The Anatomy of *Laevapex fuscus,* A Freshwater Limpet (Gastropoda: Pulmonata)

BY

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CONTENTS

ILLUSTRATIONS

FIGURES IN TEXT

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INTRODUCTION

THE fresh water limpets of the family Ancylidae have been consistently perplexing to malacologists. Because of their small size and almost indistinguishable shells, students of mollusks have neglected them. Since the group is world-wide in distribution, and obviously contains a great diversity of forms, some authors (e.g., Boettger, 1944) have suggested that the family is really of polyphyletic origin, and contains representatives of several diverse evolutionary lines.

Current interest in trematode diseases borne by molluscan vectors, coupled with the reports (Gadgil and Shah, 1955; Shah and Gadgil, 1955a, 1955b) that ancylid snails may be possible intermediate hosts for the human blood fluke *Schistosoma haematobium,* makes it imperative that accurate information about these snails be obtained.

Most of the anatomical work on ancylids has been carried out on *Ancylus fluviatilis,* the common European river limpet. The more important studies on this species are those of Moquin-Tandon (1852), Sharp (1883a. 1883b), André (1893), and Lacaze-Duthiers (1885, 1899). A few other genera have also been investigated anatomically. Pelseneer (1901) reported on the anatomy of a species of *Gundlachia,* as did Scott (1954). *Ferrissia* has been studied by Baker (1928) and also by Hoff (1940), whose paper represents the most complete study to date of a North American form. Recent work on eggs and reproduction of ancylids has been done by Bondesen (1950a, 1950b) and Basch (1959).

Most authors are in agreement with the general classification proposed by Thiele (1931), particularly with the following higher categories:

Phylum	Mollusca
Class	Gastropoda
Subclass	Pulmonata
Order	Basommatophora
(Stirps	Hygrophila)
Family	Ancylidae

Other families which Thiele placed in the Hygrophila are the Chilinidae, Latiidae, Physidae, Lymnaeidae, and Planorbidae. The last three, together with the Ancylidae, are called the "higher limnic Basommatophora" by Hubendick (1947).

In 1903 Walker divided the eastern American ancylids into two sections, *Ferrissia* and *Laevapex* (Fig. 1), based largely upon the presence or absence, respectively, of radial striations around the apex of the shell. Both sections were of equal stature within the genus *Ancylus,* and were used in the sense of subgenera. Hannibal (1912) considered these groups to be generically distinct from *Ancylus* and elevated *Laevapex* to generic status, with two subgenera, *Laevapex, sensu stricto,* and *Ferrissia.* Walker (1914), however, did not agree with this grouping and in effect reversed the positions of these names. Since that time, the practice has been to follow Walker and place all of these forms under *Ferrissia,* but some authorities feel that under the rules of priority the grouping presented by Hannibal should stand.

On the basis of the differences noted in this paper, and in particular the great discrepancy in the nature of the reproductive systems, I consider that *Laevapex* and *Ferrissia* are sufficiently distinct to warrant generic separation. Such an action would be in harmony with the accepted procedure followed in other groups of Basommatophora. This disposition of the groups is felt to be a more accurate reflection of their actual relationships, and at the same time makes unnecessary the arguments regarding the validity of the classifications proposed by Hannibal and Walker.

A number of genera, found only in the southernmost states (*Amphigyra, Neoplanorbis, Rhodacmea*) and which are not treated in this paper, appear to be very different from both *Laevapex* and *Ferrissia,* on evidence from their shells and radulae, but their limpet-like shape has caused them to be placed in the Ancylidae. They have never been studied anatomically; such an investigation would be extremely valuable in clarifying the relationships within the family. The genera *Laevapex* and *Ferrissia* may be characterized as follows:

GENUS *Laevapex* Walker, 1903.—Type: *Ancylus fuscus* C. B. Adams, 1841.

Shell patelliform, usually depressed, peritreme broadly ovate-elliptical in outline; apex relatively obtuse, smooth, lacking radial striations. Animal with pseudobranch consisting of two lobes, the upper bearing the anus. Male reproductive system without a flagellum. Habitat chiefly lacustrine.

GENUS *Ferrissia* Walker, 1903.—Type: *Ancylus rivularis* Say, 1819.

Shell patelliform, usually elevated, peritreme ovate-elliptical in outline; apex relatively acute, marked by fine radial striations representing the embryonic shell. Animal with a simple pseudobranch which bears the anus. Male reproductive system with a flagellum. Habitat chiefly fluviatile, occasionally lacustrine.

Grateful acknowledgment is made to Dr. Henry van der Schalie, Curator of Mollusks in the Museum of Zoology, University of Michigan, who placed

the full facilities of his division at my disposal and assisted at all times with helpful suggestions and criticisms. Professors T. H. Hubbell, G. H. Lauff, and W. H. Wagner read and criticised the manuscript and made many useful recommendations during the course of this study. I am greatly indebted to Mr. William L. Brudon for his kind advice regarding the preparation of the illustrations. To these and all of the other people who assisted at one time or another with this investigation I wish to express my sincere gratitude.

METHODS AND TECHNIQUES

FIELD METHODS

Periodic collections of *Laevapex fuscus* were made at several localities in the vicinity of Ann Arbor, Michigan, at all seasons from August 1956 to December 1957. It was most frequently taken along the east side of the causeway which adjoins the Geddes Avenue Bridge across the Huron River—more precisely, at the boundary line between sections 26 and 27, T. 2S, R. 4E, Washtenaw County. Additional material came from a site in Dexter, Michigan, immediately above a dam across a small tributary of the Huron River. This station is just off Highway M 132, sec. 6, T. 2S, R. 5E, Washtenaw County. Small collections were also made at various locations on the Huron River system, including its slow-flowing "backwater" areas.

For comparative purposes, specimens of *Laevapex fuscus* were secured on August 27, 1957, from the Flat River near Highway M 91 bridge, sec. 11, T. 8N, R. 8W, Ionia County, Michigan, about 100 miles WNW of Ann Arbor. These proved to be indistinguishable from those collected in Washtenaw County.

These three areas from which *L. fuscus* was collected have several characteristics in common. All are lateral expansions from a medium-sized river and are affected only slightly by the current in the main stream; consequently they are almost stagnant and pond-like. In each area there is a fairly abundant growth of rooted aquatic plants such as *Sagittaria, Peltandra,* and *Potamogeton,* and at certain times of the year floating plants such as *Lemna* appear. In all, the bottom is soft, muddy, and rich in decomposing organic matter, which may color the water to a marked degree. Sticks, logs, and debris are common, often forming a tangled, waterlogged jumble beneath the surface.

Ancylids were found by examining the submerged debris and also the bases of the stems of the submerged vegetation. The limpets have a marked preference for hard, smooth surfaces. They may congregate on such objects as discarded bottles where they prefer the bottom surface rather than the

top and sides. The snails were taken off the substrate by slipping a sharp scapel beneath the shell, and maintained in a jar of the water in which they were found until they were brought into the laboratory.

MAINTENANCE IN THE LABORATORY

Stocks of ancylids were maintained in the laboratory in order to observe behavior, egg-laying and development, and similar aspects of their biology. An attempt was made to feed them on the snail food prepared according to the formula of Lee and Lewert (1956), used with great success on planorbid snails, but the limpets did not seem to eat it. Rather, they found enough nourishment in the thin layer of algae on the sides of the aquaria, where they undoubtedly browsed, for in those tanks in which no live animals remained the algal layer increased perceptibly within a short time, indicating that it had previously been kept in check by the feeding activities of the snails.

Three kinds of aquaria, mostly of one-to-two-gallon capacity, were used. One type had an outside siphon-fed filter in which water ran through glass wool and charcoal before returning to the tank. The second had an air hose which bubbled air from the bottom of the water. The third was merely filled with pond water, covered loosely, and allowed to stand without much further attention. At least four of each type of aquarium were set up.

The third type of tank was found to be the most successful for *Laevapex fuscus* and *Ferrissia shimekii,* although it was useless for culturing forms from running water, such as *F. tarda* and *F. rivularis.* All attempts to maintain these two species in aquaria met with failure.

ANATOMICAL STUDIES

Specimens destined for dissection or sectioning were first anesthetized (or relaxed) with menthol crystals or a solution of Nembutal. The latter was prepared from "Veterinary Nembutal Sodium," a mixture of Sodium Pentobarbitol containing about 60 milligrams of the active agent per cc., manufactured by Abbott Laboratories. Van der Schalie (1953) described the use of this drug in the relaxation of amnicolid snails of the genus *Pomatiopsis.*

Relaxation of the snails with menthol is a relatively simple procedure. A few crystals are floated on the surface of the water containing the snails, and within one to three days they are relaxed in an extended position. If the relaxation process is prolonged, however, degenerative changes accompany the death of the animals and ruin the specimens for anatomical purposes. If the snails are fixed before anesthesia is complete, they will contract and distort the normal relationships of their organs.

A one to two per cent solution of Nembutal was found to be sufficient

to relax the limpets completely in one to two days. It was necessary to check the container frequently since the snails tended to crawl out of the fluid during the early stages of relaxation.

Chloretone, Evipal, and Pentothal Sodium were also used in varying concentrations, but results with these drugs were in general poorer than those obtained with menthol or Nembutal; the latter relaxing agent was found to be preferable.

Those snails which were to be sectioned were permitted to remain in clean pond water, which was changed frequently, for several days prior to relaxation to clear the stomach and intestinal tract of bits of sand commonly found in them.

After relaxation the snails were fixed in Bouin's fluid or Lavdowsky's formalin-acetic acid-alcohol solution (FAA) for several hours to a day, and then stored in 70 per cent ethyl alcohol. The FAA solution was found to be generally preferable. The stronger Bouin's fluid dissolved away the shells and also the small calcareous concretions normally found scattered throughout the subcutaneous connective tissues. While removal of the shell is necessary in material to be sectioned, it was feared that the bubbles of gas formed during the solution of the calcareous granules might have a tendency to tear or disrupt the delicate tissues. Also, the picric acid in Bouin's fluid is a strong yellow dye while the FAA solution is colorless and does not alter the original color of the organs to the same extent, although fixed tissues are usually rendered rather whitish.

The shells of animals fixed in FAA were removed by placing them in a solution of one per cent HCl in 70 per cent alcohol, or they were removed with the aid of a flat, thin spatula made from a sewing needle.

The snails were embedded in paraffin by the usual alcohol-xylol process; sections were cut at 10–15 micra in transverse, sagittal, and horizontal planes, and stained mostly with Ehrlich's haematoxylin and eosin or erythrosin counterstain, or with Mallory's triple stain.

Dissections were made by placing the snails in small watch glasses in each of which a layer of paraffin had been poured. Specimens were secured to this base with entomologists' minuten nadeln. The dissecting instruments were watchmakers' forceps, sharpened to a fine point, and good quality steel sewing needles, embedded in short glass rod handles. The needles were ground into various shapes on a fine-grained stone.

Most of the dissections were made under a stereoscopic binocular microscope, with the specimens in 70 per cent alcohol. For certain structures such as nerves and delicate membranes the following procedure was employed. Stock solutions of 0.5 per cent aqueous methylene blue dye and 5 per cent formalin were prepared. The methylene blue, in proper concentration, deposited on the surfaces of delicate structures and made them

easier to see; the alcohol tended to remove this dye whereas the formalin did not. Accordingly, specimens were pinned down and the area under study was exposed. Then a drop of dye was put on them and after a few seconds they were flooded with the formalin solution. If the specimen was found to be overstrained, the formalin was removed with a medicine dropper and alcohol was dropped onto the field until the right color appeared. At the proper time the alcohol was drained off and the formalin replaced. The dissection was subsequently carried out in formalin. Some turbulence resulted from the mixture of the two solutions, but no particular difficulty was encountered in doing gross dissections in this manner.

Whole mounts of animals and of selected organs were made by staining with alcoholic borax carmine for about one day, destaining with acid alcohol (one per cent HCl in 70 per cent alcohol) for several days, and finally dehydrating and clearing in xylol or a xylol-terpineol mixture.

Special methods for the radula will be discussed in the appropriate section below.

Histological drawings were made with the aid of a camera lucida. For the illustrations of gross morphology an ocular disc bearing a squared grid pattern was used in conjunction with corresponding squares on the drawing paper.

MORPHOLOGY

SHELL

Adams (1841) described *Laevapex fuscus* under the name *Ancylus fuscus* as follows:

"A. testa tenui, sub epidermide pellucida, subdepressa, elliptica, epidermide fusca, crassa, aspera, extra marginem prominente; apice obtusa, ad dextram, vix postera.

"*Shell* thin, transparent without the epidermis, not much elevated, elliptical, moderately curved at the sides; *epidermis* brown, visible through the shell, giving it the appearance of having the same color, thick, rough, slightly extending beyond the margin of the shell; *apex* obtuse, moderately prominent, scarcely behind the middle, inclining to the right, so as to have only two-fifths of the width on that side.

"Length, .31 inch; width, .22 inch; height, .05 inch."

It is notable that in this description of a new species not a word was devoted to the animal itself. The habitat was said to be "adhering to stones, in a small rivulet, at Andover . . . ." This is surprising in view of the fact that *L. fuscus* is almost always found in standing waters and not in "rivulets." The holotype is in the collection of the University of Michigan Museum of Zoology, UMMZ 68054.

Fig. 1. Shells of ancylid snails: A and B, *Laevapex fuscus*; C and D, *Ferrissia rivularis*; E and F, *Ferrissia shimekii*. All scale lines equal one millimeter.
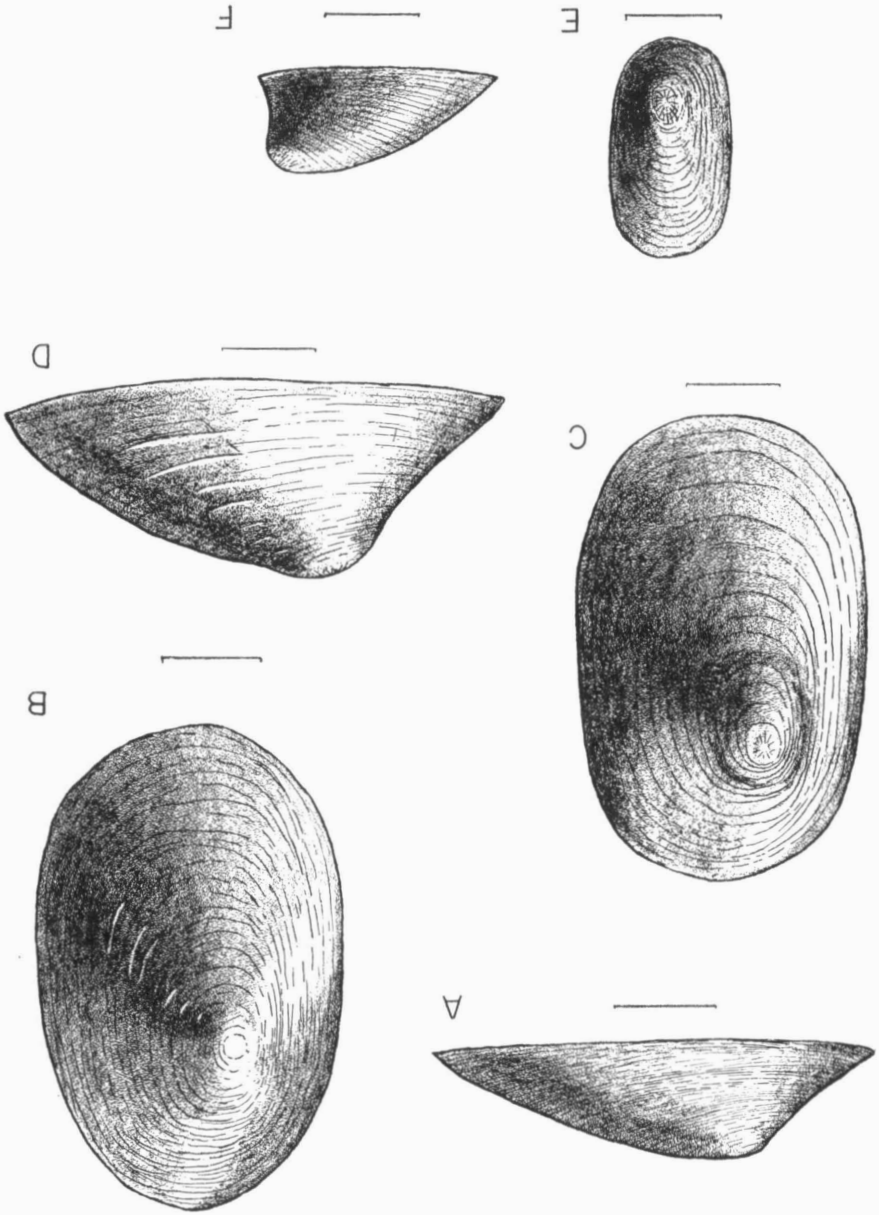
Specimens from the Geddes Bridge locality agree well with this description, except that the average sizes and dimensions are not quite the same as Adams' type. Their color is a light horny brown owing to the periostracum, which extends beyond the edge of the shell all around and permits the animal to close down tightly against a slightly irregular substrate. Table I shows the dimensions and proportions of specimens from a number of

TABLE I

DIMENSIONS IN MM. OF SHELLS OF *Laevapex fuscus*

Locality	Number Specimens	Av. Length	Av. Width	Av. Height	Length / Width	Length / Height	Width / Height
Andover, Mass.[1]	1	7.87	5.59	1.27	1.41	6.2	4.4
Winchester, Mass.[2]	1	5.5	4.0	1.25	1.35	4.4	3.2
Kent Co., Mich.[2]	1	7.25	4.5	1.75	1.61	4.14	2.56
Ottawa Co., Mich.[2] ...	1	8.25	4.5	3.0	1.83	2.75	1.5
Geddes Bridge, Washtenaw Co., Mich.[3]	25	5.34	3.75	1.72	1.42	3.10	2.16
Green Lake, Wisc.[4] ...	4	5.62	3.60	1.72	1.56	3.26	2.09
Greenbrier Co, W. Va.[5]	36	4.45	3.49	1.45	1.27	3.06	2.40
St. Louis Co, Mo.[6] ...	26	4.50	3.13	1.38	1.36	3.34	2.46
Maumee R., Ohio[7]	32	5.32	3.91	1.59	1.44	2.71	2.26
Marshall Co., Ind.[8] ...	50	4.89	3.19	1.49	1.53	3.27	2.13

[1] Type specimen; from Adams' original description.
[2] From Walker, 1903.
[3] From collections by the writer.
[4] From Baker, 1928; U. of Wisc. collections N. 4728.
[5] UMMZ 60935.
[6] UMMZ 55959.
[7] UMMZ 28764.
[8] UMMZ 68920.

different lots of *L. fuscus*. The identification of the Geddes Bridge material as *fuscus* was based upon comparison with the specimens of this species in the collection of the University of Michigan Museum of Zoology, which were identified by Bryant Walker, and also by comparison with the holotype.

At least part of the variation shown in Table I is caused by local ecological factors, for according to Walker (1903):

"When it lives on the flat side of a reed or leaf it grows normal in shape and the peritreme touches the surface all the way around. But when it lives on a round reed like *Scirpus lacustris,* which is narrower than the full grown shell, it adapts itself to its position and grows to fit the reed, the ends following the convex surface of its support and the sides lapping down around the reed itself."

Baker (1928) gave a rather complete description of the shell of *L. fuscus,* and it is not considered necessary to repeat such a description here.

EXTERNAL MORPHOLOGY

The body of *Laevapex fuscus* may be divided into several main regions: the head, the foot, and the visceral mass (Fig. 2, A, B, C). Externally, the head shows an almost perfect bilateral symmetry and is joined to the body by a poorly defined neck region. The single pair of stout subcylindrical tentacles contain a conspicuous hollow core of black pigment (Fig. 12, A; Fig. 15, F). This tentacular pigment, absent from such forms as *Ferrissia rivularis, F. tarda, F. parallela, F. shimekii,* and the two European ancylids, may be a distinguishing character of taxonomic significance. The general conformation of the tentacles seems to be similar in all ancylids, but it differs from that in the Physidae and Planorbidae, in which the tentacles are often quite long and delicate, and from that in the Lymnaeidae, where the tentacles are horizontally flattened.

A sessile eye lies at the inner base of each tentacle (Fig. 2, A), as in the other three families mentioned above; a fundamental basommatophoran character. Beneath and slightly posterior to the base of the left tentacle is the male genital opening (Fig. 2, C), which is difficult to locate externally when the penial complex is retracted.

On the ventral surface of the head, the mouth is anteriorly located, between the two lateral lobes of the velum.

The muscular foot underlies most of the remainder of the body posterior to the head. It is suboval in shape when viewed from below, is broadest near its anterior end, and tapers regularly posteriad. Intimately connected with the foot are the three shell muscles which serve to attach the animal to its shell. The dorsal surfaces of these columnar muscle masses are clearly visible when the animal is viewed from above.

The visceral region, with its underlying foot, is covered completely by the oval, dome-shaped mantle. In the space beneath the mantle on the left side of the body lies the pseudobranch, a plicated roughly triangular extension of the body wall (Fig. 2, C; Fig. 3). This structure in *L. fuscus* consists of two lobes: a larger ventral respiratory lobe with about five pairs of folds extending dorsally and ventrally from the margin, and a smaller anal lobe which bears the anus on its anterior dorsal surface. The rectum passes through the interior of this lobe, which is often thrown into one or two poorly defined folds.

Two openings are to be found near the pseudobranch. The pulmonary opening which leads to the much reduced pulmonary cavity lies dorsal to it, and the female genital opening which may be seen by pulling the pseudobranch aside and upwards lies beneath. Above the pseudobranch,
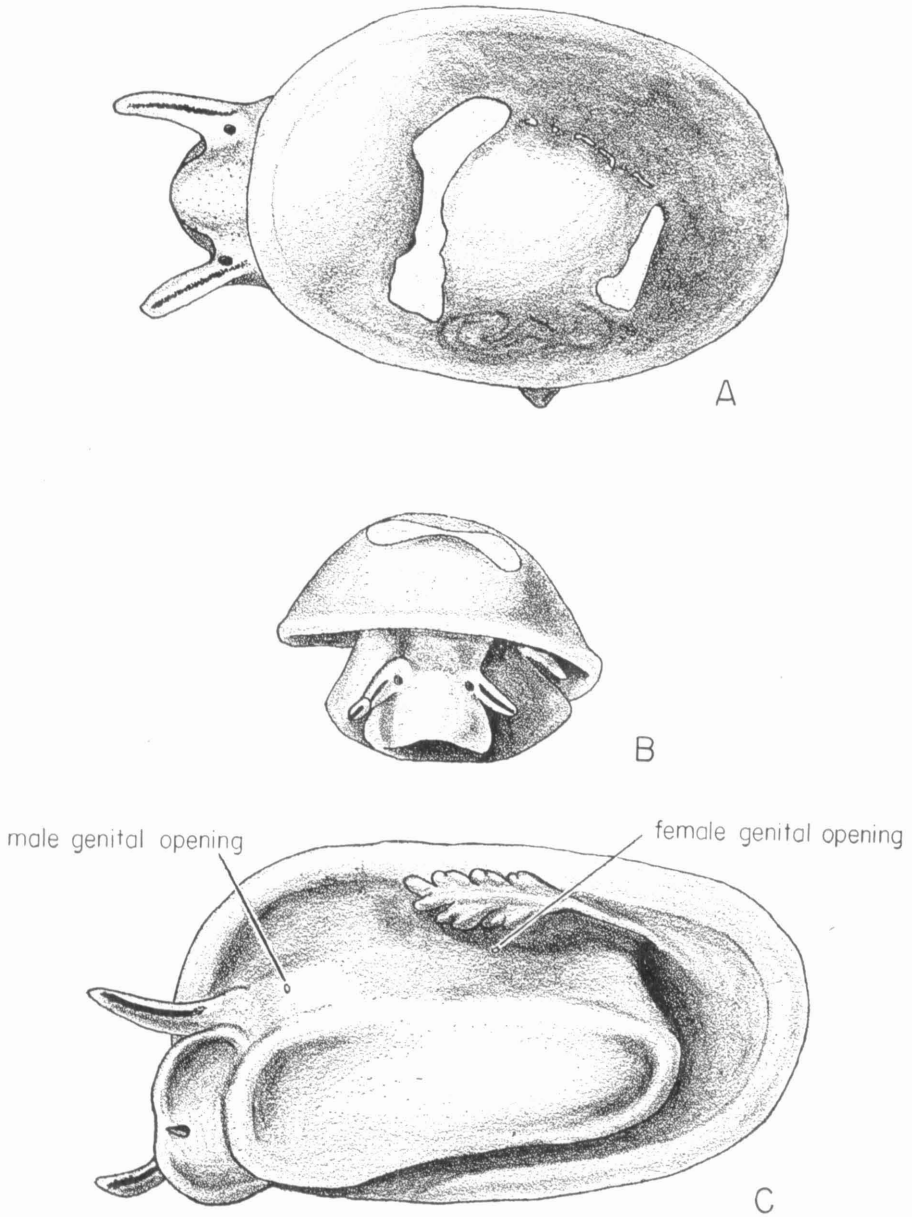
FIG. 2. External morphology of *Laevapex fuscus:* A, dorsal view of specimen with shell removed; shell muscles visible as light areas; tip of pseudobranch can be seen on left side of animal. B, face view of specimen with shell removed; note reationship of overhanging mantle to foot. C, oblique ventral view, with shell removed; note position of genital openings and pseudobranch.

on the ventral surface of the overhanging mantle, the tiny urinary orifice may be seen in favorable specimens. Its position can be determined by following the distal region of the kidney tubule to its posterior end (Fig. 5, A).

The left side of the body possesses these five openings; male and female genital openings, digestive (anal), pulmonary, and urinary. The right side of the body, in contrast, has none.

Chromatophores containing black pigment granules are generally distributed over the dorsal surface of the mantle; they are often concentrated in the right posterior quadrant and around the periphery of each shell muscle. The location of the kidney is frequently outlined by black pigment. However, the swollen edge or margin of the mantle all around the animal is free of this pigment, as is the sole of the foot and the velum. The remainder of the animal is flecked with scattered small black spots, somewhat larger on the anterior and dorsal surfaces of the head than elsewhere. Between the two anterior shell muscles, and also running posteriad from the right anterior shell muscle, a number of unpigmented spots in a variable pattern are usually to be seen (Fig. 2, A).

Species of *Ferrissia* with a high apex (e. g., *F. rivularis, F. tarda*) generally lack pigment in the central region of the dorsal surface of the mantle and are left with a vaguely defined ring of black around the periphery, with the exception of the margin itself which, as in *L. fuscus,* is unpigmented. According to Sharp (1883*a*), the inferior portion of the external surface of the mantle of *Ancylus fluviatilis* has a deposit of black pigment; this band of black is absent from *Acroloxus lacustris.*

INTEGUMENT

In its general form the skin of *L. fuscus* agrees with the description given by Graham (1957):

"The fundamental structure of the molluscan epidermis is an epithelium of columnar cells resting on a basement membrane. This, in turn, lies over a mat of connective tissue through which run muscle fibers. The epithelial cells are typically ciliated . . . ." However, some regions of the skin show interesting local modifications.

The dorsal surface of the mantle consists of two very thin layers. The outer of these normally lies in contact with the shell and is made up largely of chromatophores about 4 micra in thickness. In fixed material it is possible to peel this layer away from the subjacent membrane and mount it on a microscope slide. The pigmented layer is then seen to consist of simple squamous polygonal cells containing distinct spherical granules 1 micron or less in diameter scattered throughout the cytoplasm, but not

in the nucleus. The observations of André (1893) on the pigment cells of the mantle of *Ancylus fluviatilis* agree perfectly with this description.

With the outer pigmented layer removed, the layer of the dorsum of the mantle lying in contact with the visceral cavity is revealed as a delicate, transparent membrane 5 to 6 micra in thickness. This stratum is composed of simple squamous cells throughout most of the mantle, but near the thickened margin these give way to a single layer of columnar epithelium the function of which is presumably shell secretion (Figs. 12, 13, 14). This layer is continuous, on the ventral surface of the mantle, with an epithelium of cuboidal cells. The ventral mantle epithelium is strongly ciliated, as can be demonstrated by introducing a small drop of dye in the water in front of an animal which has been turned upside down on its shell. The cilia do not carpet the underside of the mantle completely, but occur in regularly spaced clumps or tufts, which are particularly evident in very young animals.

The skin covering most of the remainder of the body with the exception of the sole of the foot is composed of a single layer of cuboidal epithelium 7 to 9 micra in thickness, subtended by a distinct basement membrane. Occasional unicellular glands ranging to 45 micra in length open onto the surface, and many are filled with a secretion that stains with haematoxylin and aniline blue. These gland cells are often seen with a mass of secretion extruded from them. The surface of this epithelial layer is dotted with cilia.

The surface of the pseudobranch is more heavily endowed with cilia than is the general body covering. These cilia range to 15 micra in length and appear to be concentrated at the bottom of the troughs inside the folds. The illustration of the histology of the pseudobranch (Fig. 3, B) does not show the cilia, which occur on both the anal and respiratory lobes.

The sole of the foot is a distinctly differentiated area consisting of very densely packed columnar cells about 12 micra in height, and with large oval nuclei uniformly placed basally near the distinct basement membrane (Figs. 13, 14). On the free surface of these cells is a strongly thickened border which may be identical with the "brush border" or "striated border" mentioned in the histological literature. This border appears to consist of tightly packed cilia or hair-like cellular extensions 4 to 5 micra in length, and it extends over the whole of the sole of the foot.

The tentacle epithelium shows some differentiation between the dorsal and ventral surfaces. The covering of the ventral surface is a simple cuboidal epithelium of cells approximately 7 micra square, bearing tufts of cilia on their free edges. The cilia here are about 10 to 12 micra long beneath, but on the dorsal surface they are much reduced and spaced farther apart. The dorsal cells are also somewhat smaller than those on the ventral side.

The mouth shows what appears to be a cornified epithelium of simple columnar cells, about 16 by 4 micra, with a distinct basement membrane and large, basally placed oval nuclei. The cells are not ciliated, and appear to be a modification of the epithelium found on the sole of the foot. (Fig. 12, A). The jaws will be considered below with the digestive system.

An infolding of the outer epidermis forms the preputium of the male genital complex (Fig. 10, B; Fig. 11, A, D). This structure is lined with a layer of cuboidal cells 7 micra high and bearing a distinctly thickened (2 micra) distal margin. Beneath this covering layer is a stratum of dense muscle fibers and connective tissue cells along which are scattered chromatophores differing from those found in the dorsal part of the mantle. The chromatophores here (and elsewhere in the body) are irregularly shaped cells occurring singly or at most clumped in loose aggregations. They are full of black pigment granules which are seen with an oil immersion lens. The subjacent muscle layer of the preputium is 10 to 20 micra in depth and does not appear to have a very well defined limiting membrane on the side farthest from the epithelial cells.

A further specialization of the outer skin covering is found in the membranes which line the reduced pulmonary cavity. These cells are low and squamous; their nuclei lie horizontally compressed. The cilia characteristic of the ventral mantle surface and the dorsum of the pseudobranch become much reduced.

Adjacent to the inner surface of the basement membrane of the epidermis throughout the body is a subcutaneous connective tissue which varies in thickness and density in different areas. This underlying tissue is extremely scanty beneath the epithelium of the mantle, becoming somewhat more abundant nearer the edge. It is best developed in the foot region. The connective tissue consists largely of muscle fibers and other fibers which may correspond to the collagenous or elastic fibers found in vertebrate connective tissues; also, chromatophores and a variety of other cell types are found here. Calcareous granules which stain strongly with aniline blue are scattered about in this tissue in varying amounts in different individuals. These granules appear to be built up of several concentric layers, and may be a storage source of calcium carbonate which the snail requires for shell production. Sometimes they are so abundant in the living animal that the tissues have a distinctly bluish cast.

In comparison with other forms, the integuments of *L. fuscus* appear to be similar to those of other ancylids, although a detailed description has never been published. André (1893) stated that the parts of the body of *A. fluviatilis* not covered by the shell were bounded by a vibratile epithelium consisting of a single layer of elements. This author also differentiated the epithelium of the sole of the foot (which he said was composed of cells

37 micra long) from that covering the other naked parts of the animal. The sub-epithelial parts and glands are essentially the same as those found in other pulmonates.

Hoff (1940) found that the cells of the marginal ridge in *F. tarda* are not much larger than those that form the general surface of the mantle. Mucus-secreting cells were said to be frequent near the edge of the mantle. The surface of the foot is described in his paper as being composed of ciliated cells 15 micra long, with cilia 5 micra in length.

MUSCULAR SYSTEM

If the mantle and all of the viscera are removed from a specimen of *L. fuscus,* the remainder of the body behind the head consists largely of the three shell muscles and the foot together with their covering integuments. These muscles are composed of densely packed parallel fibers which attach to the shell at their upper end and penetrate deeply into the foot tissue ventrally (Fig. 13, D; Fig. 15, B, F). While the three muscles are distinct in gross terms, the individual fibers of each fan out greatly when the muscle enters the foot. Therefore, a section of this organ, made through the mid-region of the body, will cut across the intermingled fibers of all three muscles as well as the intrinsic muscle fibers of the foot itself.

André (1893) and other authors have mentioned two large muscles, variously called columellar muscles, "retracteurs du pied," "musculus cochlearis," disposed laterally and placed symmetrically on either side towards the anterior of the body in *Ancylus fluviatilis.* Apparently, *A. fluviatilis* lacks the posterior shell muscle found in *L. fuscus.*

F. C. Baker (1928) stated that the animal of *Ferrissia* is attached to its shell "by three muscles, (columellar) two anterior, and one posterior on the left side, and by a continuous band of muscle marking the free edge of the mantle; this muscle recalls the pallial muscle of bivalves . . .". His illustration (1928:388) shows a structure labeled "pallial muscle," which is not near the free edge of the mantle but well up under the shell. No trace of any muscle that corresponds either to Baker's description or illustration has been found in *L. fuscus.* The margin of mantle retractor muscles, attached to the edge of the mantle, which have been described by Hoff (1940) in *F. tarda* are microscopic fibers only and not gross muscular structures.

Histologically, the three shell muscles of *fuscus* all present a uniform appearance. The individual fibers seem to extend the full length of each muscle, although this is difficult to determine in sections since these fibers are not straight. No cross striation has been observed. The basic unit of muscle structure, the individual fiber, is 3 to 4 micra in diameter in the

foot tissue and somewhat smaller in the trunk of the muscle. Scattered nuclei are to be seen at various points throughout the muscle. Variations in methods of relaxation, killing, and fixing, and possible compression during the sectioning process might have a profound effect upon the apparent length and diameter of these structures.

Additional strands of muscle extend forward into the sides of the head, paralleling the nerves that pass anteriorly from the brain. One particularly distinctive strand passes over the base of the preputium near its attachment to the epidermal surface. Fine muscle fibers are everywhere a component of the connective tissue lying underneath the skin, as in the mantle, pseudobranch, tentacles, and other parts. Those muscle masses which are superficially concerned with the functioning of certain systems (as the buccal mass) will receive consideration when these systems are discussed.

RESPIRATORY SYSTEM

The principal organ of respiration in *L. fuscus* is the pseudobranch, a much folded, roughly triangular epidermal extension of the body lying beneath the mantle on the left side (Fig. 3; Fig. 14, E; Fig. 15, G.). Two lobes may be differentiated: an upper anal lobe in which the rectum lies, and a much larger subtending respiratory lobe: It is this latter portion which is pertinent to a discussion of respiration.

The respiratory lobe is composed of two elements. The greater part of the surface area is formed by a thin skin thrown into five accordion-like folds such that a probe inserted between any two folds on one side would lie within one of the outpocketings on the other side. Around this pleated flap of skin and continuous with its surface lies a hollow tubular margin with a lumen diameter of about 40 micra. This margin serves to give some structural rigidity to the pseudobranch, but its primary function appears to be the conduction of blood. Anteriorly, the lumen of the pseudobranch margin reaches a point just lateral to the left anterior shell muscle, where it swings dorsad for a short distance and opens into the floor of the blood sinus within the mantle. Posteriorly, it is also continuous with the mantle blood sinus; the communication here is just lateral to or sometimes just behind the posterior shell muscle. The respiratory surface is thus bounded by a blood-carrying tube which is "open" at both ends. There does not seem to be any definite direction of blood flow in the lumen of the pseudobranch margin. Circulation probably is effected by a sluggish ebb and flow corresponding to the activity of the animal.

Histologically, the pseudobranch membrane is a thin, delicate structure. It is composed of one or two thicknesses of large vacuolated cells bounded externally on either side by a thin layer of cuboidal epithelium

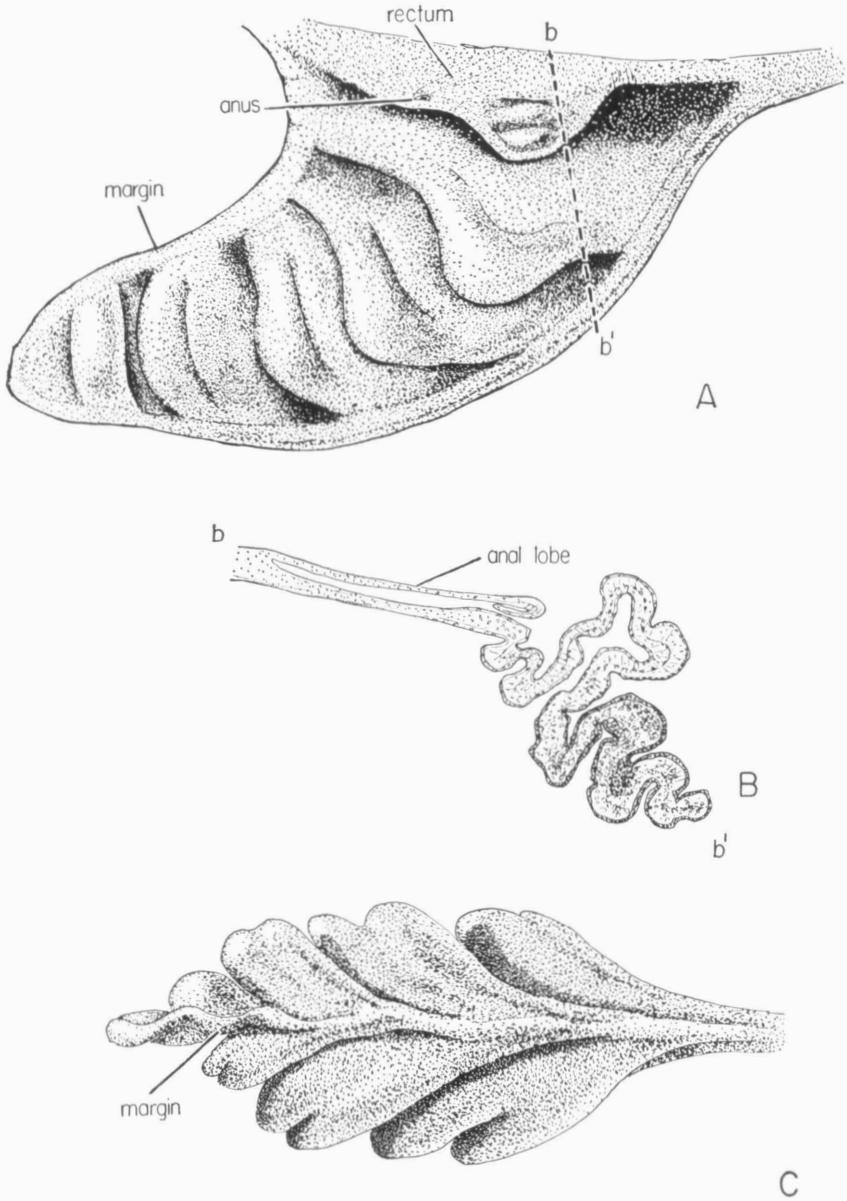FIG. 3. The pseudobranch of *Laevapex fuscus:* A, dorsal view of pseudobranch, drawn from relaxed and fixed specimen; tip of organ points to anterior; anal lobe, bearing rectum and anus, visible at top of figure. B, section through pseudobranch, from another specimen, through the approximate plane b—b′ on A; note hollow nature of folds. C, lateral view of pseudobranch, showing folds extending dorsally and ventrally from margin.

that is studded, as previously described, with small, dense tufts of cilia. The thickness of this membrane varies from 30 to 40 micra, and provides the thin tissue and large surface-to-volume ratio necessary for respiratory exchange.

As far as could be determined, no structure similar to this respiratory pseudobranch has been described in any other ancylid. The "lobe auriforme" of Moquin-Tandon (1852) and other authors has a smooth surface in *Ancylus fluviatilis,* and it "may contain a few poorly defined folds when contracted, but normally is a thin flap of material hanging between the body and the mantle" in *Ferrissia tarda* (Hoff, 1940). In both of these species the rectum passes through this lobe on which the anal orifice is situated.

Therefore (considering the position of the rectum and anus to be a relatively conservative character), the entire auriform lobe of other ancylids seems to be homologous with the relatively tiny anal lobe of *L. fuscus.* The respiratory lobe has no obvious homologue in these other ancylids.

A quotation from Hubendick (1947) may be appropriate in this regard (omissions refer to figures):

"In Lymnaeidae the lower boundary of the mantle aperture is enlarged to form a large labiate process, the lower mantle lobe. The anus opens close to the posterior edge of this process or lobe. A similar lower mantle lobe of the same shape and in the same position also occurs in Physidae. . . . The same applies to Planorbidae, but in this family there is in addition a disciform lobe or process caudal to the former . . . The anus . . . thus comes to lie in the furrow between the two lobes. As Pelseneer (1896) and others have shown, the caudal process forms a gill-shaped structure. In Ancylidae there is only one lobe, termed the auriform lobe by Hoff (1940), and the anal orifice is situated in the centre of this . . . "

Is it possible that the respiratory lobe of the pseudobranch of *L. fuscus* is really homologous with the caudal lobe described above for the family Planorbidae? Both are gill-shaped structures, and, although the respiratory lobe underlies the entire anal lobe in *L. fuscus,* the former does extend much farther posteriorly. More comparative material is needed to answer this question.

Regarding the remainder of the respiratory system, a pulmonary cavity is present, but reduced in comparison with those of other members of the pulmonate group, and may be only vestigial (Fig. 9, A, B). This cavity lies dorsal to the pseudobranch. The opening of the cavity consists of a narrow horizontal slit that extends roughly between the left anterior and the posterior shell muscles, about 1.2 mm. Anteriorly, the cavity extends into the body as far medially as the inner face of the left anterior shell muscle, and the inner edge of the cavity passes posteriad and laterad so

that at the posterior shell muscle it merges almost imperceptibly with the outer body wall. The pulmonary cavity thus approximates a right triangle in shape. One leg represents the posterior side of the left anterior shell muscle, the other the left edge of the body just above the pseudobranch, and the hypotenuse a line extending from just inside the left anterior shell muscle to just outside the posterior shell muscle. The lengths of these three sides are about 1.2, 0.7, and 1.9 mm., respectively.

The floor of the pulmonary cavity is made up of epithelium, continuous with the dorsal surface of the pseudobranch; its ceiling is the ventral surface of the mantle and the ventral pericardial membrane. Through the delicate, transparent inner wall of the pulmonary cavity the following structures are visible: the uterus and prostate, the loop of the intestine as it swings left and posteriad from the stomach, and the rectum, which passes ventrad into the anal lobe of the pseudobranch.

If the left side of the mantle (containing the heart, the ventral pericardial membrane, and the kidney) is carefully removed, the epithelium of the floor of the pulmonary cavity will lie exposed. This fine structure is thus found to be continuous with the inner of the two layers which compose the *dorsal* covering of the mantle beneath the shell.

Finally, it is quite probable, as André (1893) suggested, that the entire skin surface in contact with the water, and particularly the ventral surface of the mantle, plays a considerable part in respiration in ancylid snails.

DIGESTIVE SYSTEM

The digestive system of *Laevapex fuscus* consists of the following parts: mouth, jaws, radula, buccal mass, pharynx, esophagus, stomach, cecum, intestine, rectum, and anus, together with the salivary and digestive glands (Fig. 4).

The mouth and the buccal cavity into which it leads are covered by a layer of columnar epithelium described previously in connection with the integument. The buccal cavity lies entirely within the large buccal mass, and occupies the anterior portion of that organ. In preserved specimens the radular surface may be seen within the ventral posterior region of this cavity; in life the radula is often protruded slightly from the mouth to rasp off small bits of food material. The buccal cavity opens dorso-posteriorly through the short pharynx into the esophagus, a closed tube that leads through the dorsal musculature of the buccal mass, and then lies free on top of the medial dorsal region of the buccal mass, continuing posteriad to the stomach.

A single horseshoe-shaped salivary gland lies above the posterior portion of the buccal mass. It is not shown on Figure 4, but sections
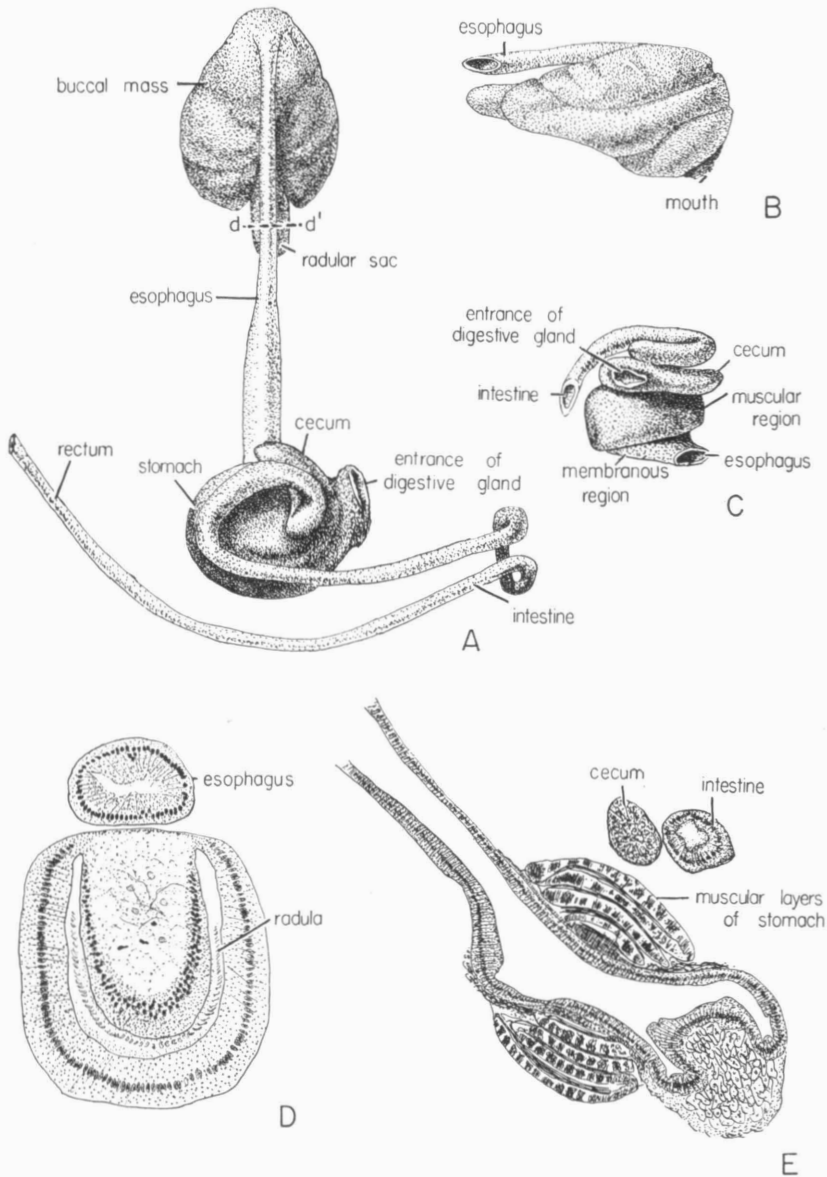
FIG. 4. The digestive system of *Laevapex fuscus:* A, dorsal view of entire system, removed from a relaxed and fixed specimen; salivary gland removed to reveal relationship of esophagus and radular sac; digestive gland removed. B, right side view of buccal mass; salivary gland and all nerves removed. C, stomach, viewed from right side. D, transverse section through plane d–d' on A; note position of radula. E, parasagittal section through stomach to show the composition of the muscular ring.

through this gland are seen on Figures 12, B, and 15, D. All other ancylids that have been investigated anatomically possess two salivary glands disposed on either side of the esophagus, and the single gland of *L. fuscus* may be thought of as the posterior fusion of these two glands. Whether this fusion may be of taxonomic significance cannot be determined without a more inclusive study of other species.

The diameter of each anterior arm of the salivary gland is about 60 micra and the gland itself is composed of a single layer of large irregularly-shaped secretory cells, many of which can be shown to be full of their secretory products. These cells surround a rather vaguely defined central lumen. At the anterior medial extremity of each arm, this lumen continues forward as the salivary duct which passes through the dorsal surface of the buccal mass and debouches into the dorsal region of the buccal cavity. Other authors are in general agreement with this description in other species, but Hubendick (1947) stated that the salivary glands of *A. fluviatilis* are richly lobate. In *L. fuscus* the glands are simple, without lobes.

Most of the volume of the buccal mass is taken up by the so-called buccal or radular cartilages, two bean-shaped bodies composed of large, vacuolated cells and many transverse muscle fibers. The radular pouch is situated between these cartilages. In *fuscus* this pouch extends but a small distance posteriad behind the buccal mass, but the radular pouch in *Ancylus fluviatilis* may be half the length of the body. *Acroloxus lacustris* and *Ferrissia tarda* both have a short radular pouch as does the *Gundlachia* sp. from New Zealand, studied by Pelseneer (1901).

The esophagus passes posteriad from the buccal mass, dorsal to the radular or odontophoral pouch, through the circumesophageal ganglion (or brain), and then expands from 100 to 200 micra in outside diameter. The wall of the esophagus is about 30 micra thick and consists of a simple columnar epithelium subtended by a thin tunica of connective tissue. The interior of the esophagus is often somewhat rugose; in fixed specimens it sometimes appears to have a typhlosole-like indentation.

About one millimeter behind the buccal mass the esophagus enters the stomach in the region often called the crop, although there seems to be no evidence that the "crop" functions in food storage. It is a thin-walled dilation of the alimentary tract which leads directly into the muscular region often referred to as the gizzard. This consists of a ring of muscular tissue surrounding an expansion of the alimentary tract, and is composed of eight to ten layers of muscle fibers alternately arranged at right angles to one another (Fig. 4, E; Fig. 14, E). As it is oriented in relaxed and fixed specimens, the ring of muscle is tilted forward to form an angle of about 45 degrees with the sole of the foot. The muscular region of the stomach of many pulmonates has been investigated by Heidermanns (1924), and the

description here given agrees rather well with that of *Ancylus fluviatilis.* According to Simroth and Hoffman (1908–1928), the *Ancylus*-type of stomach is also found in many of the smaller planorbids.

Dorsally, the muscular region of the stomach communicates with three distinct openings—the cecum, the intestine, and the opening of the digestive gland—all on the right side.

The cecum is a small digitate projection about 400 micra long arising from the dorsal swelling above the stomach (the region sometimes called the pylorus) to which all of the three openings connect. It runs immediately beneath the intestine and follows the direction of the first intestinal flexure to its blind end just above the esophagus. The cells lining this sac appear similar to those found in the intestine and the esophagus; the function of the cecum is unknown. *Ferrissia tarda* and *Acroloxus lacustris* each possesses a single cecum, while André described two such projections for *A. fluviatilis.*

The intestine appears to be similar in all ancylids. It loops first forward describing a semicircle to the left, crosses the dorsal part of the body from left to right, dips down to form another semicircular loop, and recrosses the body paralleling its more proximal region to pass through the anal lobe of the pseudobranch and end in the anus on its anterior dorsal surface. Histologically, the intestine is similar to the esophagus, consisting of a simple, closely packed columnar epithelium underlain by a sheath of connective tissue. In the dextral species, *Acroloxus lacustris,* the loops of the intestine show a mirror image of those described above for the sinistral species.

The length of the digestive tract is about 8 mm., comparing favorably with the figure (9 mm.) given for *Ancylus fluviatilis* by Hesse and Doflein (1943).

The digestive gland is probably the organ of most interest to parasitologists since it is utilized more than any other by the larval trematodes which pass through molluscan hosts. This gland is the largest organ in the body of *L. fuscus,* and forms a much divided lobulated sac whose lumen is continuous among all of the pouch-like diverticula. The wall of this organ is composed of a single layer of vacuolated glandular cells about 20 micra across which are often seen to possess a thickened free border. These cells are covered on the outside by a very low simple squamous epithelium with horizontally compressed nuclei. Many of the digestive gland cells on any one section are full of their secretion products.

Food material is sometimes seen inside the digestive gland, and it may be that most of the digestion actually takes place in the lumen of this organ. André (1893) fed some carmine to *A. fluviatilis* and observed that the cavity of the digestive gland became filled with the red dye.

Rather little is known of the functioning of the digestive system of ancylids. Pelseneer (1935) reported that hemoglobin is present in the radular musculature of *Ancylus,* and Hesse and Doflein (1943) observed that about 12 minutes was needed for a meal to traverse the entire length of the gut of *A. fluviatilis.*

JAWS AND RADULA

Jaws and radulae were removed by placing the heads of specimens in a two per cent solution of KOH for several days. Radulae were mounted unstained, or stained in a 0.5 per cent solution of acid fuchsin. They were examined with the normal and phase contrast microscope at magnifications up to 1500 times. Jaws were dissected out together with a small amount of the buccal mass tissue in which they are embedded, stained lightly, and examined as glycerine mounts. Sections through the jaws are seen on Figure 12, A, and through the radula on Figure 12, A and B, Figure 15, C, and Figure 4, D. The jaws are near the point marked by the leader line from the word "mouth" on Figure 4, B.

The superior jaw is very thin and contains fewer plates than the 18 described by Baker (1928), most commonly eight to ten. The lateral jaws each consist of about 26 small rod-shaped segments or plates, varying greatly in size and shape between individuals.

The radula is very similar to Baker's (1928) illustration and is not figured here. The figures of the radula of *L. fuscus* given by Walker (1918, 1923) are comparatively much poorer. The formula for the Geddes Bridge specimens was 23–1–23, agreeing with Walker (1918) ; Baker could count only 20–1–20 on his specimens from Wisconsin.

EXCRETORY SYSTEM

The kidney of *Laevapex fuscus* lies entirely within the mantle on the left side of the body lateral to the two shell muscles on that side (Fig. 5; Fig. 8, A). It is clearly visible through the thin ventral mantle epithelium in the living animal when viewed from beneath, as is possible through the glass side of an aquarium; it is also vaguely outlined by the distribution of pigment on the dorsal surface of the mantle. Basically, the kidney is a single continuous tube with four sharp bends or flexures. The first of these is near the posterior shell muscle, while the other three lie in the anterior half of the kidney.

The kidney drains fluid from the pericardial sinus by means of the renopericardial duct, a small tube 150 micra long and about 30 micra in diameter. This duct connects the posterior lateral wall of the pericardial sinus with the large saccous dilation at the very beginning of the proximal
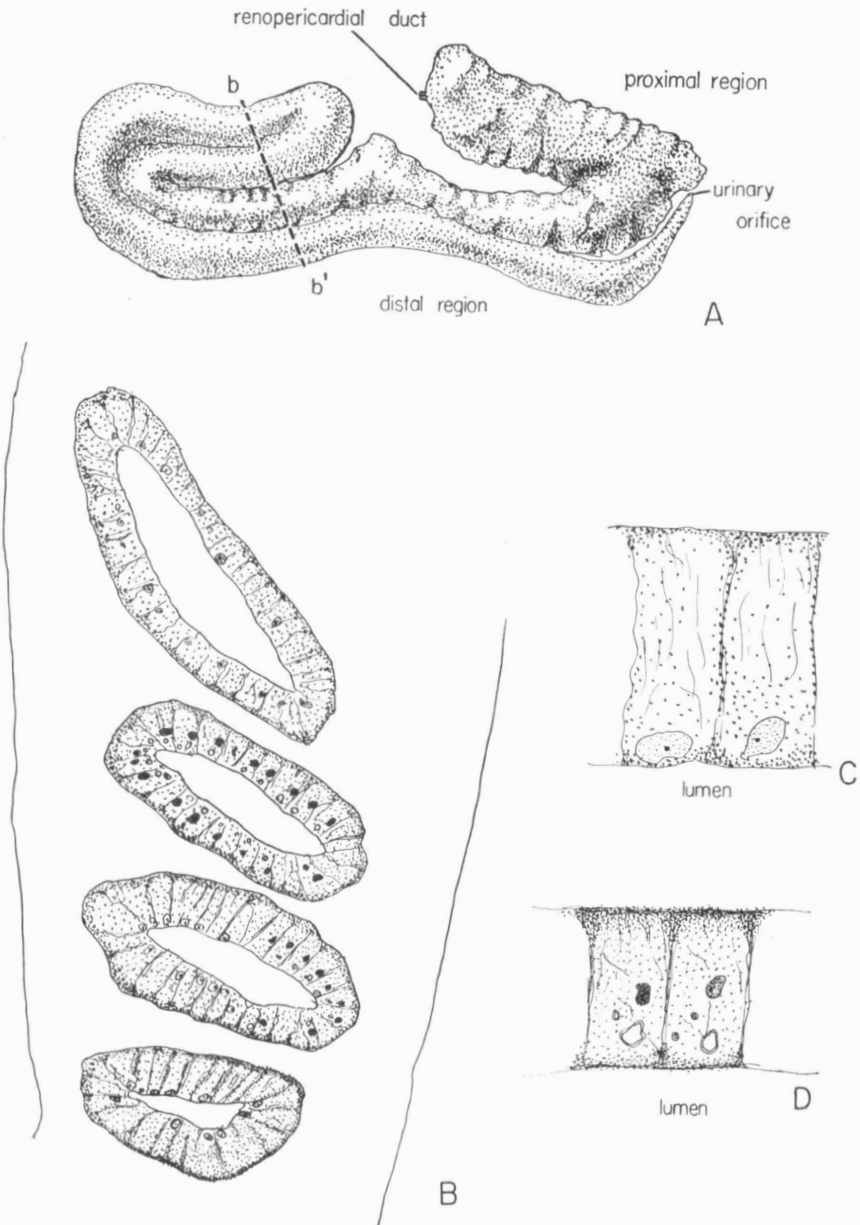
FIG. 5. The excretory system of *Laevapex fuscus:* A, kidney of a relaxed and fixed specimen; left side view. B, section through kidney of another specimen, through plane b—b' on A; vertical lines represent mantle, with ventral surface on right. C, detail of cells from distal region. D, detail of cells from proximal region.

region of the kidney. This connection is difficult to observe in gross dissections, but can often be seen by removing the roof of the kidney in this area. The duct runs sagittally in a plane parallel with and very close to the ventral mantle epithelium. The cells of the wall of the renopericardial duct are small and cuboidal, 6 to 7 micra on a side. Extending into the lumen of the duct are large, massive cilia, the largest observed anywhere in the animal. These cilia, which stain red with Mallory's triple stain in contrast to the blue-staining wall cells, are 30 to 40 micra long. The fluid which they propel from the pericardial sinus into the kidney is not blood, but seems to be some filtrate which may be forced through the rather porous wall of the ventricle when it contracts. The intimate connection between heart and kidney is well illustrated in the following observation by Kozloff (1954), who studied the ciliate *Curimostoma renalis* which lives in the kidney of *Ferrissia peninsulae* from Florida:

"As the limpets are small and the tubule is rather superficial, the ciliates may readily be observed within a living limpet examined with transmitted light under a low power objective. They may swim actively in the fluid of the tubule, and are also rocked by movements of the fluid induced by pulsations of the circulatory system."

He also found that the fluid is probably isotonic with a 0.3 per cent solution of NaCl.

Connecting abruptly with the renopericardial duct is the large saccous extension referred to above as the beginning of the proximal region of the kidney. The kidney is roughly divisible on the basis of its histologic structure into two regions, proximal and distal. The first of these extends from the renopericardial duct to the area of the first flexure, at which point the distal region merges gradually with it and continues to the urinary orifice.

The entire proximal region is about 2 mm. long. Histologically the walls of the tube are made up of a single layer of columnar cells whose appearance is characteristic and constantly different from the cells of the remainder of the kidney. The proximal cells are about 22 micra high; the nucleus is placed centrally and, because of its heavily granular nature, stains darkly with haematoxylin or acid fuchsin. Between the nucleus and the border of the cell nearest the lumen there is almost invariably an irregularly-shaped object reminiscent of the mineral concretions commonly found in the subcutaneous connective tissue. These granules may be the precipitated excretory product. In this regard Pelseneer (1935) quoted Lettelier (1887) as having determined that *Lymnaea, Physa,* and *Planorbis* excrete uric acid. Nothing is said about the Ancylidae, but it may be assumed that the biochemistry of excretion in this family is not fundamentally different from that of the other limnic Basommatophora. Staining with Mallory's triple

stain reveals that the granules take the aniline blue, while the remainder of the cell stains red.

The lining of the distal tubule consists of a single layer of cells which are generally somewhat larger than the proximal cells and differ conspicuously from them. The blue-staining granules are absent from the distal cells whose nuclei are located at the edge of the cell where they crowd the free border near the lumen. This position is very unusual in columnar cells, where the nuclei usually are basally placed.

The entire kidney lies within the blood sinus of the mantle, to whose ventral surface it is attached by a number of fine connective tissue strands. Aside from the cells of the renopericardial duct, the remainder of the kidney does not appear to be ciliated, contrary to the observation of Sharp (1883*a*) for the kidney of *Ancylus fluviatilis*.

The tubules vary in shape, but generally they are roughly circular or oval in cross section, and flattened in a plane parallel to the edge of the mantle. The entire organ will fit into a rectangle 0.6 mm. by 1.8 mm. in size, and the total length of the passage is about 5 mm. The size of the lumen varies considerably in different specimens and in different parts of the tube, but average measurements are about 70 micra in diameter or at most 30 by 150 micra for strongly flattened tubes.

Comparatively, this kidney is very similar to those described by Sharp (1883*a*) and André (1893) for *A. fluviatilis*, and by Hoff (1940) for *Ferrissia tarda*. It differs basically from that of *Acroloxus lacustris,* where the tubules are arranged differently. The precordial gland described by Moquin-Tandon (1852) as a respiratory structure in *A. fluviatilis* is probably the kidney.

NERVOUS SYSTEM

EYES.—The eyes lie in the head just inside the base of each tentacle (Fig. 2, A and B). The optic nerve, a delicate branch of the large tentacular nerve, passes to the eye on either side. The eyes are very weakly supplied with muscles and apparently are not able to rotate or move very well. Because of this and the extremely small optic nerve, it is probable that *L. fuscus* does not rely very heavily upon its eyes in carrying out its normal activities.

The eye itself is a complex organ analogous with the eyes of vertebrates (Fig. 6, D). The black appearance is given to the eye by a heavy layer of pigment lying between the lens and the sensitive cells of the retina with which the optic nerve connects. This pigment layer is about 13 micra in its thickest part and resembles a sphere with a circular portion cut out of its anterior face. In the black layer of the eye is found by far the heaviest concentration of pigment in the entire animal. Overlying the clear portion

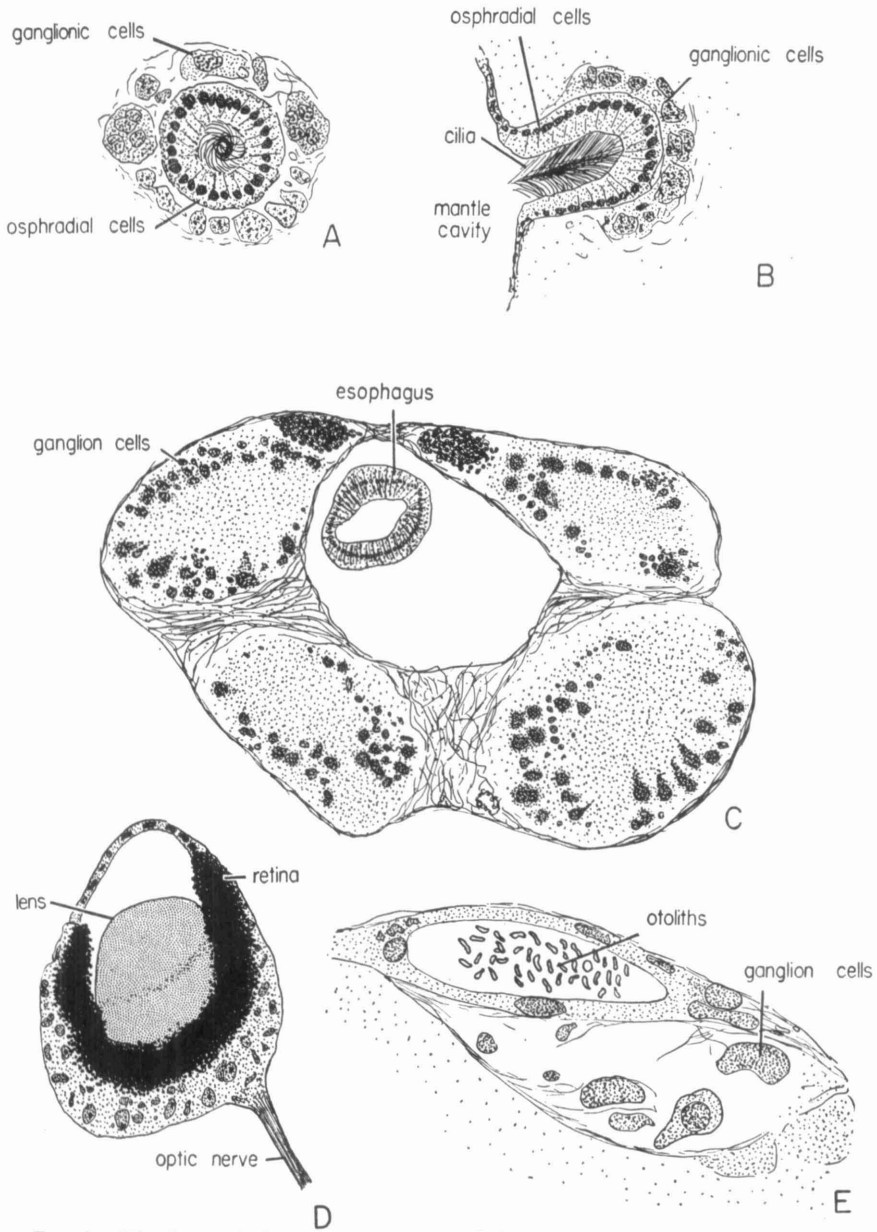FIG. 6. Histology of the nervous system of *Laevapex fuscus:* A and B, cross and longitudinal sections of osphradium showing "cap" of ganglionic cells around inner end of osphradial depression. C, cross section through cerebral commissure; large neurone cells visible peripherally; note smaller "c-cells" of Lever near the word "esophagus." D, section through eye. E, cross section through statocyst showing relation to pedal ganglion.

where there is no pigment is a single layer of thin cuboidal cells, about 5 micra in thickness, which may be called the cornea. The hyaline lens is an approximately spherical structure about 40 micra in diameter, and resembles a small transparent bead when it is forced from the eye of a fresh or preserved animal. The eye extends about 100 micra in its greatest dimension and its general conformation is similar to that found in other pulmonates.

OSPHRADIUM.—This small sense organ lies in the mantle on the left side of the body just in front of the anterior edge of the kidney (Fig. 6, A, B; Fig. 8, A, B). Since its size varies among different specimens, the following description is quite generalized.

The organ itself consists of a tubular invagination from the ventral mantle epithelium (the "infundibulum" of some authors) which is directed dorsally and often curves posteriorly near the edge of the kidney. The tube varies in length to about 300 micra and it is about 20 micra in diameter. The cells that compose its walls are strongly ciliated, and the blind end of the tube is capped by a cup of large ganglionic cells morphologically similar to the neurones within the brain (the "ganglion olfactorum"). One of the branches of the left pallial nerve connects with these cells. The osphradium is generally similar in all ancylids studied. In lymnaeids it is frequently branched and more complex.

The osphradium, first described by Lacaze-Duthiers in 1872, is sometimes referred to as the "Lacaze Organ." This organ is at present little understood, but Hulbert and Yonge (1937) suggested that its function is connected with estimating the amount of sediment which is carried into the mantle cavity of certain mollusks. In describing the osphradium of *Siphonaria alternata,* a primitive patelliform pulmonate, Yonge (1952) verified his earlier opinion.

STATOCYSTS.—Lying on the dorsal surface of the pedal ganglia are two hollow lenticular chambers 45 to 50 micra in diameter containing 30 or more ovoid granules 3 to 5 micra long and 1 to 2 micra wide (Fig. 6, E). These chambers are the statocysts, and the granules enclosed within them are otoliths. Presumably this organ functions in balance and orientation. The fine membrane that covers the statocyst is continuous with the sheath covering the rest of the pedal ganglion; no opening in its wall has been observed.

Moquin-Tandon (1852) described the statocysts of *Ancylus fluviatilis* quite clearly, stating that he could see over 100 otoliths. André (1893) and other authors have mentioned the statocysts in their descriptions. Hoff (1940) agreed with the statement of André that a fine nerve (auditory nerve) passes from the cerebral ganglion to the statocyst. I have been unable to find such a nerve in *L. fuscus.*

BRAIN AND MAJOR NERVES.—The brain of *L. fuscus* (Fig. 7) consists of nine major ganglia: a pair each of cerebral, visceral, pedal, and buccal ganglia, and a pleural ganglion on the left side. The terminology applied to the various parts of the brain and the larger nerves of pulmonates has not been standardized in the literature. Consequently those names have been selected which seem best to describe the parts with the least confusion.

With the exception of the buccal ganglia, which lie on the dorsal surface of the buccal mass near its posterior end, the parts of the brain are distributed in a ring around the narrow portion of the esophagus. The cerebral commissure which connects the two cerebral ganglia lies dorsal to the esophagus, and the other ganglia are lateral to and beneath it.

The shape of the ganglia varies considerably in different specimens, as does also the precise mode of branching of many of the nerves. In some specimens a swelling is detected between the right cerebral and visceral ganglia, which may represent the right pleural ganglion. The entire brain and the major cephalic nerves are invested by a tough membrane or sheath (neurilemma) marked with pigment flecks. The three nerves of the cerebral ganglia are bound by this membrane during the course of their passage through the cephalic hemocele between the buccal mass and the inner face of the body wall. Many of the smaller nerves are very fine and tenuous, and therefore extremely difficult to trace both in gross dissections and on serial sections.

The buccal ganglia are paired subspherical bodies lying on the buccal mass, as previously described, and are connected to the cerebral ganglia on either side by a flattened buccocerebral connective. The buccal commissure between these paired ganglia is bound by a fine membrane to the dorsal surface of the buccal mass and appears to give off a pair of nerves to it medially. On either side arises a single nerve, which runs around the side of the buccal mass, branches, and then enters it laterally. This is the lateral buccal nerve. Dorsally, each of the buccal ganglia gives rise to a short trunk that divides immediately into a salivary nerve supplying an arm of that gland, and an esophageal nerve which passes anteriorly and posteriorly along either side of the esophagus. Apparently all of the nerves of the buccal ganglia are motor in function.

Behind the buccal ganglia and connected with them are the tapering cerebral ganglia. Three stout nerves arise from each of these ganglia; all serve the head region. The uppermost of these three nerves connects with the tentacle, at the base of which it enlarges to form a ganglion with a small lateral spur. The delicate optic nerve arises from the medial side of this tentacular nerve a short distance from its origin in the brain, and then passes without branching directly to the eye.
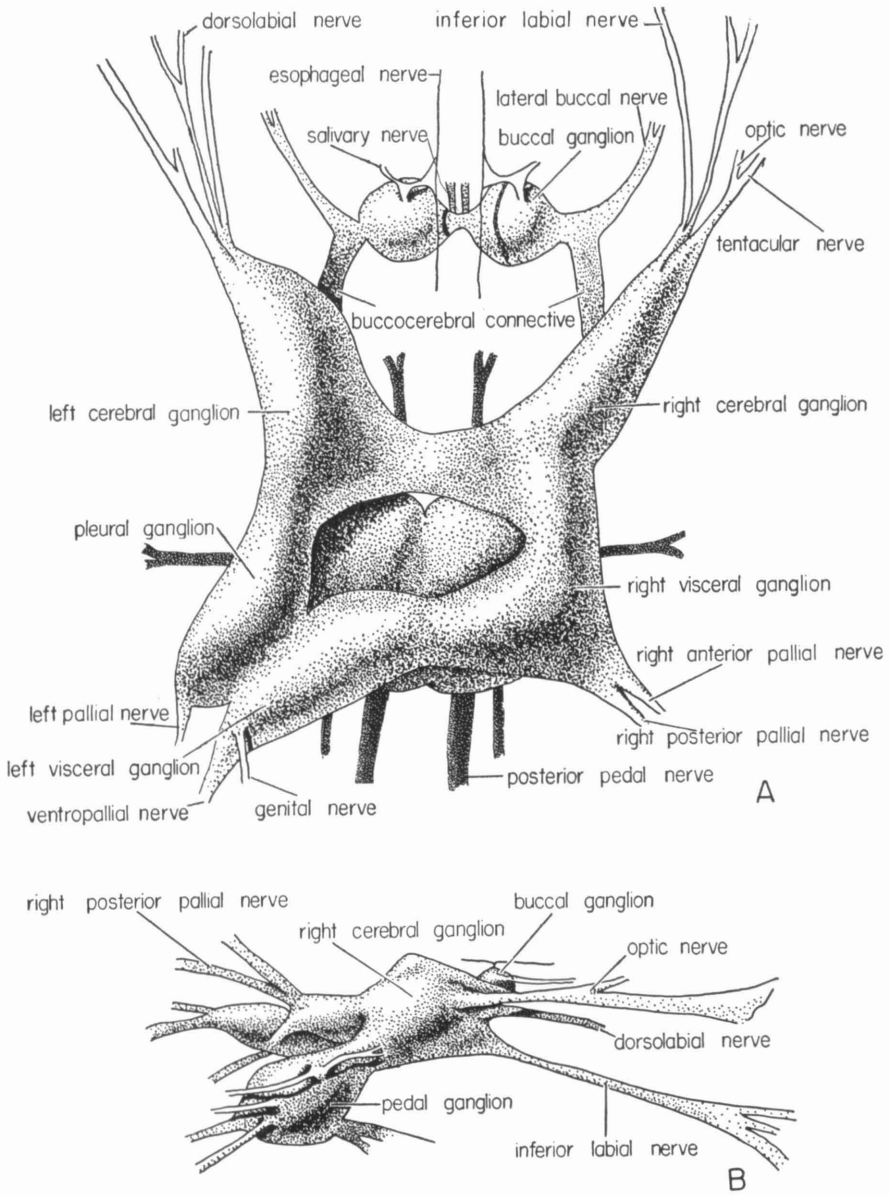
FIG. 7 The brain of *Laevapex fuscus:* A, dorsal view of brain, from a relaxed and fixed specimen. B, right side view of brain of another specimen.

Beneath the tentacular nerve, on each side, the dorsolabial nerve emerges. This nerve follows the outer border of the cephalic hemocele for a short distance, gives off a fine lateral branch about halfway along its course, and passes, usually without further branching, to the side of the mouth, where it divides into several extremely small nerve endings.

The lowermost of the cerebral nerves is the inferior labial nerve, an abundantly dividing nerve which serves the ventral portion of the velum lateral to the mouth. Three main trunks are given off along its course, which is approximately parallel to and below the dorsolabial nerve. These three trunks arise at about the same level, a point about two thirds of the distance between the origin of the inferior labial nerve and the mouth opening. Two of these branches swing laterad where they divide repeatedly and finally terminate around the margin of the velum in very fine branching subdivisions. The third continues in the direction of the main nerve and ends at the mouth near the terminal arborization of the dorsolabial nerve All of the nerves of the cerebral ganglia seem to be sensory in function.

The pleural ganglion on the left side gives off a single large and very important nerve which serves the left side of the mantle with its included organs. This left pallial nerve passes directly into the left anterior shell muscle in which it turns abruptly to continue dorsad, parallel with the muscle fibers. Still within the muscle, it divides into two branches, the first of which passes to the left anterior quadrant of the mantle where it divides variously and ends in a very fine series of nerves at the mantle edge. The second and posterior branch divides again almost immediately, still within the substance of the left anterior shell muscle. One very short limb of this second division leads directly to the osphradium, while the other swings up and over the kidney just under the dorsal surface of the mantle, and ends to the left of the midline of the body behind the posterior shell muscle, having given off numerous lateral branches to the mantle margin along its course. The left pallial nerve with its three major branches appears to have a sensory function.

Somewhat complimentary to the left pallial nerve are the two pallial nerves arising from the right visceral ganglion. The first of these, the right anterior pallial nerve, passes through the right anterior shell muscle in a manner similar to the left pallial nerve on the other side, and serves the right anterior quadrant of the mantle in the same fashion, covering with its subdivisions the entire edge of the mantle in this area.

The second nerve from the right visceral ganglion, the right posterior pallial nerve, does not enter a muscle, but passes along the inside of the right anterior shell muscle, posterior to it, and then dorsally where
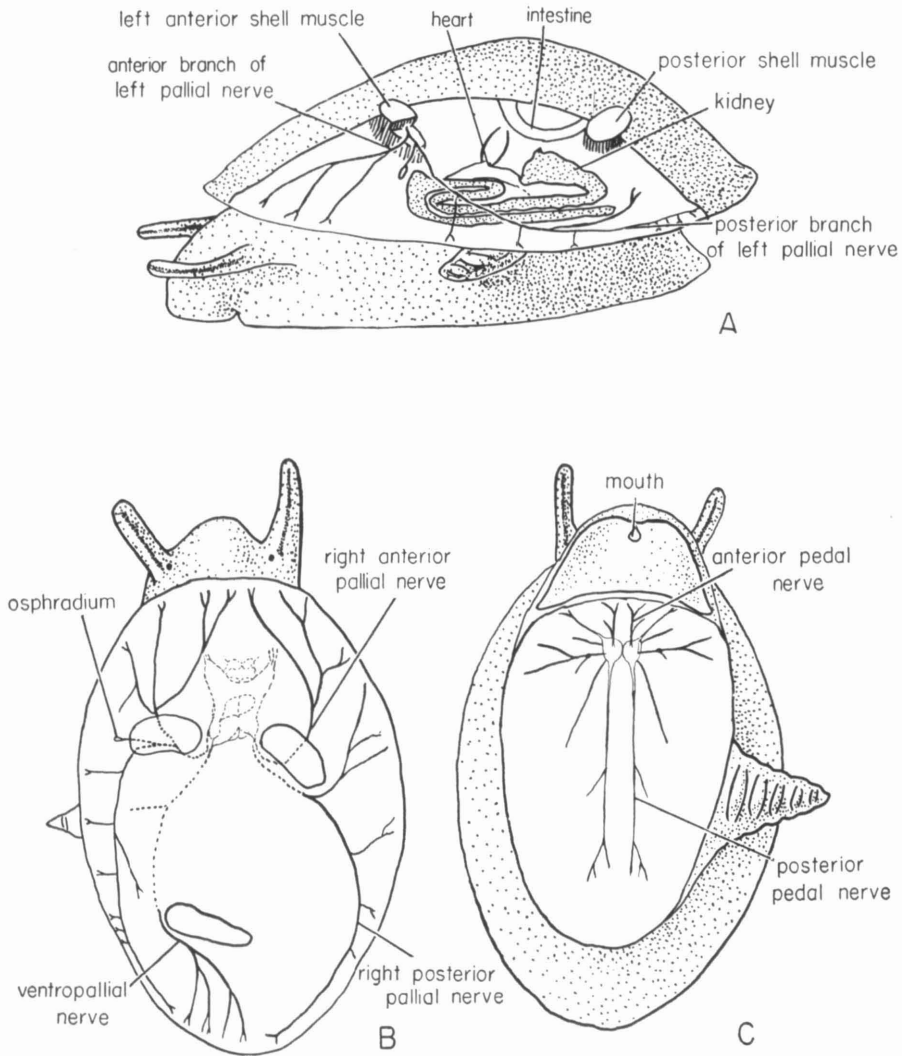
FIG. 8. The nervous system of *Laevapex fuscus:* A, major nerves to left side of mantle, showing ramifications of left pallial nerve. B, dorsal superficial nerves, showing distribution around mantle. C, nerves from pedal ganglia.

it ramifies in the mantle much as the posterior branch of the left pallial nerve does on the opposite side of the body.

The medial posterior portion of the mantle is served by still another nerve arising from the left visceral ganglion. This is the ventropallial nerve, whose course through the body is reminiscent of that of the right posterior pallial nerve. The ventropallial nerve runs free inside the body, around the left anterior shell muscle, along the inside of the left body wall, where it gives off a lateral branch to the pseudobranch, and finally posteriad and dorsad around the posterior shell muscle to end after serveral divisions in the mid-posterior region of the mantle.

The mantle is thus seen to be highly supplied with nerves from five major branches arising from three ganglia. Such a rich nervous supply reflects the importance of the mantle in the general economy and well-being of the animal.

Aside from the ventropallial nerve, the left visceral ganglion gives off a fine, tenuous nerve to the genital system. This nerve runs free through the body cavity to an attachment in the region of the prostate. Tracing of the subsequent course of this nerve has unfortunately not been possible, and the nerves which must activate many of the visceral organs have not been found.

The pedal ganglia supply nerves to the foot region and the lower portion of the body generally. More nerves connect with this lowermost pair of ganglia than with any of the others, and many of these are extremely delicate and difficult to trace. Moreover, there seems to be some variability in the placement and course of the smaller nerves. I shall confine this discussion to some of the major pedal nerves.

Anteriorly, three pairs of nerves are given off by the pedal ganglia, to serve the front region of the foot. The innermost pair originates on the ventral anterior surface of the pedal ganglia and extends the short distance between the ganglia and the front edge of the foot (but not to the velum). Each of these anterior pedal nerves sends off two short branches within this distance. Lateral to these and emerging from the outer anterior "corners" of the pedal ganglia are two nerves on each side which branch variously into the foot and the base of the anterior shell muscles. These and others in this area may be considered as "cervical" nerves. One pair of nerves from the medial ventral face of each pedal ganglion runs laterally to the areas of the foot at the sides of the brain, and two nerves from each ganglion run posteriad from the pedal ganglia into the main mass of the foot. The inner of these, the posterior pedal nerves, are the longest nerves arising from the pedal ganglia, and extend through the foot, giving off several

branches. They show a few ganglionic swellings along their course until their ramifications become too fine to follow in the very posterior part of the foot. The outer of this pair of posteriorly directed nerves is much finer and more delicate than the posterior pedal nerve, and angles laterally, presumably to the body wall on each side.

Histologically, the elements of the brain and nervous system present a characteristic picture differing from that of all other tissues of the body. The ganglia show a central mass of velvety-textured tissue with a few scattered small nuclei in which fibrous tracts can simetimes be distinguished (Fig. 6, C). Around this area is a cortex of large ganglionic cells. These cells typically have heavily granular round to oval nuclei about 10 micra in diameter, in which a nucleolus is sometimes observable. The nuclei are surrounded by a coat of smooth-textured cytoplasm of conical shape with a long tapering apex leading into the central mass. Lever (1957) distinguished at least seven different types of such cells, and also found neurosecretory phenomena in the form of granules which are passed along the nerve fibers in an unidentified species of *Ferressia*. Several extremely large ganglion cells are found in the median ventral region of the pedal ganglia. These enormous cells measure 40 micra across with a nucleus 20 micra in diameter.

The commissures and connections between the various ganglia are bridges of a definitely fibrous construction resembling the larger nerves in this respect. The cerebral commissure between the two cerebral ganglia is of this type, but, in addition, it has a dorsal covering of small crowded cells which extends laterally into the dorsal region of both cerebral ganglia and appears to be set off by a fine membrane from the rest of the ganglion cells. These small cells are undoubtedly the same as the "c-cells" described by Lever as being present in the latero-dorsal and medio-dorsal bodies in his species of *Ferrissia*. In that case, the two sets of "bodies" stood out quite prominently from the surface of the ganglia, a situation also common in such ancylids as *Ferrissia tarda*. These bodies, or their homologues, are also present in *L. fuscus*, although they cannot be seen in a gross dissection. In Lever's species, the "c-cells" apparently did not cross the cerebral commissure, while they do so very clearly in *L. fuscus*. The phylogentic significance, if any, of the distribution of cell types in the central nervous system is not known.

From the work of Sharp (1883a), Lacaze-Duthiers (1885), and André (1893), it appears that the central nervous system of *Ancylus fluviatilis* consists of ten ganglia, and that of *Acroloxus lacustris,* as well as *Ferrissia tarda,* described by Hoff (1940), has nine. The brain figured by Lever (1957) also has nine.

CIRCULATORY SYSTEM

The circulatory system of *Laevapex fuscus* consists of a two-chambered heart (Fig 8, A; Fig. 9) and a poorly defined arterial system, together with the blood sinuses in the tissues. The heart lies in the pericardial sinus or space situated between the two shell muscles on the left side and medial to the kidney. The funnel-shaped lumen of the auricle actually lies outside the pericardial space in the marginal blood sinus of the mantle. The medial portion of the intimately associated kidney is often drawn for a short distance into the auricle. The thin membrane that composes the auricular wall extends from the posterior lateral edge of the left anterior shell muscle, around the conical auricle, and back to a point at a level with the beginning of the saccous portion of the kidney. Here the wall of the pericardial sinus continues mesiad around this part of the kidney and lateral to the first loop of the intestine, swinging anteriad to the inner edge of the left anterior shell muscle. The pericardial space is limited ventrally by the fine membrane composing the roof of the pulmonary cavity, which lies beneath, and dorsally by the dorsal mantle epithelium. The only opening into the pericardial space appears to be the tiny renopericardial duct, which communicates with the mid-ventral part of its posterior wall. The auricle and ventricle are actually a continuous tube through the middle of this cavity, connecting with the marginal blood sinus of the mantle on one side and the aorta above the stomach on the other. Numerous dissections of this area have failed to show a single instance where the pericardial sinus itself contained any blood. The fluid drawn into the kidney by the ciliary action within the renopericardial duct is not blood, but pericardial fluid, presumably a filtrate (through the walls of the ventricle?) containing some components of whole blood and lacking others.

Between the two parts of the heart lies a conical valve, about 50 micra long, with its base facing the auricle. The ventricle is formed of a type of cell found only in this organ. These are long, ribbon-like muscle cells, 4 to 6 micra wide, that branch abundantly to form a syncytial network. Nuclei are distributed throughout the fibers, which dilate slightly to accommodate them, and also in the triangular areas where the three arms of a branching fiber come together.

The aorta, which leads from the medial end of the ventricle, immediately breaks up into a fine tissue that fills the loop of the intestine above the stomach. Various authors (Sharp, 1883a; Moquin-Tandon, 1852; André, 1893; Hoff, 1940) stated that in the species of ancylids studied by them the aorta divides into cephalic and visceral branches, but no such branches could be distinguished in *L. fuscus*.

Beneath the brain, and extending to the ventral surface of the buccal mass, is a tubular net of tissues which presumably acts to direct blood to
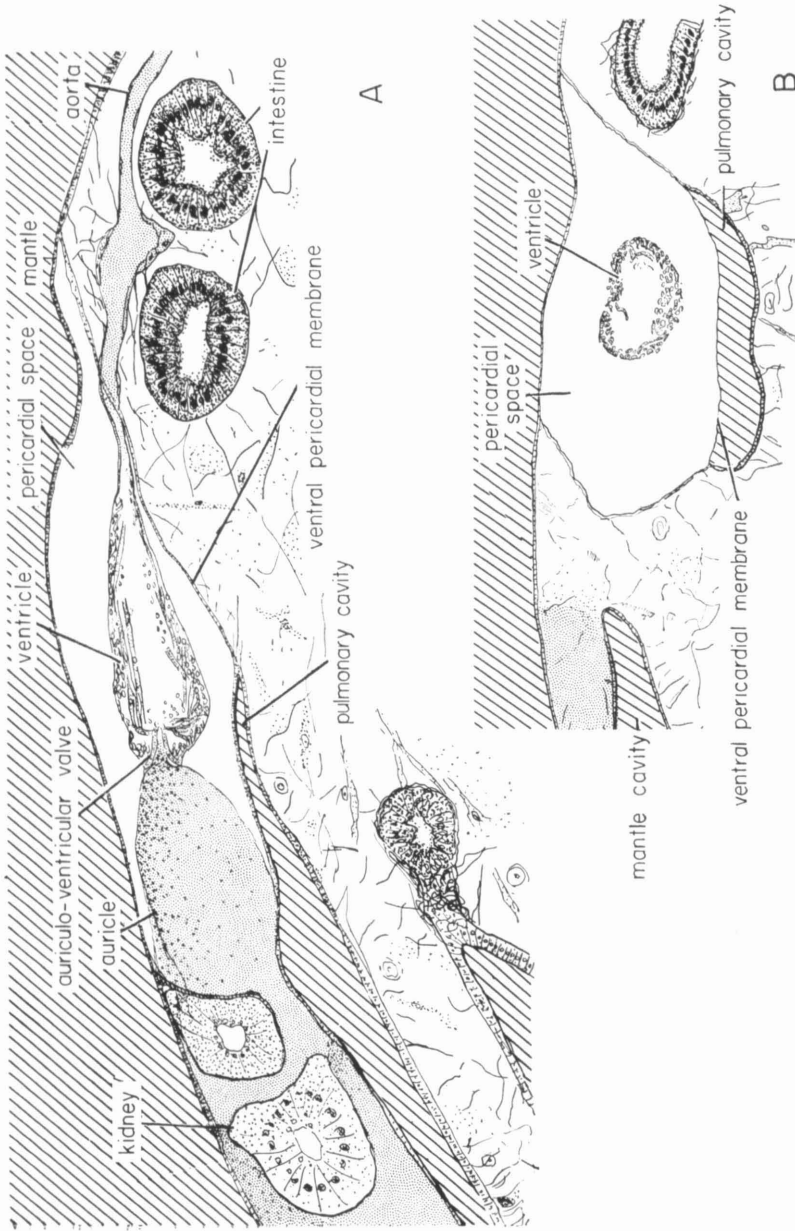
FIG. 9. The heart of *Laevapex fuscus*: A, cross section through heart region; blood represented by fine stippling. Parallel diagonal lines show regions external to body. B, longitudinal section through heart region.

the buccal mass. Extending between the two anterior shell muscles are two very fine membranes, more poorly developed in *L. fuscus* than in *F. tarda,* which may serve a hemostatic function, or may be vestiges of a structure that served such a function.

In a gross dissection of a preserved animal the blood appears as a fluffy, cottony mass filling the ventricle; often packed into the interstices between the kidney folds, and spreading out generally throughout the inside of the mantle. Occasionally blood is found packed around the brain and rarely also around the buccal mass, but it is not known if this situation represents a pathological hemorrhage induced by the anesthesia and fixation.

Microscopically, the blood is a rather uniformly-textured, light-staining, acellular fluid. The auricular wall, similar in nature to the other delicate membranes found in the body, is composed of a single extremely thin layer of unpigmented squamous cells.

There is no venous system. The body contains undefined blood sinuses, of which the inside of the mantle is one. The system is "open" as compared with the "closed" system of the vertebrates.

The structure of the heart in other ancylids that have been studied is generally similar to that of *L. fuscus,* except that the heart of *Acroloxus lacustris* lies on the right side, as do most of the body openings in that species.

REPRODUCTIVE SYSTEM

In common with other pulmonates, *L. fuscus* has elements of both male and female systems intermingled in its reproductive tract (Fig. 10). Some units of the reproductive system play a part in both male and female functions, and some may be said to belong exclusively to one or the other "sex." The common elements include the ovotestis and hermaphroditic duct (with the exception of the seminal vesicle). The male organs are the prostate, vas deferens, and penial complex. The enlargement of the hermaphroditic duct which serves as the seminal vesicle should probably be included here also. The albumen gland, uterus and vagina, nidamental gland, and the seminal receptacle or spermatheca comprise the female portion of the reproductive system.

The ovotestis (Fig. 10, A) is a roughly hemispherical gland about one mm. in diameter. It is divided into 20 or more elongated acini or follicles whose long axes lie in a plane perpendicular to the flat surface of the organ. Within these acini all of the stages of spermatogenesis and oogenesis are observable, but details of these processes will not be elaborated here. The primordial germ cells are concentrated along the walls of the acini, the open lumina of which usually contain large numbers of sperm cells. Clusters of maturing sperm cells gathered around the Sertoli or nurse cells near the upper portion of the gland are easily found. Developing eggs are seen in
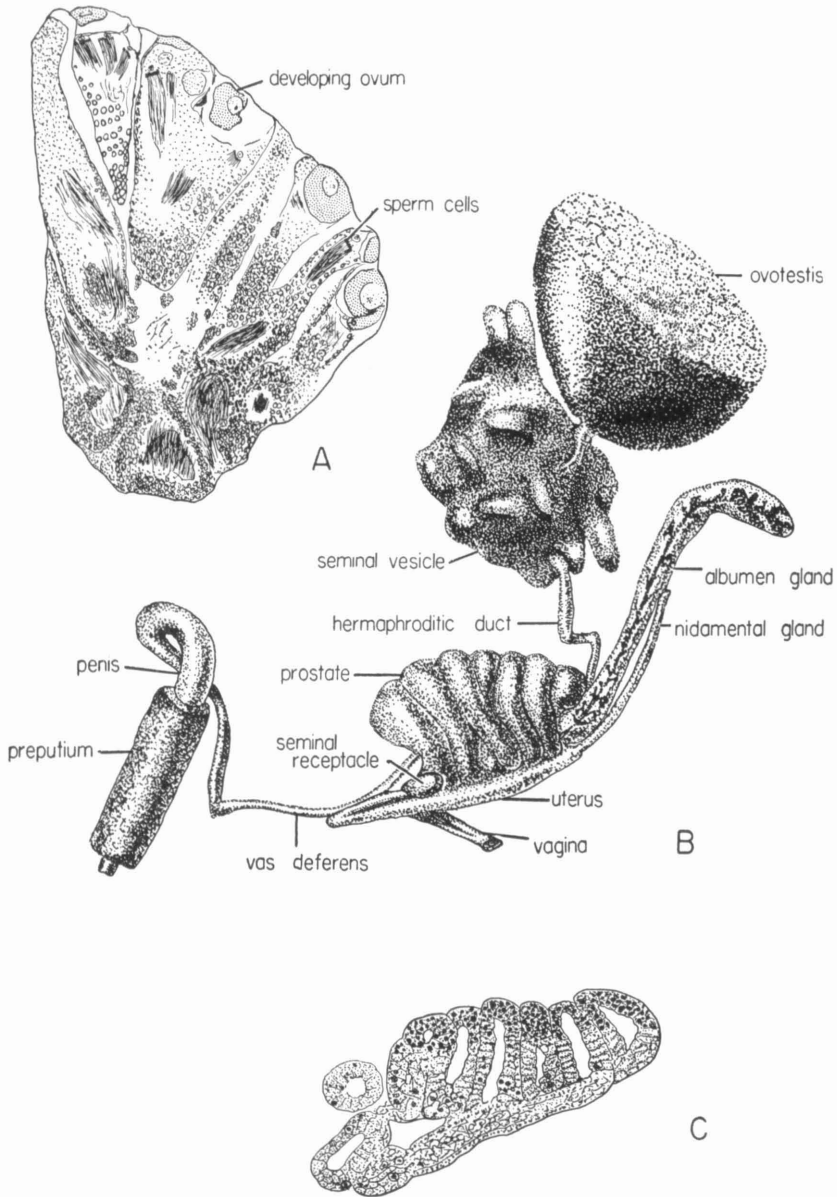
Fig. 10. The reproductive system of *Laevapex fuscus:* A, section through ovotestis showing regions of developing sperm cells and ova. B, entire reproductive system from a relaxed and fixed animal. C, longitudinal section through prostate, showing follicles. Heavy black dots represent droplets of secretion.

the uppermost part of the ovotestis. These ova are generally about 60 micra across and are characterized by a distinct germinal vesicle nucleus, 30 micra in diameter, which contains several large densely staining granules; one or more of these may be nucleoli.

In comparing the ovotestis of *L. fuscus* with that of other ancylids, the general impression is that the gland in this species is more massive and is composed of many more follicles. *Ferrissia tarda* has five to seven follicles, and the drawing of the ovotestis of *A. fluviatilis* by Lacaze-Duthiers (1899) indicates about 15, rather distinct and clearly separated. The figures of *A. fluviatilis* in the paper by Stepanoff (1866) are very poor and useless for comparison. In proportion to the size of the body, the ovotestis of *L. fuscus* is larger than that of other ancylids.

The hermaphroditic duct leads from the ventral anterior face of the ovotestis and within a very short distance dilates enormously to form the thin-walled seminal vesicle. This structure varies greatly in size, depending on the condition of the individual, and is often about as large as the ovotestis itself. The seminal vesicle is normally densely packed with sperm cells numbering many thousands. Presumably these cells undergo some sort of maturation process during their stay in this organ (Fig. 14, E). The surface of the seminal vesicle is marked by a variable number of very definite digitate projections extending in all directions from the main body of the organ. Its wall consists of a single layer of squamous or low cuboidal, unciliated epithelium about 4 micra thick. The seminal vesicle lies just anterior and medial to the ovotestis and, like it, is embedded within the digestive gland, which must be picked away in gross dissections to reveal it.

This form of seminal vesicle has never before been described for an ancylid snail. Both Baker (1928), in his description of the genitalia of *Ferrissia parallela*, and Lacaze-Duthiers (1899), for *A. fluviatilis*, showed a rather small number (six to nine) of follicles or ceca, each about the same diameter as the hermaphroditic duct itself and each ending blindly within a very short distance. The total volume of sperm cells that these might contain would amount to only a fraction of that found in the seminal vesicle of *L. fuscus*. *F. tarda* has a single, simple bulbous evagination near the middle of the hermaphroditic duct (Hoff, 1940), again relatively tiny in comparison with that of *L. fuscus*.

Leading from the seminal vesicle more or less transversely across the body is the distal continuation of the hermaphroditic duct, which connects at its other end with the complex set of glands and organs constituting the bulk of the reproductive systems.

These organs lie almost entirely to the left of the midline of the body and extend from the region of the buccal mass to behind the posterior shell

muscle. The interconnections between constituent parts are not evident unless they are very carefully separated with fine instruments.

At its distal end the hermaphroditic duct opens into a small, irregularly shaped chamber from which three tubes are seen to lead. This area may be called the carrefour. It is not seen when the organs are in their normal positions, as they are on Figure 10, B. A posterior duct from the albumen gland opens into this chamber, as does the duct from the prostate which lies anteriorly. The fourth opening from the carrefour is lateral and communicates with the uterus which, through the vagina, leads to the female genital opening just beneath the pseudobranch. The carrefour is in the normal position in comparison with other forms, but the papilla found in *F. tarda* and *F. parallela* appears to be absent from *L. fuscus*.

THE FEMALE PART OF THE SYSTEM.—The albumen gland in *Laevapex fuscus* is a flat, ribbon-like body roughly 1.5 mm. long and 0.2 mm. wide. It lies against the floor of the visceral cavity and is wrapped around the inner face of the posterior shell muscle. It is composed of a large number of closely appressed lobules, each of which consists of a layer of cuboidal secretory cells around a central cavity into which their products are elaborated. The cavities of all the lobules are continuous with an irregular lumen passing through the center of the albumen gland and opening as previously described into the posterior wall of the carrefour.

Ebner (1912) made a special investigation of the albumen gland of *Ancylus fluviatilis* and found fibrillar structures or lamellae inside the cells reaching about to the height of the nucleus and playing a part in the formation of the secretion. Similar cytological structures have not been found in *L. fuscus,* although a difference in technique might have revealed them.

The albumen gland is quite variable in gross structure. In *F. parallela* it is a large, rounded, somewhat irregular body, composed of many elongated, tube-like follicles. In *A. fluviatilis* it is a rather loose mass of feathery lobulations, each elongated and pear-shaped. A flat, leafy shape is assumed by the albumen gland of *F. tarda,* but according to Hoff (1940), the shape varies considerably.

The nidamental gland, which runs parallel and lateral to the albumen gland, is a rather puzzling structure. If, as appears, it is a dorsal prolongation of the glandular upper wall of the uterus with which its small cells merge rather indistinctly, the size and shape of this gland cannot be given definitely. The free portion near the albumen gland is about .75 mm. long and .05 mm. wide, and is more nearly circular in cross section than the latter. The normal position of this gland in the other families of Basommatophora is at the summit of the uterus, and in the Planorbidae it "follows the uterus and is usually placed over the uterus and oviduct" (Baker,

1945). In *Ancylus fluviatilis* and *Ferrissia tarda* the nidamental gland is near the proximal end of the uterus.

The uterus is a flattened tube which varies greatly in size and histologic appearance with the condition of the individual. The best-developed uteri are found in animals collected in midsummer; in these the squarish anterior extremity is frequently found to extend forward along the inner edge of the left anterior shell muscle and underlie the penial loop, passing almost as far forward as the buccal mass. In these individuals the dorsal and ventral surfaces of the uterus are heavily invested with a yellowish glandular coat with well-defined edges, beginning about one-fourth of the distance back on the uterus and extending to its posterior extremity. It is this glandular material that also appears to compose the nidamental gland. The inner wall of the uterus is folded in preserved specimens and the entire inner epithelial surface is heavily covered with cilia. Its walls are thickened and rather muscular.

Connecting with the uterus at its anterior end is the vagina, which turns abruptly and forms an angle of 180 degrees with the uterus, connecting this organ with the female genital orifice. The inner wall of this portion of the vagina resembles that of the uterus, since it also is heavily ciliated. Almost immediately inside the female genital opening, the vagina bifurcates, one arm passes up and forward to the uterus as described, and the second branch leads to the seminal receptacle, or spermatheca of some authors. The wall of the latter portion presents a very different histological picture. It is lined by a layer of small, dense columnar cells surrounded by a thick muscular coat. The lumen is greatly compressed, and the whole appearance is very similar to that of the terminal end of the rectum near the anus. This histological arrangement continues into the seminal receptacle itself; the entire bulbous structure is covered by a thick muscular coat different in appearance from the rest of the female system. The seminal receptacle usually is full of some orange-colored secretion. Well-formed sperm cells are encountered there only rarely, although they are commonly seen in the anterior branch of the vagina leading to the uterus. This plan of structure is essentially the same as that found in other basommatophores, and is similar to that in the other species of ancylids which have been studied in detail.

THE MALE PART OF THE SYSTEM.—Following through the male part of the system from its junction with the hermaphroditic duct at the carrefour, the only gland encountered is the large, folded prostate. This gland consists of seven to nine tubular lobes folded over upon themselves much the same way that the fingers are folded over the palm of the hand in a fist. The free distal edge of the prostate lobes lies approximate to and usually slightly over the uterus, and it is possible in favorable materials to fold
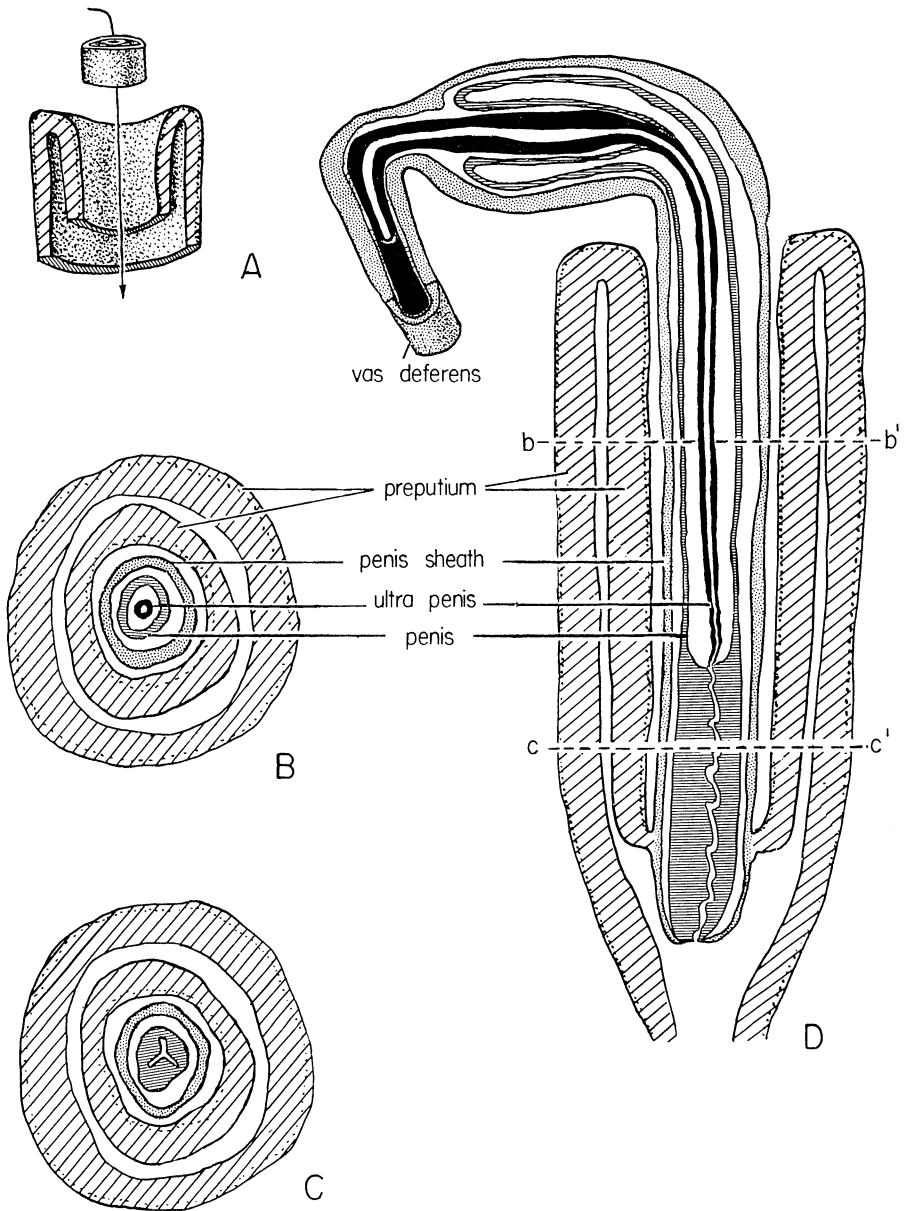
vas deferens

preputium

penis sheath

ultra penis

penis

A

B

C

D

b b'

c c'

FIG. 11. The penial complex of *Laevapex fuscus:* A, cutaway view through upper end of preputium; arrow indicates position occupied by penis. B, cross section through plane b–b' on D. C, cross section through plane c–c' on D. D, longitudinal section through male organ; reconstructed from cleared whole mounts and serial sections.

this half of the prostate back to reveal the passage of the vas deferens through the ventral portion beneath. Histologically, the lobes of the prostate are actually follicles formed of sacs of cells surrounding a central lumen. These secretory cells, as in many other glands, are in a single layer varying from large columnar cells 25 by 12 micra in size to various smaller columnar and cuboidal forms. They show, better than any other cells, extremely active secretory activity, with droplets of the secretory product visible practically everywhere. With Mallory's triple stain these droplets appear bright orange in the part of the gland approximate to the vas deferens and more reddish distally. They are also much larger in the proximal region. Haematoxylin with eosin or erythrosin reveals these droplets as highly refractile granules, shining brightly with the microscope slightly out of focus. The composition of the droplets is unknown, but it is assumed that the secretion of the prostate adds to the fluid in which the sperm is transferred during copulation.

Hubendick (1946) made a special study of the prostate in the Basommatophora, and defined the structure to which this name should be applied:

"The term prostate should only be used for glandular formations that have developed from part of the vas deferens (or in cases of monauly from the male part of the common duct) situated proximal to its passage through the musculature of the body wall. The fully developed prostate organs cannot always be assumed to constitute homologous structures. But the potentially prostatogenous region is probably genetically uniform."

The form of the prostate differs greatly from that in some other ancylids. This gland in *Ancylus fluviatilis* is merely a saccous extension of the vas deferens which has three digitate pouches called by Lacaze-Duthiers (1899) "trois culs-de-sac." In *Ferrissia tarda* it is represented by Hoff (1940) as an oval-shaped body in which the vas deferens makes a coiled loop before proceeding distally. Baker's (1928) figure of the prostate of *F. parallela* is more like that found in *L. fuscus,* showing seven long narrow tubes laid longitudinally across the vas deferens.

Continuing with the male system of *L. fuscus,* the vas deferens passes from the anterior lateral corner of the proximal portion of the prostate, swings laterad to the body wall very near and a little posterior to the vagina, turns 90 degrees and runs forward within the body wall lateral to (but not through) the left anterior shell muscle to a point just posterior to the attachment of the base of the preputium beneath the left tentacle. Here it turns 90 degrees once more and swings inward again to about the middle of the body where it makes a loop and joins the penis.

The male copulatory organ in *L. fuscus* is a simple series of concentric tubes without a flagellum and in this respect differs basically from all other
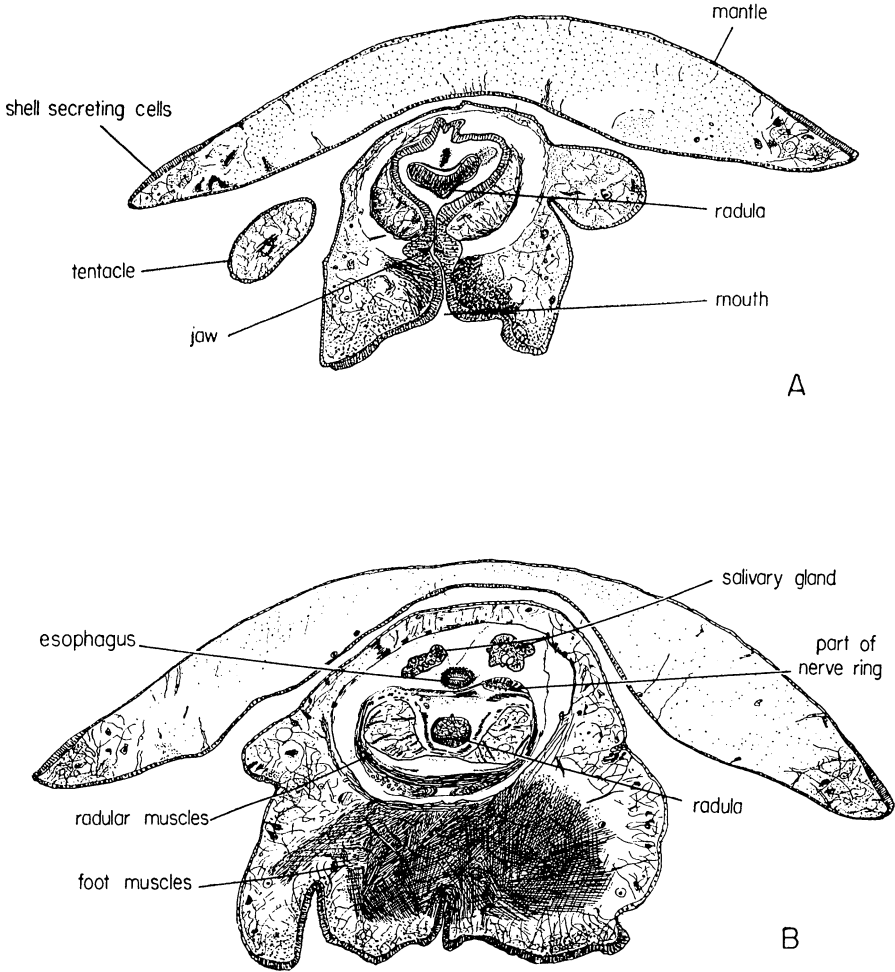
FIG. 12. Cross sections through *Laevapex fuscus:* A, through mouth region. B, through head just posterior to mouth.
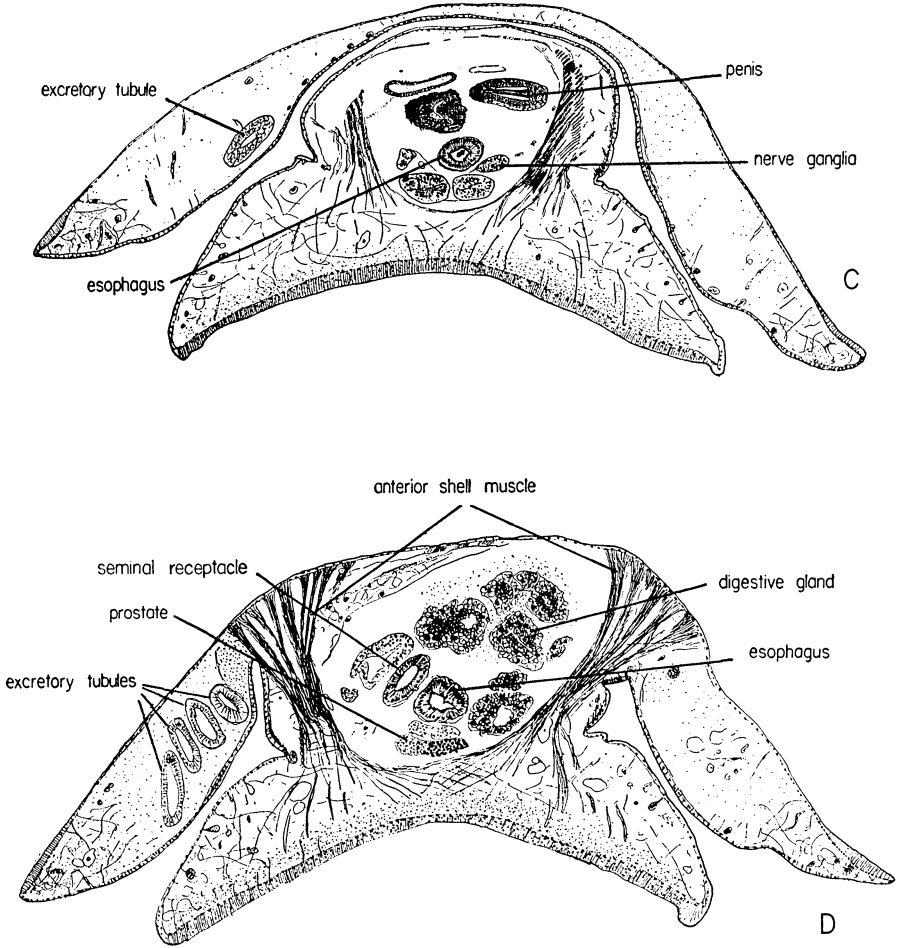
FIG. 13. Cross sections through *Laevapex fuscus:* (continued): C, through neck region posterior to buccal mass; anterior tip of kidney visible. D, through anterior shell muscles; hollow glandular organ to left of seminal receptacle is uterus.
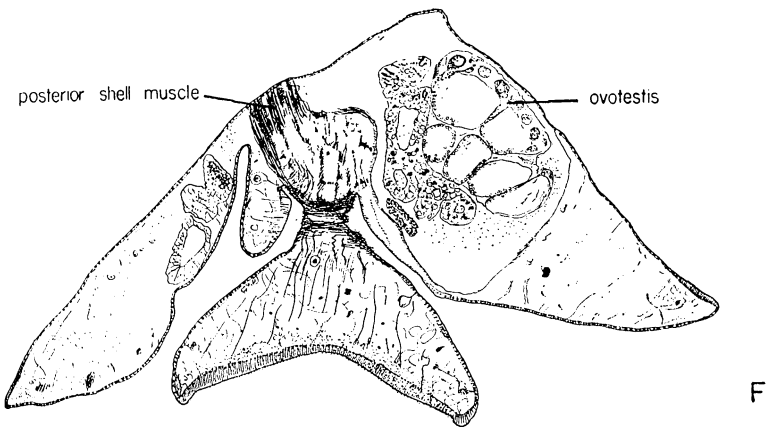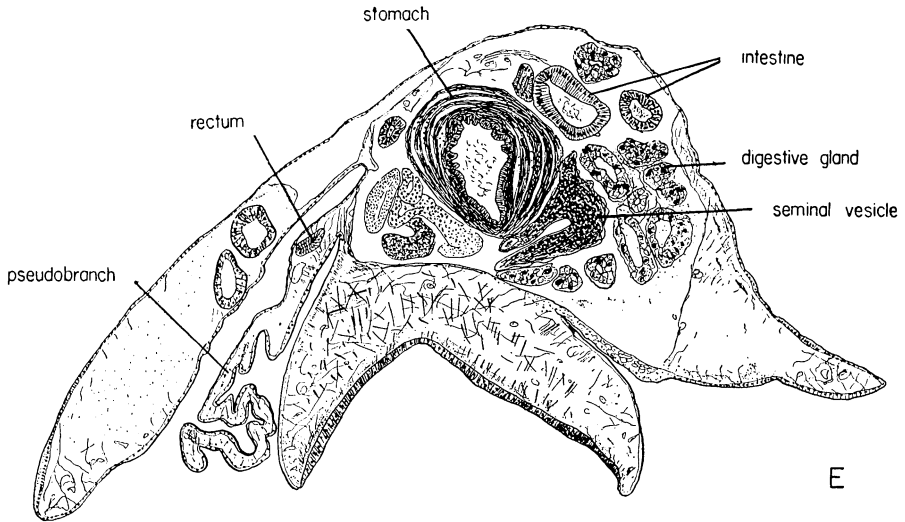
FIG. 14. Cross sections through *Laevapex fuscus* (continued): E, through body near posterior part of pseudobranch. F, through region of ovotestis.

ancylid forms yet investigated. Hundreds of specimens from several different localities have been dissected without revealing a flagellum.

Ancylus fluviatilis possesses a long flagellum, as Lacaze-Duthiers (1899), Hubendick (1947), and others have reported. In the American species that have been studied, the flagellum is much shorter and club-shaped. Baker (1928) and Hoff (1940) are not in agreement as to the mode of entrance of the flagellar duct into the main lumen of the penis.

The male copulatory organ differs moreover in the possession of an ultra-penis type of arrangement. This structure was described by Hubendick (1948) under the name of "pseudo-penis," in his investigation of the genus *Bulinus,* but the terminology has recently been standardized to "ultra-penis" (Hubendick, 1955).

In the ultra-penis, a secondary split within the original penis results in a "tube-within-a-tube" plan, often permitting the contained ultra-penis, actually a prolongation of the vas deferens, to coil within it. This type of organization is present in some planorbids (e. g., *Bulinus, Indoplanorbis, Physopis*) and also in some lymnaeids. Such an arrangement has never before been reported for an ancylid snail.

There is some question whether the ultra-penis is actually connected with the thickened distal region of the penis in *L. fuscus* (Fig. 11, D), or extends into the lumen of the penial duct in this region and ends there. The association is certainly close, but an actual continuation of the cells of the ultra-penis with the cells of the penis itself has not been demonstrated unequivocally despite the numerous whole mounts and serial sections that have been studied.

In the normal, retracted condition, the preputium is folded back upon itself (Fig. 11, A).

The differences here detailed in the structure of the penial complex of *L. fuscus,* as compared with other ancylids, are undoubtedly of considerable phylogenetic and taxonomic significance. However, the present state of knowledge concerning the anatomy of other forms is so poor that an intelligent evaluation of the true meaning of these differences is impossible.

DISCUSSION

An attempt has been made to discuss as completely as possible the anatomical features found in *Laevapex fuscus,* and to compare each with the corresponding structures in all other ancylid species that have been investigated by other workers. Thus, this study may serve both as a summary of the present state of knowledge concerning ancylid anatomy and as a basis from which further research can be developed. The distinction of generic rank found between *Laevapex fuscus* and *Ferrissia* was not antici-
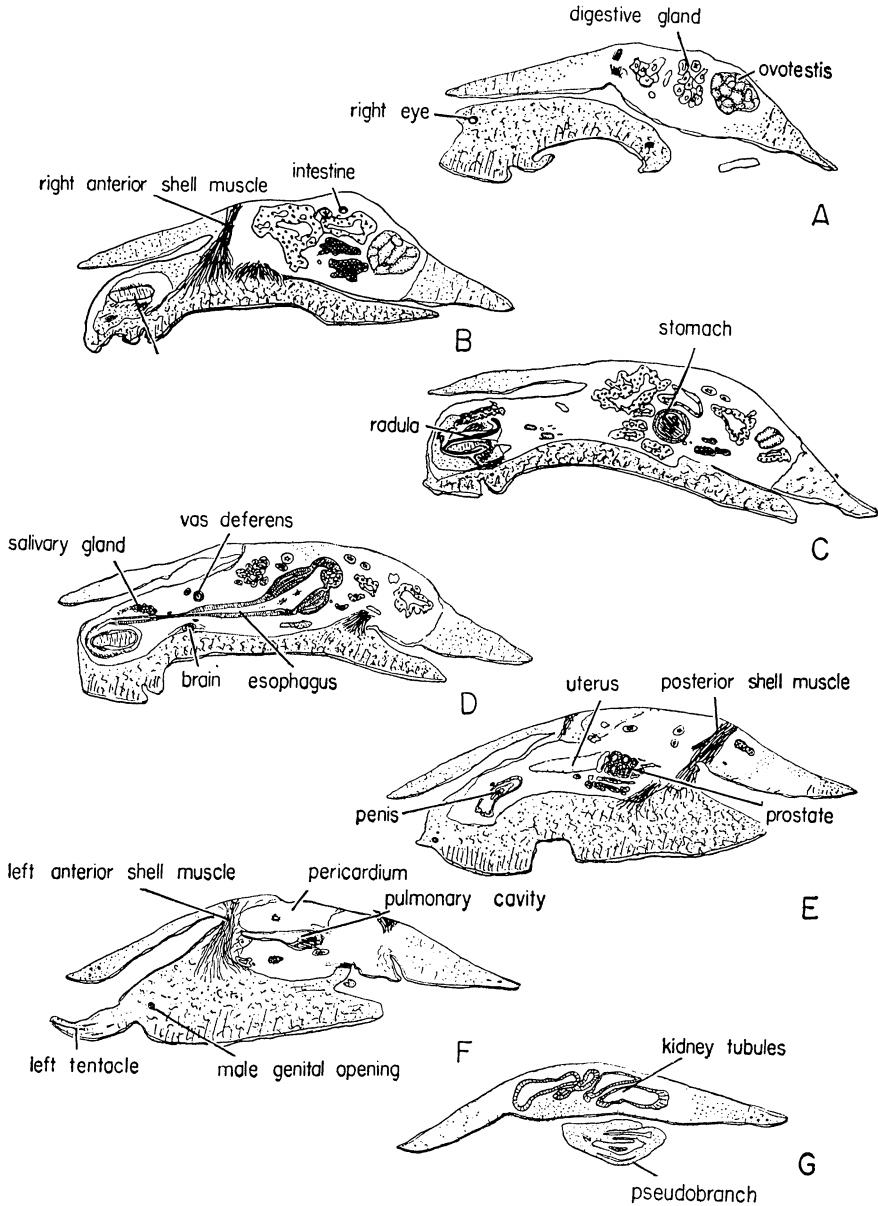
FIG. 15. Sagittal sections through *Laevapex fuscus:* A, through right side of body. B, through region of right anterior shell muscle; seminal vesicle shown in crosshatch. C, just to right of midline. D, medial section showing course of esophagus to stomach. E, to left of midline. F, section near left edge of body; cf. Fig 9, B. G, through mantle and pseudobranch lateral to left side of body.

pated when the study was initiated, and it is entirely possible that the dissection of other species of freshwater limpets will reveal further unexpected relationships or divergences within this puzzling group. However, notwithstanding the differences summarized in Table II, *Laevapex* and *Ferrissia* are probably closely related. Nevertheless, the differences in the respiratory and reproductive systems bespeak an isolation of long standing between members of these two genera.

TABLE II

Major Anatomical Differences Between *Laevapex fuscus* and *Ferrissia tarda*

Structure	L. fuscus	F. tarda
Shell	relatively lower; apex smooth, rounded	relatively higher; apex striated, subacute
Pigment	hollow black core in tentacles; on mantle under shell	none in tentacles or under middle of shell
Salivary glands	fused; horseshoe-shaped	separate; sausage-shaped
Reproductive system:		
ovotestis	many (ca. 20) follicles	few (5–7) follicles
seminal vesicle	large with digitate extensions	small, simple
prostate	large, lobed, folded	small, simple
flagellum	absent	present, club-shaped
penis	ultra-penis; large	normal penis; small
albumen gland	strap-shaped	leafy
nidamental gland	around uterus; thin, ribbon-shaped	leafy

The striking contrast in habitat between *Laevapex fuscus* and such forms as *Ferrissia tarda* or *F. rivularis* are undoubtedly of significance in understanding the differences in morphology between these forms. The primary morphological feature of ecological significance is the nature of the pseudobranch. Even though the total oxygen consumption of lentic and lotic freshwater limpets may be the same (Berg, 1952), the availability of oxygen in the two habitats may be quite different. The richly folded pseudobranch of *L. fuscus* is, therefore, considered to be an adaptation

for life in an oxygen-poor environment, in contrast to the simple flap-like structure found in *Ferrissia* from well oxygenated streams.

The relatively greater pigment concentration in *L. fuscus* may be related to problems of heat conservation in more unstable lentic environments, including ponded, stagnant embayments from larger streams such as the Huron River. Another possible function of general body darkening may be protection from predation by such animals as fish that seek food in the still waters rich in dissolved organic matter and, therefore, considerably more deeply colored than the main body of the stream. The pigment within the tentacles may serve a similar function rendering them less conspicuous as they probe about from beneath the shell.

The significance of the comparatively large reproductive system of *L. fuscus* is as yet unknown. It is possible that the high concentrations of leeches, ostracods, and other harmful animals in *L. fuscus* habitats lead to an increased mortality of young and a consequent necessity for greater egg production in order to maintain population levels. The greater fluctuations in environmental factors such as temperature may also be significant in this regard. Such ideas as these are purely conjectural; it remains to be determined whether individuals of *L. fuscus* actually produce more eggs than lotic forms such as *F. tarda*. The need for detailed ecological study of these species is evident.

Functionally, the relative hypertrophy of the prostate in *Laevapex fuscus* may be related in some way to the absence of a flagellum in this species, but this view, again, must be tested by suitable physiological studies.

SUMMARY

1. This study deals mainly with the anatomy of *Laevapex fuscus* (C. B. Adams), 1841, an ancylid snail. Most of the specimens dissected were collected in the vicinity of Ann Arbor, Washtenaw County, Michigan.

2. Animals used for dissection or sectioning were anesthetized with menthol or Nembutal, fixed in Bouin's fluid or FAA, and preserved in 70 per cent ethyl alcohol.

3. Aquaria containing pond water and kept loosely covered without additional air were best for the maintenance of *L. fuscus*.

4. The dimensions of shells of *L. fuscus* from Ann Arbor are typical of specimens from many areas of eastern United States.

5. The distribution of pigment inside the tentacles and over the dorsum of the mantle contrasts distinctly with the pigment pattern of other ancylids and may be a character of taxonomic significance.

6. The integument, shell muscles, digestive system, nervous system, and circulatory systems are in general similar to those of other eastern American ancylid species. The salivary glands are fused posteriorly.

7. The pseudobranch is different from all other ancylids that have been studied. A small upper lobe bears the rectum and anus and may be homologous with the entire auriform lobe of other species. The lower lobe is very much larger, and is composed of a single pleated triangular flap of tissue surrounded by a hollow tubular margin which acts as a blood sinus. The homologies of the lower lobe are uncertain. A reduced pulmonary cavity is also present.

8. The reproductive system is very distinctive. An extremely large seminal vesicle is found midway along the hermaphroditic duct. The albumen gland and nidamental gland of the female system and the prostate gland of the male system present characteristic structural differences from other forms. The structure of the ultra-penis and the complete absence of a flagellum distinguish the male copulatory structures of *Laevapex fuscus* very clearly from those of other ancylid snails.

9. The differences noted above are considered to be sufficient to separate the genera *Laevapex* and *Ferrissia,* previously considered to be closely related subgenera.

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