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VIII

ANATOMY OF LANX, A LIMPET-LIKE LYMNÆID MOLLUSK

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In a recent paper, Dr. Henry A. Pilsbry[1] pointed out that the genus Lanx differed from the Ancylidæ in the position of the apex of the shell, in the absence of a distinct pseudobranch, and in the Lymnæid form of the jaw and dentition. For these reasons, he decided that the Lancidæ should be separated as a family, with Lymnæid rather than Ancylid affinities.

About the same time, Dr. G. Dallas Hanna, Curator of Paleontology, California Academy of Sciences, wrote me that he had specimens of Lanx with the animal, originally preserved in formalin, and very generously put them at my disposal. One lot, from which the dissections were made, consisted of seven specimens of *Lanx alta* (Tryon) from Klamath River (on rocks in swift water), Klamathton, California, collected by G. A. Coleman (Nov. 13, 1924). Although considerably retracted and stiffened by the formalin, they made very satisfactory material for dissection. The other set consisted of smaller and somewhat lower specimens (slightly approaching *Lanx subrotundata)* from Rogue River, 6 miles south of Grants Pass, Oregon, collected by G. D. Hanna (Nov. 15,

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[1] 1925, Naut. XXXVIII, 73-75.

1924); it was used in the preparation of a second series of transverse sections. The identifications were made by Dr. Pilsbry, whose many helpful criticisms were of greatest assistance. The dissections were worked out and figured at the Zoölogical Laboratory of the University of Pennsylvania.

Especial acknowledgment is due Dr. Eleanor Carothers, of the same laboratory, for the preparation of two very valuable series of transverse sections. As those cut from a Rogue River specimen show less maceration than the series from typical *Lanx alta,* the former are used for some of the histological figures, but only in cases where the essential structure is the same in both forms. The series are stained with alum-cochineal and counter-stained with orange G.

In order to facilitate comparison of the figures made from different animals, the measurements in millimeters are given below for the shells of the individuals studied.

		Length	Width	Height	
Klamath River;	No. 1	15.9	77 (12.3)	50 (8.1)	Figs. 2-4, 16
	No. 2	14.5	75 (10.9)	50 (7.2)	Figs. 5, 6, 14, 15
	No. 3	13.0	76 (9.9)	48 (6.2)	Figs. 7-13, 17-19, 21
	No. 4	12.9	72 (9.3)	45 (5.8)	Figs. 23, 24
	No. 5	12.8	79 (10.1)	52 (6.6)	Fig. 1
	No. 6	12.2	79 (9.6)	54 (6.6)	
	No. 7	11.1	83 (9.2)	54 (6.1)	
Rogue River;	No. 8	9.3	82 (7.6)	43 (4.0)	Figs. 20, 22, 27

Eleven specimens, from some of which the animals were taken for dissection, are in the collection of type material of the California Academy of Sciences where they bear Nos. 1783-1794. Others from the same lots have been deposited in the Academy of Natural Sciences of Philadelphia.

Like the shell, the body is broadly conical, with the apex distinctly in front of the center and slightly to the left (fig. 2). The dorsal side of the cephalic end shows transverse wrinkles between and around the bases of the broadly triangular tentacles, just in front of which are the rather prominent eyes. The male sex-opening is an inconspicuous orifice at the bottom of a conical depression, just behind the posterior end of the right tentacle (fig. 1). The roughly crescentic ventral surface of the head is covered with coarse bosses; the

T-shaped mouth is on a prominence a short distance in front of the groove which borders the foot.

The foot is large and has a very thick, muscular sole, well adapted for attachment to rocks in swift water. Its sides are somewhat wrinkled, due to the retraction, but are otherwise quite smooth and lightly pigmented. Its epidermis is a simple columnar epithelium, while its interior contains a rather loose network of interlacing muscle-fibers. Just above the sole (F, fig. 11), the interspaces are filled with masses of mucous cells, but above this denser zone is a much broader one with numerous sinuses (S, fig. 11). The female sex-opening appears as a prominent longitudinal slit with thick lips, in the upper portion of the right side of the foot, about ⅓ the body-length from the anterior end of the animal (fig. 1).

When the shell is removed (fig. 2), the cut ends of the columellar muscle-fibers appear as a white band which completely surrounds the visceral dome, except for a small gap (sometimes closed dorsally) just above the lung. Immediately behind this gap, a stout column of muscle (M, fig. 3) is separated from the remainder of the ring ventrally, but partially fuses near the shell. All of the muscle-strands descend ventrad from the shell (or scar) as a dense mass (M, fig. 11), to spread out widely between the sinuses of the foot. This is a very different arrangement from the three columns of muscle in *Hebetancylus moricandi* (von Ihering; 1891, Bull. Sci. France-Belg. XXIII, fig. iv-8).

The visceral dome inside of this columellar ring is covered by a very thin, darkly-pigmented, but slightly translucent membrane, which practically consists of a single layer of flattened cells; this is fused to the inside of the ring a short distance below the attachment of the latter to the shell. Outside of the muscle-scar, the mantle forms a broad, continuous, jet-black band, covered with concentric wrinkles (figs. 8-10), and margined with white at its free border. This band is slightly narrower on the left side (appears much more so in fig. 2, due to the steeper slope of the left side) and is slightly notched at the center of its anterior end. The epidermis of this black band consists of simple columnar epithelium which is full of very opaque pigment. The outer, white band develops higher, but

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non-pigmented cells (figs. 8-10) ; below these, numerous neurocytes suggest that this zone has a sensory function.

The thick, muscular, free mantle juts out some distance all around the foot. Under its edge is a thickened fold (fig. 1), which forms the special organ for aëration; this is heaviest just behind the gap in the muscle-ring and decreases in prominence in both directions until it is practically obsolete at the anterior mantle-notch. The large sinuses in this fold (S, figs. 8-10) are drained by two mantle veins which join, opposite the muscle-gap, to form the principal pulmonary vessel or vena cava. The common opening of the lung and hind-gut is a little to the right of the posterior end in the very edge of the mantle (A, figs. 1-3). The lower side of the free mantle is covered by a simple columnar epithelium similar to that of the foot. Although clumps of nerve cells are quite frequent in this vicinity, I am unable to distinguish a definite "osphradium" in any of my preparations, unless the plications of the cavity behind the confluence of the lung and hind-gut (A, fig. 8) represent such a structure.

The lung is clearly vestigial and must play practically no role in respiration. It is roughly comma-shaped (broken lines, fig. 2), with the point of the comma at the confluence with the hind-gut and the elongate dot across the front of the visceral dome (Z, fig. 11), mainly behind the pericardium. Its lining consists of a single layer of very flat cells (fig. 7) and does not appear to be associated with any special blood-spaces. The enormous pericardium (fig. 6) lies between the lung and the anterior region of the muscle-ring (H, fig. 2). The renopericardial orifice (X, fig. 6) is opposite the middle of the ventricle of the heart. The elongate kidney lies (K, fig. 2) above the lung parallel to the pericardium. The lumen of the main portion is rendered complexly sacculate (fig. 6) by cords and trabeculæ (K, fig. 11) of the same rather low, columnar cells that form its lining; these partitions disappear as the kidney passes gradually into the ureter (U, fig. 9), which is also surrounded by similar epithelium. These renal epithelia (fig. 7) are characterized by the peculiar position of the nuclei near the luminal ends of the cells and by the rather large vacuoles nearer their outer ends; the tissue appears to have a marked affinity for the orange G but practically none for the red stain. Inside of the mantle, the ureter (U) is about half as large as and lies laterad to the lung (Z, fig. 10), into which it opens (fig. 9) about 2 mm. above the confluence of the latter with the hind-gut (fig. 8).

From the above, it will be seen that the pallial complex of Lanx is Lymnæid in its general plan, and has nothing in common with that of the Ancylidæ; even the gill-like fold is of quite different character from the pseudobranch of the latter family. In comparison with *Lymnæa stagnalis*[2] and *Lymnæa reflexa*[3], the reduction in size of the lung is not out of proportion to that of the entire visceral mass. However, the lack of venation and the confluence with the hind-gut appear to indicate that the lung of Lanx plays a relatively unimportant part in the aëration of the blood. In addition, the entire visceral dome and the pallial cavity appear to be twisted posteriad and to the right, as if the spire had more than uncoiled; the position of the shell-apex slightly to the left and in front of the center also seems to indicate a slight degree of hyperstrophy. As will be described below, this torsion is accompanied by a peculiar dislocation of the visceral and abdominal ganglia (fig. 16).

Attention is also called to the fact that, in many features, the arrangement of the pallial complex shows a remarkable parallelism with that of the Veronicellidæ[4], in which group the "lung" appears to have degenerated even more completely into a sort of secondary ureter. *Protancylus pileolus* Sarasin[5] also has a common opening for the lung and hind-gut, but this is near the middle of the left side of the body; this last species develops a left pseudobranch, quite like that of the Planorbidæ and Ancylidæ, in addition to blood-sinuses in the right mantle[6].

The thick-walled ventricle (fig. 6, 11) is very large, and heart-shaped, with the point (aorta) towards the left side and the emarginate border towards the right. The auricle is much more slender and has very thin walls. The preservation of the

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[2] Pilsbry; 1900, Proc. Acad. Nat. Sci. Philadelphia, LII, fig. xvii-2.
[3] F. C. Baker; 1911, Chicago Acad. Sci., Sp. Publ. 3, pl. I.
[4] Sarasin; 1899, Land-Moll. Celebes, figs. xiv, 124-127 and Pelseneer, 1901, Mem. ac. r. Belg. LIV, 21-26, figs. vi-49, 52-55.
[5] 1898; Süssw.-Moll. Celebes, 86-88, pl. xiii.
[6] op. cit., figs. 170, 177.

specimens impedes a detailed study of the arterial system, but the main aorta does curve ventrad, pass under the bursal sac and bifurcate to form a cephalic aorta which goes first to the gizzard, and a visceral (intestinal) aorta with large branches to the genitalia and visceral mass. The pulmonary vein (vena cava), which passes through the muscle gap, is formed by the confluence of the two mantle veins and vessels from the sinuses of the foot. The large "right" mantle vein drains the sinuses of the posterior and sinistral portions of the gill-fold, while the smaller "left" one comes from the limb along the anterior portion of the right mantle edge.

This circulatory system appears quite like that of *Lymnæa emarginata mighelsi*[7], but the pulmonary network is practically lacking and the mantle veins are correspondingly enlarged. The enormous relative size of the heart in *Lanx alta* must insure a rapid circulation of the blood, which would compensate in part for the reduction in area of the aërating membranes and the apparent dependence on dissolved oxygen. However, it is just possible that the animal can breathe air, as I found bubbles in the lung of one preserved specimen. The pallial complex and mantle fold of the Rogue River form are very similar to those of typical *Lanx alta,* but the lung and ureter occupy a relatively larger portion of the free mantle while the aërating sinuses are correspondingly smaller.

As already mentioned, the closed mouth (fig. 1) of Lanx is T-shaped and opens on the ventral side. The cross-bar of the T is reinforced dorsally by the principal jaw, while the lateral sides of the longitudinal slit are strengthened by the two, so-called accessory jaws. The last (fig. 24) are simply vaguely-outlined thickenings of a general, "horny" stratum that covers the margins of the mouth and is continuous with that of the true jaw. This median jaw (fig. 24) is broadly crescentic with the cutting margin slightly emarginate, either side of the middle, so as to form a slight median projection. Its upper side is finely striate at right angles to the cutting margin, while its inner side is strengthened by a crescentic thickening which runs parallel to the imbedded edge.

[7] F. C. Baker; 1900, Bull. Chicago Acad. Sci. II, pl. vi.

The radular formula of *Lanx alta* is about 16-6-1-6-16; the transverse rows are almost straight in the central and lateral fields, but are directed obliquely anteriad in the marginal region. The small central (fig. 23) is asymmetrical and bicuspid, with a stout, aculeate, major cusp and a left minor one. The large 1st lateral has a small base and a large, squarish, very thin, bicuspid reflection; the major cusp (mesocone) has a low entoconal angulation and a higher one on the ectoconal side. The ectocone itself is small, acuminate, and sometimes slightly hooked. The other lateral teeth are slightly smaller and the entoconal wing becomes higher until the 7th tooth is distinctly tricuspid. The marginal teeth have very small bases and elongate reflections; usually the 9th develops another entoconal notch which on the 10th separates a distinct cusp. The remainder of the teeth are practically all 4-cusped, although one or two of the minute outermost ones commonly develop more points.

Through the generosity of Dr. Pilsbry, I have been able to examine radulæ mounted by him from *Lanx subrotundata* (Tryon), *L. patelloides* (Lea), and *L. (Walkerola) klamathensis* Hannibal. A radula of *L. subrotundata* from Elkton, Oregon (A.N.S.P. 78630) has very similar inner teeth to those of *L. alta,* but all of the marginals could not be counted in the specimen examined. The radular formula of specimens of *L. patelloides* from Redding, California (A.N.S.P. 72741), is about 12-6-1-6-12. The teeth in the three radulæ examined are all very similar to those of *L. alta* and have the same asymmetrical, bicuspid centrals; while the occasional presence of another minor cusp on the latter[8] would not be extraordinary, I doubt whether the central is ever symmetrical. The radular formula of *L. (Walkerola) klamathensis* from Upper Klamath Lake, California (A.N.S.P. 113843), is about 15-6-1-6-15. The teeth are very similar to those of *L. alta,* but the minor cusp of the central is slightly reduced and the bases of the laterals are a little larger in proportion to the reflection. Walker's figure (1918, fig. 53) clearly shows these characters, but the smaller number of teeth (12-5-1-5-12) suggests that his radula is from a younger or smaller animal.

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[8] Walker; 1918, Univ. Mich. Mus. Zool., Misc. Coll. 6, fig. 51.

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A radula of *Lanx (Fisherola) lancides* (Hannibal) from a dried specimen (A.N.S.P. 113838), collected in the Snake River at Lewiston, Idaho, by H. Hemphill (1911) shows a quite different dentition. The radular formula is 28-8-1-8-28 and the rows are shaped somewhat as in *L. alta.* The minor cusp of the asymmetrical, bicuspid central (fig. 25) is almost obsolete. The laterals have much smaller reflections and the mesocone and ectocone are connected by a thin shelf which commonly develops two weak and extremely variable cusplets. This shelf decreases in prominence on the outer laterals, while the entoconal wing becomes higher, until the 9th tooth has only one vestigial cusplet between the ectocone and mesocone but shows a distinct entocone. Beyond the 9th, each marginal has a rather short reflection which bears three cusps: a sub-spatulate mesocone, a small, sharp entocone, and a larger, pointed ectocone. One or two of the minute outermost teeth often develop additional cusplets, but the tricuspid condition is maintained with remarkable uniformity through most of the marginal series. The median jaw (fig. 26) of this species is much thinner and more elongate than that of *L. alta;* the lateral thickenings show signs of their derivation from a plaited condition.

Superficially, the buccal mass of *Lanx alta* (fig. 4) is a large, ovoid body, from which the short, blunt radular pouch projects, slightly below the center of the posterior end. Several minor protractor muscles are present, but long retractors appear to be lacking. The two, small, light-colored, amorphous, salivary glands (S) are above the œsophagus but extend anteriad around both sides of the buccal mass; their ducts enter the substance of the mass and empty into the dorsum of the pharynx, either side of the gullet. Histologically, they consist of small alveoli composed of vacuolate cells, which are remarkably similar in appearance to those of the mucous glands of the foot.

The flattened ventral portion (B. fig. 22) of the buccal cavity is roofed by the radular membrane (R), which curves around the anterior end of the radular cartilage. The last is a large, bilobed structure (C) with large spaces between the anastamosing trabeculæ of harder substance (fig. 27). Ventrad and anteriad (R, fig. 22), it presents a smooth, even curve, over which the radula is slightly convex, while dorsad, it develops a U-shaped grove (U), into which the radula is concavely folded. This groove is continuous with the almost cylindrical radular pouch, which lies between the two, bluntly-rounded, posterior horns of the cartilage. The pharynx (P) is not separable from the buccal cavity; both are lined by simple columnar epithelium which is somewhat lower than that of the epidermis. Under the radular membranes, this epithelium becomes still lower, so that it consists of a layer of practically cuboid cells.

The oesophagus opens out of the dorsal side of the pharyngeal portion of the buccal cavity just opposite the anterior end of the radular cartilage; at first, it is enclosed in the walls of the buccal mass above the radular pouch (G, fig. 22), but appears superficially (G, fig. 11) on the posterior end of the mass. From here, it extends to the gizzard, which lies a little behind and to the left of the center of the animal. No sharply demarcated crop is present, but the posterior end of the gullet is externally thrown up into longitudinal ridges and would appear to be adapted for considerable distension. The rather thin walls of the oesophagus are mainly composed of a layer of very high, darkly-staining, columnar cells, which internally form coarse, longitudinal folds that increase in prominence towards the gizzard.

The entire stomach is obliquely tilted dorsad, with the elongate, cone-shaped, thin-walled pylorus above and twisted first to the right and then abruptly to the left. The gizzard is bilobed as in Lymnæa[9], has extremely thick, muscular walls, and contains rounded bits of sand, diatom shells, pieces of tubular algae and much unidentifiable material. The upper end of the pylorus receives two large ducts (L, figs. 4, 5) from the anterior and posterior lobes of the liver. Its very tip, beyond these ducts, is slightly separated by a weak constriction and bears ventrally (posteriad) a small, ovoid diverticulum. (In another specimen, this is considerably longer than in D, fig. 5). This pouch is lined by high, columnar epithelium, very similar to that of the pylorus and gizzard.

[9] F. C. Baker; 1900, figs. iv, C-E.

From the stomach, the intestine (fig. 3) runs almost to the left side (where it appears on the dorsal surface of the visceral mass), then bends across the anterior border of the liver (just under the edge), loops through the posterior portion of this digestive gland to return to the anterior border at the right side, where it turns abruptly downward, and passes posteriad along the left side of the lung to the posterior opening of the common cavity (A, figs. 8, 9, 10). Like all of the digestive tract, the intestine is lined by simple columnar epithelium; this is slightly lower in the first limb than in the fourth, but is lowest in the fifth limb or hind-gut, which, however, has clumps of higher cells that form the plicæ. Besides the slender columnar cells with dense, darkly-staining cytoplasm, there occur larger, rounded goblet-cells with large vacuoles; in the hind-gut (fig. 12), these are mainly restricted to the higher folds. As already mentioned, the lung (Z, fig. 10) joins the hind-gut (A) a short distance above the common opening; in this region, the cavity is enlarged, very coarsely plicate, and lined by higher, columnar epithelium somewhat similar to that of the epidermis.

The bilobed liver or pancreas forms an alveolate, lenticular mass which almost covers the posterior ¾ of the visceral mass. The small anterior (L, fig. 3; morphologically right?) lobe lies above the gizzard and between the first two limbs of the intestine, while the much larger posterior (morphologically left?) portion lies between the first, third and fourth limbs, extends slightly outside of the last and invades the base of the free mantle (L, fig. 10) through the muscle-gap; this invasion is greater in a Rogue River specimen and may be due in part to the retraction of the animals studied. The large hepatic alveoli are mainly composed (fig. 13) of very large columnar cells (liver cells) with large vacuoles, around the small, subbasal nuclei, and more opaque globules in the cytoplasm near the lumen of the gland. These principal cells are interspersed with clumps of lower, more rounded cells (lime-cells) with much larger nuclei and denser cytoplasm. These two types stand out very distinctly in the stained sections as the liver cells are colored yellow, while the lime cells are bright red.

The genitalia (fig. 14) are bulkier than all of the remainder of the viscera taken together. The ovotestis is larger (T, fig. 3) than the liver, but is mainly imbedded beneath the latter. It is also irregularly lens-shaped with an emarginate anterior margin, is light yellow in color, and consists of complexly intertwined series of cords with closely-packed alveoli, like excessively attenuate bunches of raisins[10]. These all lead into an ovoid sac a little back of the center of the mass. All of the individuals examined, regardless of their size (see above), appear to be sexually mature; the spermatozoa are much more conspicuous than the ova (note dates of collection).

The anterior portion of the ovisperm duct, just behind the ovoid sac, is slender and naked, but the major portion is covered by a dense mass of large, very thin-walled alveoli, which are closely packed into the right side of posterior end of the ovotestis and actually appear on the dorsal surface of the visceral mass between the third and fourth limbs of the intestine (D, fig. 3). The cavities of these sacs are crowded full of spermatozoa and must act as seminal vesicles or reservoirs. In the ovotestis, the sperm are grouped with their heads together in disc-shaped masses, each of which lies against a large cell somewhat similar to the Sertoli cells of vertebrates, but, in the reservoirs, they are quite irregularly massed, although they still tend to lie parallel to each other. The ovisperm duct itself bifurcates on the surface of the carrefour; one twig goes to the seminal duct while the other develops a small spherical body (talon?) and enters the carrefour itself.

The oviduct may be divided into four regions: (1) the carrefour[11]; (2) the prebulbar oviduct; (3) the bulbous enlargement; and (4) the postbulbar or vaginal portion; in addition, it develops two glandular diverticula: (1) the albumen gland; and (2) the oviducal diverticulum or "nidamental gland." The carrefour or spermoviduct (uterus of authors) receives the ovisperm duct and that of the albumen gland; it is a narrow, transversely sacculate and complexly plicate tube which lies between the head of the false prostate and the base of the albumen gland. Its walls are almost entirely composed of a simple epithelium which varies in height from the very slender,

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[10] Cf. F. C. Baker; 1900, fig. iii-F.
[11] Lacaze-Duthiers; 1899, Arch. Zool. Exp. (3) VII, 110.

columnar cells of the plicæ, to the almost cuboid ones of the intermediate regions. The albumen gland is gray in color, semicircular and considerably flattened; it lies under the ovotestis towards the left (right in a Rogue River specimen) side of the floor of the hæmocœle. The sections show it to be divided into numerous alveoli which are lined by a single layer of rather low, columnar cells that stain a bright red and are superficially similar in appearance to those of the oviducal bulb but contain much larger vacuoles and larger nuclei (fig. 21).

The oviducal diverticulum or "nidamental" gland (second accessory albuminiparous gland of F. C. Baker, 1911) is an ovoid body which opens at the junction of the carrefour and prebulbar oviduct. Both in gross and histological structure, this body looks like a small edition of the oviducal bulb; its lumen is similarly reduced by numerous laminæ, which are composed of two layers of columnar cells that are stained a brilliant red in the serial sections.

The prebulbar portion of the oviduct is a rather stout tube, with a few, coarse, internal plicæ. The simple columnar epithelium which composes the main portion of its wall (fig. 20) consists of remarkably large cells with small, basal or central nuclei and numerous, clear vacuoles, which, under low magnification, give this tissue the very distinctive appearance of delicate lace-work. Outside of these gland-cells is a very thin layer of squamous cells with scattered muscle-fibers.

The oviducal bulb or uterus is a pear-shaped enlargement which is sharply demarcated from the preceding tube but tapers rather gradually into the postbulbar portion. While somewhat flattened, it does not show as prominent a longitudinal groove as does the "first accessory albuminiparous gland"[12] in most species of Lymnæa. In *Lanx alta,* this groove is actually a thin region of the wall (fig. 14-A); if the bulb is split lengthwise along this line, the closely-packed, laminate plications of the remainder of the wall can be spread out like the leaves of a book and are seen to be oblique to the long axis of the organ. These plicæ consist of a double layer of the simple columnar epithelium which lines the bulb; the dense

[12] F. C. Baker; 1911, pl. x-xv.

cytoplasm of its large cells are stained a brilliant red in the serial sections. This tissue must be very similar to that which composes the folds of the "third division of the oviduct or uterus"[13] in *Lymnæa ovata.* Outside of the epithelium, the walls develop a very thin layer of fibrous tissue and squamous cells.

The postbulbar or vaginal portion of the oviduct is similar in diameter to the prebulbar tube, although it is slightly enlarged just above its confluence with the bursal stalk. Its thick walls are largely composed of circular muscle, although varying amounts of longitudinal fibers are usually gathered into two groups on opposite sides of the tube. The deeply plicate lumen (fig. 14-B) is lined by a comparatively thin, rather featureless, simple columnar epithelium.

The stalk of the bursa (spermatheca) is rather slender, although very slightly enlarged near its base, and lies along the dorsal side of the bulbar and postbulbar portions of the oviduct. Its terminal sac, which is imbedded (B, figs. 3, 11) near the left side of the hæmocœle, is roughly heart-shaped and very large. In addition to the thin outer layer of fibrous cells, both stalk and sac have a lining of very peculiar, simple columnar epithelium, which is thrown up into weak plications (B, fig. 11). The cells of this tissue (fig. 18) are very slender; their cytoplasm is dense and stains rather darkly, but the large, subcentral nuclei are markedly vacuolate, so as to give to a tangential section somewhat the appearance of the cartilage of vertebrates. The luminal ends of these cells are produced into anastamosing, ameboid masses from which separate roughly globular pieces of what appears to be the cytoplasm of the cell itself. The spacious lumen of the bursal sac contains many of these corpuscular structures[14] in a mass of granular material; this leads me to suspect that the bursa is actually a gland which secretes some sort of thick, viscous material as an aid in copulation. The vagina proper, beyond the confluence of the bursal stalk and the oviduct, is very short, almost obsolete, but the peculiar form and heavy walls of the postbulbar oviduct give it much the appearance of the vagina of some of the terrestrial pulmonates.

[13] J. Klotz; 1889, Jena. Zeitschr. Nat. XXIII, figs. ii-11, 17.
[14] Cf. Lacaze-Duthiers; 1899, fig. iv-9.

The very long and tortuous seminal duct can be divided into six rather distinct regions: (1) the first or false prostate; (2) the very short duct between the first and second prostates; (3) the second or true prostate; and (4, 5, 6) the first free, the imbedded, and the second free portions of the extremely long vas deferens. Ventral to the carrefour, the first prostate begins as a flattened, plicate, fan-shaped, blind sac; the portion below the entrance of the ovisperm duct forms an elongate, flattened, irregularly-lobed body which is folded into a compact mass near the left side of the body below the oviduct. (In a Rogue River specimen, it is on the right side and the blind end extends through the muscle-gap into the base of the mantle.) Its flattened lumen (fig. 14-C) is much more spacious and its walls correspondingly thinner than those of the true prostate. The columnar cells (fig. 19) which line the cavity have small nuclei surrounded by large vacuoles which restrict the cytoplasm to very thin trabeculæ; often the luminal ends of several cells support a large bubble of transparent secretion. Unlike the vacuolate cells of the albumen gland (fig. 21), these on the male side are but slightly stained in the serial sections. Like most parts of the reproductive system, the outside of the organ is covered with a very thin layer of pigmented cells; these give the surface of this glandular sac an areolate appearance.

The second or true prostate is roughly tongue-shaped and lies (P, fig. 3) just anterior to the oviducal bulb. It consists of an enlargement of the seminal duct, lined by ciliated, cuboid epithelium, and surrounded by closely-packed, radiating, tubular glands (fig. 14-D). Each of these secretory pouches is made up of large rounded cells with their long axes parallel to that of its very small central lumen, so that a transverse section of a tubule shows five or six at one time. The nucleus of each cell (fig. 17) is on the side opposite the lumen of its pouch and the cytoplasm is crowded with rather large, quite dense globules. The structure of this prostate must be quite similar to that of *Lymnæa ovata*, although the published figures[15] do not show the lumina of the tubules or the cell boundaries.

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[15] Klotz; 1899, figs. ii-12.

Below the prostate, the first free portion of the vas deferens is rather stout and quite long; it is coiled near the right side of the hæmocœle, mainly anteriad to the oviduct and bursal stalk. The imbedded section is somewhat narrower and scarcely convoluted; it passes out through the muscle-gap and runs along the outside of the columellar muscle-ring (I, fig. 11) from the base of the oviduct to that of the penis. The second free portion extends in a tortuous course through the hæmocœle (H. fig. 3) over to the left side of the body and back again to enter at the apex of the penis; although narrower than the first free portion, the greater part of its length is quite stout and thick-walled. The last few millimeters, which are mainly coiled around the penis and under the anterior pallial nerve, are considerably narrowed, so that their convoluted lumen is visible through the walls. The entire vas deferens is lined by a single layer of ciliated, cuboid epithelium. Outside of this is a thick envelope of circular muscle, usually with two groups of longitudinal fibers on opposite sides but rather close to the epithelial lining. I am unable to detect any gland cells outside of the epithelium; those figured from the vas deferens of *Lymnæa ovata*[16] look very much like cross-sections of longitudinal muscle but they are represented as much larger than the circular fibers in the same figure.

The entire male copulatory organ, termed here the penis, is very similar to that of *Lymnæa*[17]; that is, it consists of an elongate-ovoid, preputial portion (penis-sac) and a somewhat constricted *hyperphallus* (penis, F. C. Baker) with a faint terminal knob. The hyperphallus (fig. iii-15) or capsule of the verge is not sharply demarcated externally from the remainder of the penis and is about ¼ the total length of the organ. Its walls are rather thin and contain numerous sinuses which give them somewhat the appearance of erectile tissue. The hyperphallar lumen is almost completely filled by the elongate, pointe, penial papilla or verge (glans or penis of authors), which is probably the only portion that penetrates the vagina of the female. The vas deferens, with its convoluted lumen, enters the base of the verge; the continuation of the sperm canal, which extends to the very tip, is quite narrow and cir-

[16] Klotz; 1889, fig. ii-14.
[17] F. C. Baker; 1911, pl. x-xv.

cularly plicate. This arrangement appears quite similar to that in *Lymnæa ovata*[18]. The larger sac of the penis has rather thick, solid, muscular walls, which internally develop transverse plications and two large pilasters (fig. 14-E), that certainly resemble those of *Lymnæa auricularia*[19]. The penis is lined by high, columnar epithelium which extends up into the cavity of the hyperphallus.

The main body of the penis receives two branched muscles on its anterior side and three on its posterior. A slip (cut in fig. 14) from the upper of the anterior two, is attached to the apex of the hyperphallus so that, in my retracted specimens, this structure is bent back on the anterior side of the larger sac of the penis. The posterior muscles extend to the base of the thickened column of muscle behind the gap in the columellar ring.

This origin of the hyperphallar retractor from an anterior muscle appears to be quite different from the arrangement in *Lymnæa*[20], but it must be remembered that, in *Lanx alta,* all of these muscle bands arise from some part of the columellar muscle-ring. Otherwise, the genitalia are so similar to those of *Lymnæa* that they might almost pass for those of a species of that genus, although the enormous size of the ovotestis and the seminal reservoirs would appear to be rather distinctive.

On account of the stiffness of the organs, which prevent their safe manipulation without rupture, the study of the nervous system from my material is especially difficult. The general arrangement appears quite similar to that of *Lymnæa stagnalis* and *L. peregra*[21] and to that of *L. reflexa*[22], but the ganglionic ring is concentrated along the long axis of the body and stretched transversely to the right (fig. 16). This dextral distortion, which especially affects the visceral-abdominal complex, has already been correlated with the posterior position of the common pulmonary and anal opening.

The cerebral commissure is rather long. Each cerebral ganglion is roughly triangular, with enlargements (lobes) at each corner. The nerves from the left one are: acoustic,

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[18] Klotz; 1889, figs. ii-15, 16.
[19] Hugo Eisig; 1869, Zeitschr. Wiss. Zool. XIX, figs. xxv-8, 9.
[20] F. C. Baker; 1911, pl. x-xv.
[21] Lacaze-Duthiers; 1872, Arch. Zool. Exp. I, pl. xvii.
[22] F. C. Baker; 1911, pl. v.

optic (O, fig. 16), tentacular (T), superior frontolabial (L), middle labials (C), nuchal (N) and the subcerebral commissure (X; satellite of anterior labial artery). In addition, the right one gives off the penial and hyperphallar (H); these can be separated almost to their bases and appear to branch off just below a special, ridge-like enlargement of the ganglion. The cerebrobuccal connectives are rather long, but loop transversely so that the buccal ganglia are quite close to the cerebral (moved away in my figure). These buccal or stomatogastric ganglia are relatively large and give off at least the radular (R), deep pharyngeal, lateral pharyngeal and anterior pharyngeal branches; the last sends a twig (S) to the salivary glands along their ducts.

The cerebropleural connectives are very short so that the pleural ganglia are closely approximated to the cerebral. The left pleurovisceral connective is relatively long but the right visceral and pleural ganglia are in close juxtaposition. Each visceral ganglion gives off an anterior (M) and a posterior (P) pallial nerve; those of the right side are larger. The left visceral is closely united to the abdominal ganglion, although a distinct, stout connective is present between the latter and the right visceral. The abdominal ganglion gives off the subintestinal (G; genital), the aortic (A; anal), a root to the right anterior pallial, and one or two minute nerves to the body wall.

The cerebropedal and pleuropedal connectives are short and stout, but the pedal commissure is a little longer. The pedal ganglia are large and not greatly affected by the dextral distortion of the abdominal complex. Each gives off six sizable branches: superior (K) and inferior (I) cervicals, superior (D, anterior), central (E) and inferior (F, posterior) pedals and a columellar (U). The otocysts are near the anterior ends of the dorsal surfaces of the pedal ganglia.

The general shape and buried position of the eyes is quite similar to that in *Lymnæa stagnalis*[23], but a large sinus surrounds the outer half of each; it forms a rather large cavity between the thin corneal epithelium and the inconspicuous layer of connective tissue which underlies the thickened epidermis.

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[23] Simroth; 1876, Zeitschr. Wiss. Zool. XXVI, fig. xv-12.

This sinus is so large and the overlying epidermis and subdermis so opaque (in preserved specimens) that a small, rounded boss is the only superficial indication of the position of each eye. The lens is large and the pigmented layer very thick, especially at its inner end, but the outer fibrillar processes of the retinal cells are poorly developed except in a little cup directly behind the center of the lens. The optic nerve is quite widely separated from the tentacular one.

In the posterior portion of each tentacle, the transverse sections show the presence of a small, sensory pocket, with a groove which runs posteriad and ventrad from it. On the ventral side of this pocket is a mass of ganglionic tissue. The retracted condition of my specimens prevent the accurate description of the shape of this structure, as the deep folds of the tentacle obscure its position. Mucous glands, similar to those in the foot, are present in and around the base of the tentacles. My failure to find a definitely localized osphradium or organ of Lacaze-Duthiers has already been reported.

These anatomical data all substantiate Dr. Pilsbry's demonstration that Lanx is a derivative of the Lymnæidæ and is not closely related to the Ancylidæ. As Dr. Pilsbry has often pointed out, the terrestrial pulmonates appear to have a constantly recurrent tendency to produce slug-like forms. A similar propensity in the Basommatophora seems to lead towards ancyliform shells and bodies. In the Lancidæ, specialization of the other organs has not gone so far as in the Ancylid derivatives of the Planorbidæ; in fact, it is very remarkable that Lanx combines such profound changes of external form with such trifling divergencies in the internal anatomy, especially in that of the genital and digestive systems.

On the basis of much of the anatomy, Lanx could scarcely be separated from the Lymnæidæ, but its peculiar modification of the pallial complex appears to be sufficient grounds for the retention of the Lancidæ as a distinct family, with the following definitive characters:

1. The limpet-like shell and the reduction of the visceral mass, especially at the expense of the digestive glands.
2. The almost complete ring of columellar muscle.

3. The development of the mantle edge into a special organ for aeration, with the coincident enlargement of the heart and mantle veins.

4. The vestigial "lung" and its confluence with the hind-gut.

5. The distinctly posterior allocation of the common opening of the lung and hind-gut, which appears to be correlated with the distortion of the ganglionic ring in the same direction and with the hyperstrophic position of the apex of the shell.

6. The enormous size of the ovotestis and seminal reservoirs.

7. The asymmetrical, bicuspid central and the squarish reflections of the laterals in the radula.

Description of Figures

All drawings are made with the aid of the camera lucida. The histological figures represent somewhat idealized optical sections; the cells are oriented so that the lumen of the gland or organ is towards the top of the plate.

Plate 11

Scales represent lengths of five millimeters.

Fig. 1. Ventral view of retracted animal within outline of shell. Common opening of the lung and hind-gut (A) and positions of male and female sex openings indicated. Magnification the same as in fig. 2.

Fig. 2. Dorsal view of animal after removal of shell. Visceral dome, surrounded by columellar muscle-ring, represented as slightly more transparent than is actually the case. Broken lines give outlines of lung, ureter and end of hind-gut.

A....................common opening of lung and hind-gut.
H....................auricle of heart (dotted outline).
K....................kidney (dotted outline).
U....................opening of ureter into lung.

Fig. 3. Dorsal view of visceral mass inside of columellar muscle-ring (cut at anterior end), after removal of roofing membrane, pallial complex and most of free mantle. Lines of demarcation between anterior and posterior lobes of liver and between latter and ovotestis are accentuated. Broken lines show course of hind-gut through free mantle. Scale is upper one of the two.

A....................common opening of lung and hind-gut.
B....................bursal sac.
D....................seminal reservoirs of ovisperm duct.
H....................second free portion of vas deferens.
L....................anterior (smaller) lobe of liver.
M....................heaviest column of muscle-ring.
O....................oviducal bulb.
P....................second or true prostate.
T....................ovotestis (lighter than liver).

Fig. 4. Anterior portion of digestive system, removed and straightened out. Buccal mass, salivary glands (S), oesophagus, gizzard (bilobed), pylorus with ends of two hepatic ducts (L), and beginning of intestine. Magnification practically the same as in fig. 3.

Fig. 5. Left side of junction between pylorus (at left) and intestine (at right). Magnification about that of fig. 6.

D....................pyloric diverticulum.
L....................cut end of left hepatic duct.

Fig. 6. Kidney and pericardium, dissected loose and turned back sharply to right, so as to be viewed from ventral side. Ureter still remains in normal position, as viewed dorsally. Scale is placed under that of fig. 3.

X....................position of renopericardial orifice.

Fig. 7. Optical section across partition between ureter (above) and lung (below) to show columnar epithelium of former and squamous lining of latter. This is an enlargement of a small portion of fig. 10. Magnification as in fig. 12.

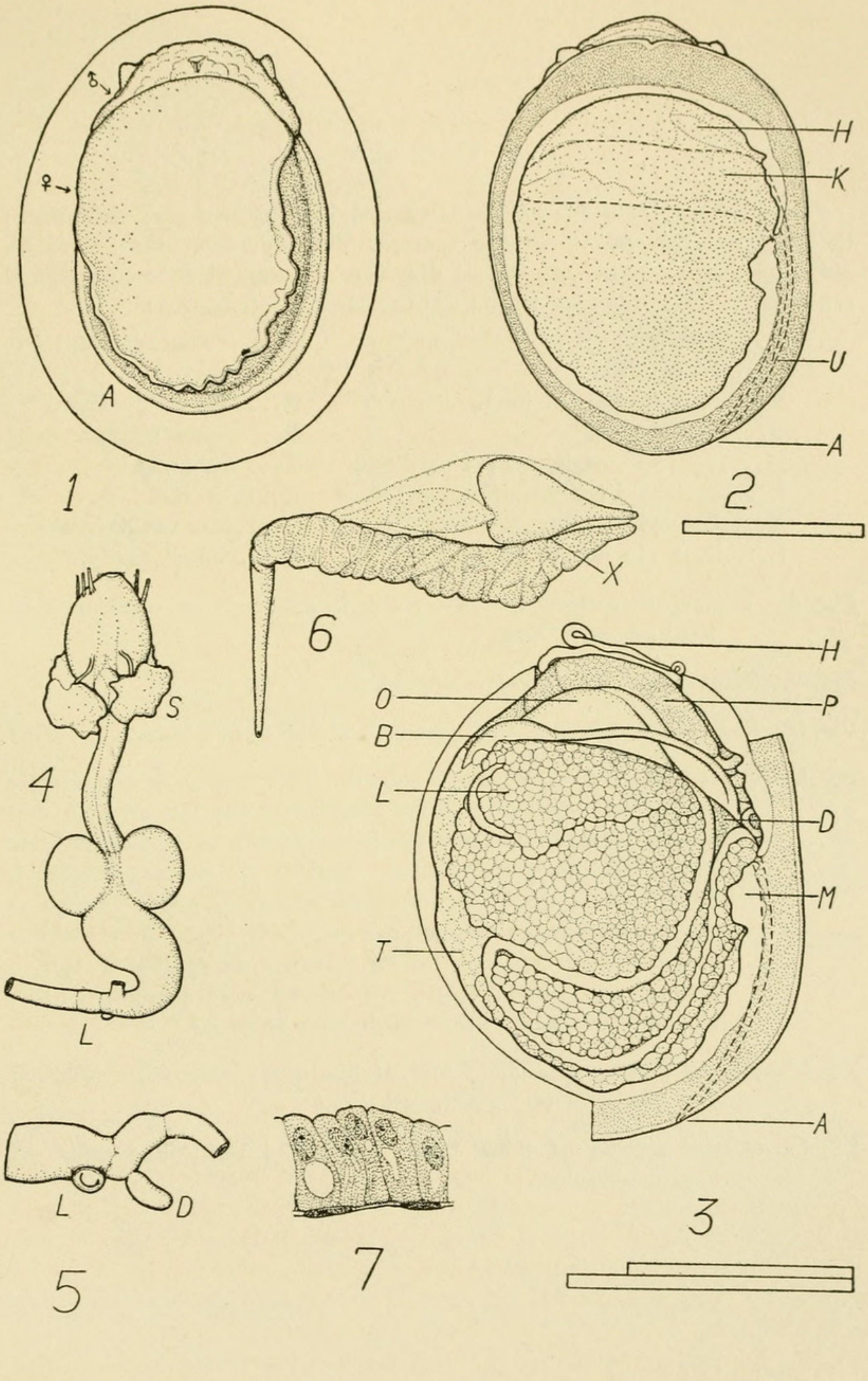

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PLATE 12

Scales of figs. 8 to 10 (under last) and 11 represent one millimeter; those of figs. 12 and 13 (under former) fifty microns. Figs. 8 to 11, although diagrammatic, are actual drawings of stained sections (animal retracted). The following letters are the same in all figures:

A....hind gut.	M....columellar muscle.
B....bursal sac.	O....oviduct.
F....foot (dense portion).	P....second prostate.
G....oesophagus.	S....blood sinuses.
H....ventricle of heart, pericardium.	T....ovotestis.
I.....imbedded portion of vas deferens.	U....Ureter.
K....kidney.	V....free vas deferens.
L....liver (in muscle gap).	Z...."lung" cavity.

Fig. 8. Transverse section through right free mantle at confluence of hind-gut and "lung."

Fig. 9. Same at external ureteric opening.

Fig. 10. Same at muscle gap, near junction of ureter and kidney.

Fig. 11. Cross-section through entire animal. This section is not exactly transverse, but passes more anteriad at the left side, so that it cuts ventricle of heart (in pericardium) as well as anterior region of kidney and "lung." Besides the structures labeled, three more loops of free portions of vas deferens, as well as all four regions of oviduct, are included. Also, tip of radular pouch and of left horn of its cartilage appear below and to left of oesophagus (G). All organs have shrunk slightly, so hæmocœle appears extraordinarily spacious.

Fig. 12. Optical section through a fold of hind-gut; intestinal epithelium (above) with two goblet-cells.

Fig. 13. Optical section of three "liver cells" and two "lime cells" of hepatic alveolus.

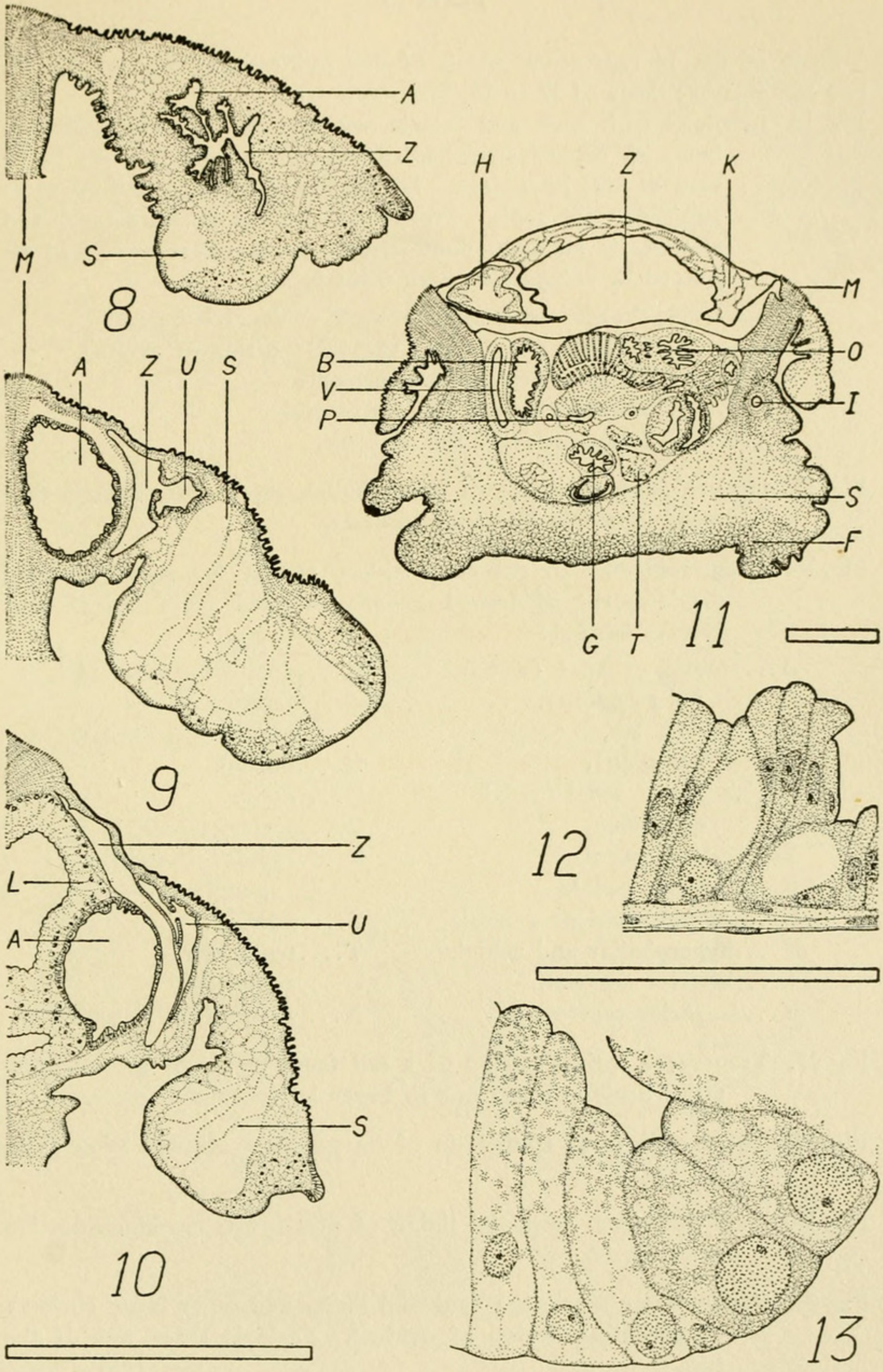
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PLATE 13

Scale of fig. 14 represents length of five millimeters; that of fig. 16, two millimeters; those of 17 to 20, fifty microns.

Fig. 14. Genitalia with male and female sex openings in usual relations, but with organs straightened out and arranged so as to be seen at best advantage. Hyperphallar retractor cut so as to straighten out penis. Transverse sections cut with razor and viewed by surface illumination. Scale of sections can be judged by comparison with main figure.

A..........Transverse section through oviducal bulb.
B..........Through postbulbar (vaginal) portion of oviduct.
C..........Through first or false prostate.
D..........Through second or true prostate.
E..........Through larger sac of penis.

Fig. 15. Optical, sagittal section of hyperphallus, made from slightly flattened mount in Farrant's medium.

Fig. 16. Ganglionic ring in natural position, except for slight anteriad displacement of buccal ganglia; viewed from dorsal side. Nerves labeled:

A....aortic or anal (abdominal ganglion).
C....middle labial (cerebral ganglion).
D....superior pedal (pedal ganglion).
E....central pedal.
F....inferior pedal.
G....subintestinal or genital.
H....hyperphallar and penial.
I.....inferior cervical.
K....superior cervical.
L.....anterior frontolabial.
M....anterior pallial (visceral gang.).
N....nuchal.
O....optic.
P....posterior pallial.
R....radular (buccal ganglion).
S....salivary.
T....tentacular.
U....columellar.
X....subcerebral commissure.

Fig. 17. Transverse optical section of a cell from tubule of second prostate. Scale is upper one in lower left corner of plate.

Fig. 18. Three cells from epithelium of bursal sac. Magnification as in fig. 12.

Fig. 19. Two cells from epithelial lining of first prostate. Magnification as in fig. 12.

Fig. 20. Rogue River specimen; epithelial lining and outer layer (below) of prebulbar region of oviduct. Scale is lower one of the two.

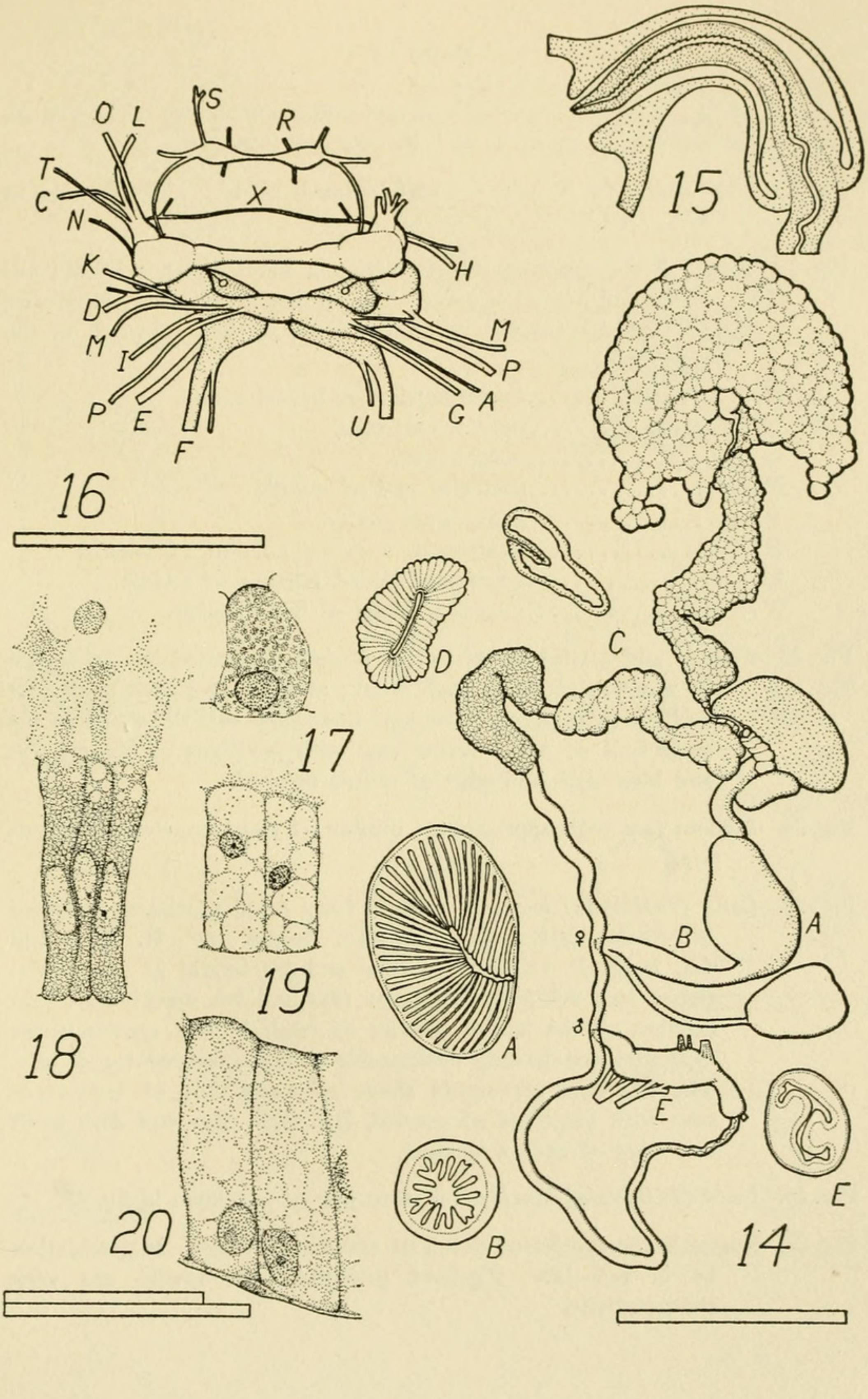
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Plate 14

Scale of fig. 22 represents length of one millimeter; those of 24 and 26, one-half millimeter; those of 23 and 25, fifty microns.

Fig. 21. Three cells from epithelium of albumen gland. Magnification as in fig. ii-12.

Fig. 22. Rogue River specimen; cross-section a short distance behind anterior end of buccal mass. The section is not quite transverse, so that the radular cartilage is cut farther anteriad on the right side.

B .... lower portion of buccal cavity.
C .... radular cartilage.
G .... oesophagus.
M .... posterior end of mouth.
P .... pharyngeal cavity.
R .... functional, anterior portion of radula.
U .... posterior, folded portion of radula.
W .... muscular walls of buccal mass.

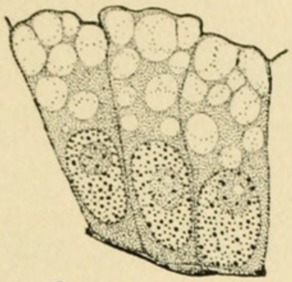
Fig. 23. Central and 1st lateral of radula slightly separated but otherwise in usual relations to each other; also 7th and 14th teeth (1st and 8th marginals). The hair-line represents the shape of the right half of a transverse row with positions of central, 7th and 14th teeth and edge of radula marked.

Fig. 24. Median jaw with approximate outline of right accessory thickening.

Fig. 25. *Lanx (Fisherola) lancides;* radula from dried specimen, collected in Snake River at Lewiston, Idaho, by H. Hemphill (A. N. S. P. 113838). Central and 1st lateral in usual relations; also 9th and 17th teeth (1st and 9th marginals). On account of the larger number of teeth in this species, these examples are directly comparable to those figured for *L. alta.* The hair-line represents shape of right half of transverse row with positions of central, 7th, 14th, 21st and 28th teeth and edge of radula marked.

Fig. 26. *Lanx (Fisherola) lancides;* median jaw of specimen in fig. 25.

Fig. 27. Rogue River specimen; detail of radular cartilage. Magnification as in fig. 12. Pigment granules near nuclei are very characteristic.



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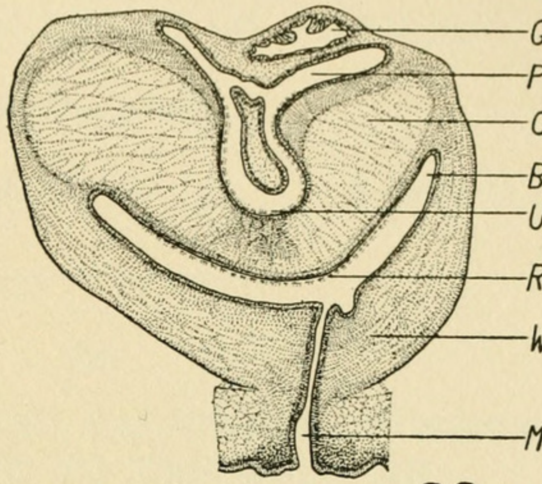

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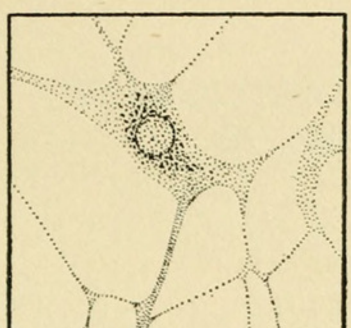

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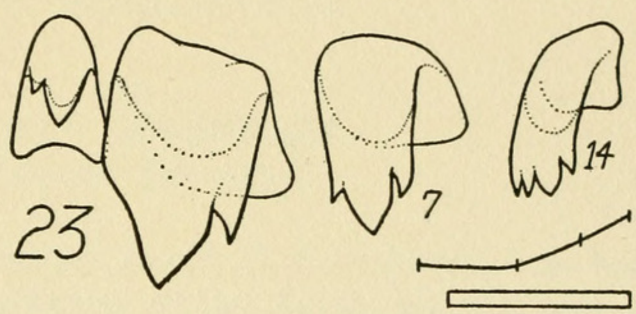

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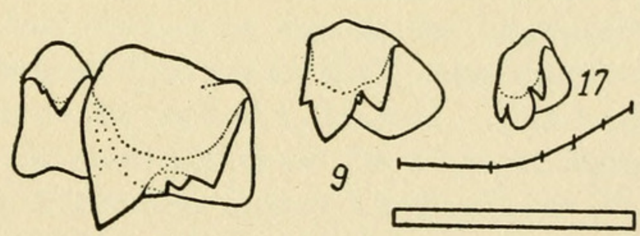

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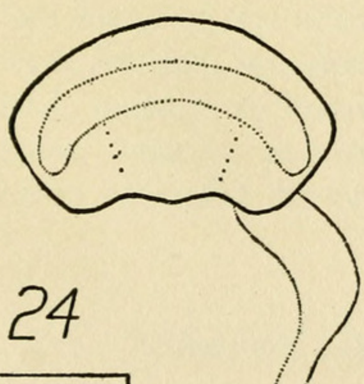

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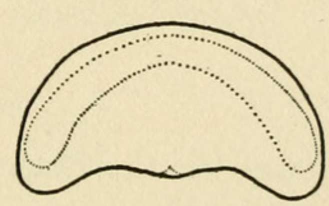

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