandible in a slight bulb. At this point it branches into three delicate nerves that can be traced only a very short distance. For the most part, the ventrolabial nerve passes only superficially into the wall of the cephalic hemocoele. The superior labial nerve generally runs dorsal to the longitudinal muscles of the wall of the hemocoele and the inferior labial generally ventral to them.

The origin of the velar nerves of *L. humilis* varies and this has been particularly observed on the right side. The anterior and posterior velar nerves may arise as separate nerves from the inferior labial, the anterior arising at a level midway between the anterior and posterior ends of the buccal mass, the posterior at a level near the junction of the esophagus and the buccal mass. The nerve may also arise from a common trunk which divides immediately. This trunk is usually located near the junction of the esophagus and buccal mass.

The buccocerebral connectives (BC.C.) arise ventral to the inferior labial nerve uniting the buccal and cerebral ganglia.

The penial nerve (PE.N.) is a branch of the right inferior labial nerve and innervates the preputium branching several times. A small branch of the penial nerve passes to the anterior penial retractor muscle.

Buccal Ganglia (Figs. 8, 9)

These ganglia are joined by the small buccal connective, and send out the principal nerves innervating the greater part of the alimentary canal (12). The nerve supply of the alimentary canal has been thoroughly worked out for *L. stagnalis* by Carriker (12). As in *L. stagnalis* six main nerve trunks arise from these ganglia: the paired ventrobuccal (VB.N.), laterobuccal (LB.N.), dorsobuccal (DB.N.), salivary (S.N.), and gastric nerves (G.N.) and the unpaired postbuccal nerve arising from the buccal connective (Fig. 8). Their distribution, as far as could be traced, is the same as in *L. stagnalis*.

Pleural Ganglia (Figs. 6, 9)

These ganglia give rise to no nerves.

Parietal Ganglia (Figs. 5, 6, 9)

The left pallial nerve (L.PL.N.), the only nerve arising from the left ganglion, passes posterodorsad and penetrates the posterior part of the roof of the cephalic hemocoele where it divides twice and occasionally three times. The right pallial nerve (R.PL.N.), which is the stoutest nerve of the central nervous system of *L. humilis*, also passes in a posterior direction dorsal to the vagina, the duct of the seminal receptacle, and the vas deferens (Figs. 5 and 6). The anterior pallial nerve (A.PL.N.) arises ventral to the right pallial and remains within a common sheath surrounding both these nerves to near the point where the anterior pallial nerve connects with the median pallial nerve (M.PL.N.).

Abdominal Ganglion (Figs. 6, 9)

The ventropallial nerve (VPL.N.) arises from the left side of the abdominal ganglion and passes back beneath the esophagus through the cervical septum and penetrates the longitudinal muscles of the left side near their junction with those of the right (to form the columellar muscle) (Figs. 5 and 9).

The splanchnic nerve (SPL.N.) arises dorsal to the median pallial nerve and follows a course and gives rise to branches in a manner similar to *L. stagnalis* (12) (Figs. 5, 6, and 9). The median pallial nerve from the abdominal ganglion unites with the anterior pallial from the right parietal ganglion and forms the internal pallial nerve (I.PL.N.), which passes ventral to the vas deferens and vagina (Figs. 5 and 9). Where the median pallial and anterior pallial nerves unite there is a small swelling, and a delicate nerve arises from it and passes to the body wall. The aortic nerve (AO.N.), a small and delicate nerve, follows a course similar to *L. stagnalis* (12) and passes along the cephalic artery (Fig. 9).

Elo (15) figured four nerves arising from the abdominal ganglion,—an intestinal nerve, a genital nerve, a cutaneous pallial nerve, and an anal nerve. The intestinal nerve is apparently the splanchnic nerve of Carriker (12) and is recognized as such here. Elo (15) renamed the aortic nerve (which remains unchanged in Carrikers' (12) work) the genital nerve because he maintained that it supplied the seminal receptacle. As far as could be determined, the aortic nerve does not innervate the seminal receptacle of *L. humilis*. According to Elo (15) the cutaneous pallial nerve serves a small region of the mantle. A corresponding nerve was not found in *L. humilis*. The anal nerve of Elo appears to be the median pallial nerve of Carriker (12) and the present study.

Pedal Ganglia (Figs. 6, 7, 9)

The paired pedal ganglia of *L. humilis* function primarily in the control of locomotion. The innervation of the foot of lymnaeid snails has not received as much attention as other structures of these snails. Lacaze Duthiers (21) and Elo (15) described the main trunks of the pedal ganglia (the former author in *L. stagnalis* and *L. pereger*; the latter in *L. stagnalis* only) but do not follow their detailed ramifications. The pedal nerves were not dealt with by Carriker (12). Both Lacaze Duthiers (21) and Elo (15) described six pairs of nerves arising from the pedal ganglia of *L. stagnalis*: the columellar nerves, superior cervical nerves, inferior cervical nerves, and the superior pedal, inferior pedal, and intermediate or median pedal nerves. The superior, inferior, and median pedal nerves are better named the anterior (A.P.N.), posterior (P.P.N.), and central pedal nerves (C.P.N.) because they are primarily oriented in an anteroposterior direction in the foot (Figs. 7 and 9). Schmalz (22) described 15 pairs of nerves arising from the pedal ganglia of *H. pomatia*.

Elo (15) homologized the pedal nerves of *H. pomatia* and *L. stagnalis* in the following way:

Lymnaea stagnalis	*Helix pomatia*
N. cervicalis superior	*N. cutaneus pedalis primus*
N. cervicalis inferior	*N. cutaneus pedalis secundus*
N. columellaris	*N. cutaneus pedalis tertius*
N. pedalis superior, medius, and inferior	*N. musculi pedali* I–XI

The 'nervus arteriae pedalis anterior' and 'posterior' of Schmalz (22) were not homologized by Elo (15).

In this study an attempt has been made to trace the innervation of the foot of *L. humilis* as far as possible. The paired pedal ganglia of *L. humilis* each give rise to six main nerve trunks; the anterior (A.P.N.), central (C.P.N.), and posterior pedal nerves (P.P.N.); the superior (S.C.N.) and inferior cervical nerves (IN.C.N.), and the columellar nerve (Figs. 7 and 9). In the present study, 13 newly named or described branches of these six main trunks are given.

The anterior pedal nerve arises from the ventral, anterior portion of the pedal ganglion and proceeds anteroventrad dividing immediately posterior to the buccal mass into the internal (I.P.N.) and external pedal nerves (E.P.N.). Both these nerves pass into the floor of the hemocoele lateral to the buccal mass. The internal pedal nerve divides into two nerves of approximately equal size, the medial (M.V.N.) and lateral velar nerves (L.V.N.), which pass into the velum. The anterior pedal nerve is ventral to the inferior labial nerve.

The central pedal nerve takes its origin from a ventrolateral aspect, and, near the wall of the hemocoele sends a small branch, the first anterocentral pedal nerve (F.A.C.P.), through the floor of the hemocoele into the foot. The central pedal continues laterad and gives rise to a second nerve which passes anteriad, the second anterocentral pedal nerve (S.A.C.P.). Turning slightly posteriad, the central pedal continues almost to the edge of the foot.

From its ventroposterior origin, the stout posterior pedal nerve passes directly posteriad and disappears into the posterior part of the floor of the cephalic hemocoele. Before disappearing, a lateral branch arises from it, the first lateroposterior pedal nerve (F.L.P.P.N.). This nerve curves laterad. The posterior pedal nerve continues posteriad and a second nerve, the second lateroposterior pedal nerve (S.L.P.P.N.), arises from it and proceeds in a manner similar to the first. Beyond the second lateroposterior pedal nerve, the posterior pedal curves slightly mesiad and then disappears in the tissues of the foot. Throughout its course, the posterior pedal runs approximately parallel to the ventral surface of the foot.

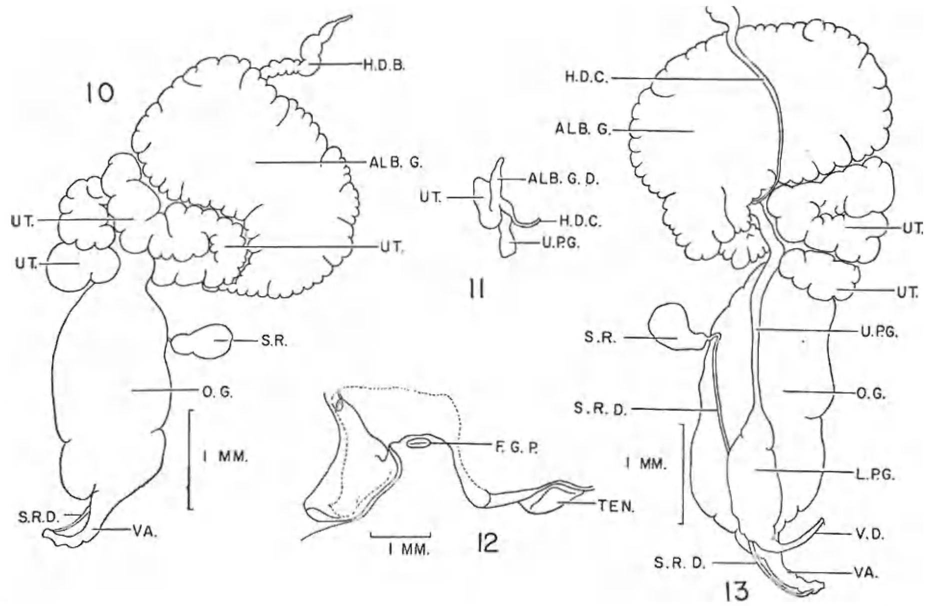
The superior cervical nerve arises between and dorsal to the anterior and central pedal nerves and divides into two nerves, the medial (M.S.C.N.) and lateral superior cervical nerves (L.S.C.N.), which penetrate the longitudinal muscles of the cephalic hemocoele wall through a distinct elongate slit (Figs. 6, 7, and 9). The superior cervical nerve passes laterad and anterodorsad.

The inferior cervical nerve originates near the pleuropedal connective and also penetrates the longitudinal musculature through a conspicuous longitudinal slit. It runs posterolaterad. Lacaze Duthiers (21) described this nerve in *L. stagnalis* as furnishing branches which extend as far as the junction of the mantle with the body. Immediately after leaving the cephalic hemocoele, the inferior cervical nerve divides into the medial (M.IN.C.N.) and lateral inferior cervical nerves (L.IN.C.N.) (Figs. 7 and 9.)

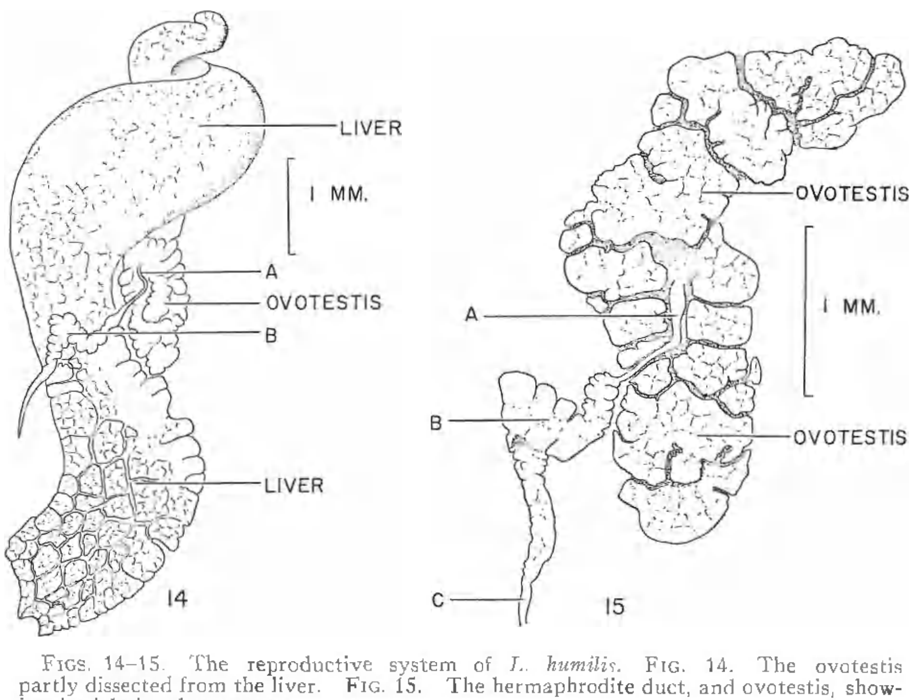
The columellar nerve (CO.N.) arises dorsomedial to the posterior pedal and disappears into the musculature of the posterior wall of the hemocoele. It gives rise to a small lateral branch, the lateral ramus of the columellar nerve (L.R.CO.N.). The general distribution of the columellar nerve of *L. humilis* agrees with that found by Lacaze Duthiers (21) in *L. stagnalis* and *L. pereger*. The columellar nerve described here must not be confused with the columellar nerve of Carriker (12). This columellar nerve is a branch of the splanchnic nerve (which arises from the abdominal ganglion) and passes over the columellar muscle (12). However, the paired columellar nerves of Lacaze Duthiers (21) are appropriately named for they pass into the musculature of the posterior wall of the cephalic hemocoele of *L. humilis* at the point where the longitudinal muscles of the lateral walls of the cephalic hemocoele converge to form the columellar muscle.

Reproductive System

As in other Lymnaeidae (14, 17, 9) the reproductive system of *L. humilis* is divided into three portions: (1) the ovotestis and its duct, (2) the female system, and (3) the male system (Figs. 10 to 15). The female system consists of the oviduct, which is much reduced in *L. humilis*, the uterus (UT.), the öothecal gland (O.G.) of Holm (17), and the vagina (VA.). The mass membrane gland of Crabb (14) constitutes part of the öothecal gland of Holm (17). Described as accessory glands in *L. stagnalis* by Holm (17) are the albumen gland (ALB.G.), which is very large in *L. humilis*, the muciparous gland, and the seminal receptacle (S.R.). The muciparous gland is the egg membrane gland of Crabb (14) and the nidamental gland of older authors. The muciparous gland is not a distinct entity in the gross morphology of *L. humilis*. The seminal receptacle is closely associated with the left posterior portion of the öothecal gland and is visible topographically under the heart (Fig. 4).



FIGS. 10–13. The reproductive system of *L. humilis*. FIG. 10. Dorsal view of the reproductive system. FIG. 11. The junction of the uterus, albumen gland duct, third portion of the hermaphrodite duct, and upper prostate gland. FIG. 12. The location of the female genital pore. FIG. 13. Ventral view of the reproductive system.



FIGS. 14–15. The reproductive system of *L. humilis*. FIG. 14. The ovotestis partly dissected from the liver. FIG. 15. The hermaphrodite duct, and ovotestis, showing its lobulated structure.

The principal structures of the male reproductive tract are the prostate (U.P.G., L.P.G.), the vas deferens (V.D.), and the large copulatory organ (PRE., PE.S., Figs. 5 and 6). The vas efferens is considered absent in *L. humilis*.

In reproductively active snails the female system is by far the larger of the two systems and completely obscures the prostate from dorsal view. Most of the prostate is confined to the mid-ventral surface of the öothecal gland. As in *L. stagnalis* the two systems are closely apposed to one another along their length except at their external outlets. The öothecal gland and part of the uterus are more or less centrally located but the remaining portion of the female tract is on the left side of the body.

The öothecal gland is directed from the left side toward the right tentacle and makes an angle of about 35 degrees with the left edge of the foot. The columellar muscle is approximately ventral to the anterior portion of the öothecal gland but gradually is situated under the right posterior portion of this gland.

The ovotestis (or hermaphrodite gland) (Figs. 14 and 15) is an elongate gland, embedded in the columellar surface of the liver. It is yellow in color and externally it is irregularly lobulated into about 25 lobules. In *L. stagnalis* it is said to be a dichotomously lobulated sac composed of about 100 lobules which are separated from the liver lobules by loose connective tissue and blood spaces (4). The ovotestis begins about the middle of the second whorl. It is dissected out of the liver with relative ease.

The hermaphrodite duct arises from the central columellar surface of the ovotestis; in live specimens it is yellow in color. This duct is divided into three distinct parts (Fig. 15). The first (A.), a portion of which lies within a short but rather deep sulcus in the ovotestis, is narrow and tapers gradually to the second or vesicular part. In relaxed and fixed material it is usually elbowed. The transition between the first and second parts is abrupt. This portion (B.) is wide and flat and is usually looped upon itself two or three times. It has about 20 diverticula, which, because they are almost always filled with spermatozoa, are sometimes called seminal vesicles. The vesicular portion merges into the third division (C.) which is a long narrow tube that passes under the ventral surface of the albumen gland and turns dorsad disappearing between this gland and the uterus–öothecal gland complex.

The hermaphrodite duct becomes very fine and hair-like at its distal end (Fig. 13, H.D.C.). Repeated dissections have shown that it terminates in a small bulbous expansion which joins with the short, stout, pigmented albumen gland duct (ALB.G.D.), which in turn is united with the upper prostate (U.P.G.) and the beginning of the uterus (UT.) (Fig. 11). This arrangement is quite different from that in *L. stagnalis* where the hermaphrodite duct bifurcates into an oviduct, and a thin, short, vas efferens (14, 17), which passes to the prostate gland. According to Holm (17) in *L. stagnalis* the albumen gland duct passes into a translucent finger-like vesicle which opens at its base into the coiled uterus. The oviduct passes dorsally around the base of this vesicle and is divided into two branches. One opens into the cavity of this vesicle and the other opens into the uterus. The small expansion at the end of the hermaphrodite duct in *L. humilis* may represent a fusion of the divided oviduct and vas efferens of *L. stagnalis*. In *L. humilis*, there is no evidence of a vesicle to which the albumen gland duct is connected as in *L. stagnalis*. Such structural consolidation is understandable in *L. humilis* since it is usually not more than one quarter the length of *L. stagnalis*.

The uterus is a white, loosely-coiled, saccular structure which surrounds the posterior portion of the öothecal gland and upper prostate. A membrane stretches between the coils of the uterus making it difficult to uncoil it. In gross dissection, there is no evidence of a muciparous gland which can be distinguished from the saccular uterus as in *L. stagnalis* (17). According to Holm (17) the muciparous gland functions to embed eggs in a mucous matrix within the egg mass.

The uterus merges into the öothecal gland, which, with the exception of a very short, upper narrow portion, is a stout organ in *L. humilis* whose sides are more or less parallel. In *L. stagnalis* the upper portion of the öothecal gland is a translucent cylindrical tube of some length while the lower portion is pear-shaped (14, 17). Transverse striae are present externally on this gland, as in *L. stagnalis*.

The vagina (VA.) arises from an elongate promontory on the anteroventral surface of the öothecal gland. The vagina is relatively broad and opens through the right wall of the cephalic hemocoele (Fig. 12). The position and shape of the pore have already been described. Where the duct of the seminal receptacle (S.R.D.) passes into the anterior face of the vagina there is usually a slight swelling. The duct of the seminal receptacle passes diagonally across the ventral surface of the öothecal gland and is partly obscured ventrally by the lower prostate. The duct is thread-like and the seminal receptacle is pear-shaped and a bright orange in the living snail.

The narrow, upper portion of the prostate (U.P.G.) is about twice the length of the lower bulbous part (L.P.G.). The upper prostate is yellow and the lower white in the living snail. The upper region is a long oval or flat tube which tapers somewhat as it merges into the lower portion which is occasionally heavily pigmented.

The vas deferens (V.D.) is broad at first but gradually narrows as it approaches the right body wall, which it penetrates anterior to the vagina (Fig. 5). It slopes slightly ventrad within the wall of the cephalic hemocoele and emerges slightly posterior to the male genital pore and follows a winding course until it continues into the penis sheath. Proportionately, it is shorter than that of *L. stagnalis*.

The penis sheath (Fig. 5, PE.S.) is about equal in length to the muscular preputium (PRE.). The preputium is always broad and square-shouldered where it receives the penis sheath. Near the genital pore several bands of muscle act as protractors of the preputium and a similar group near the penis sheath serve as retractors. This arrangement is similar to that in *L. stagnalis* (17).

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