ON THE ANATOMY OF *INDOPLANORBIS EXUSTUS* (MOLLUSCA PULMONATA).

By H. Srinivasa Rao, *M.A.*, *Research Assistant, Zoological Survey of India.*

In their paper on the Aquatic and Amphibious molluscs of Manipur Drs. Annandale and Prashad[1] have touched on some points in the anatomy of *I. exustus* and given reasons for establishing a new genus as different from the true *Planorbis* of Müller (with the European *Planorbis corneus* Linn., as type-species).

At the suggestion of Dr. Annandale I took up a detailed study of the anatomy of *I. exustus* with special reference to *P. corneus* and the smaller Indian Planorbids belonging to the genera *Gyraulus*, *Segmentina*, and *Intha*. Of the latter, the Zoological Survey collection contains some amount of well-preserved unnamed material obtained by Dr. Gravely from the Central Provinces, while Dr. Annandale kindly gave me two large preserved examples of the former taken by him at Edinburgh. I have had also the opportunity of examining a small collection of the smaller Planorbids from Manipur and the Inlê lake.

My sincere thanks are due to Dr. Annandale for his constant guidance and valuable suggestions in the course of my work, and for going through the manuscript with me.

Indoplanorbis exustus (Desh.) is the largest Planorbid known in India and is widely distributed in the Oriental region. It resembles in some respects the European *P. corneus* Linn., the type-species of the genus *Planorbis*, but is well differentiated by anatomical characters.

The shell is discoidal and sinistral with the whorls convex and has a wide ear-shaped aperture.[2] The living animal usually carries the shell with the broader end of the aperture on its right and the narrower on its left. In this position the upper extremity of the shell corresponding to the spire (which is flattened in such forms) is on the animal's left, and the lower on its right. The sinistral nature of the shell can be readily recognised when it is held with the aperture facing the observer and on his left.

If the body and penultimate whorls are carefully broken off, the remaining shell, which consists of the innermost whorls, is Physa-like. It is noteworthy that the very young shell of *I. exustus*[3] has a similar form.

When the animal crawls in a fully expanded state the portion of the body exposed is roughly boot-shaped, with the broad anterior region corresponding to the heel and the narrow posterior extremity of the foot to the toe, and consists of the head, foot, and neck.

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[1] Annandale and Prashad, *Rec. Ind. Mus.*, XXII, pp. 577—582 (1921).
[2] Annandale and Prashad, *op. cit*, pp. 578—581.
[3] Germain, *Rec. Ind. Mus.*, XXI, pp. 40—41, text figs. 12—14.

The head is anterior, moderately convex, slightly longer than broad and anteriorly produced into a short, rounded snout. The lower anterior margin of the head is expanded into a flattened, roughly rectangular, lobe, deeply emarginate in the middle of the anterior margin, and gradually sloping to the sides. In outline this expansion resembles that of the hammer-head shark. It is highly mobile in life, and is always extended in front of the anterior margin of the foot. The mouth is a Y-shaped or T-shaped slit in the middle of the lower surface of the head a little anterior to the foot. At the upper end of the head on each side is a moderately long, filiform tentacle, with two semicircular expansions at its base. Of the latter the outer is the larger, and is innervated by three or four branches from the tentacular nerve. The inner is smaller, and has no supply of nerves. A groove is formed between the two expansions. The male genital aperture opens at the base of the outer expansion on the left side. At the inner base of each tentacle lies the eye, which is a small spherical mass of dark pigment placed below the integument.

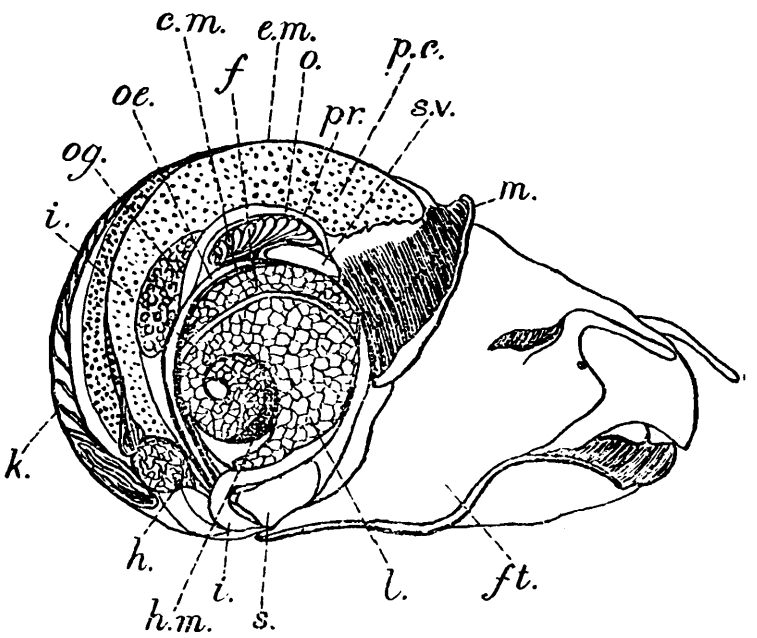

Fig. 1.—*Indoplanorbis exustus*: Viewed from the right. The right half of the mantle and the thin membrane covering the internal organs have been removed. *c.m.*, columellar muscle; *e.m.*, external membrane; *f.*, first loop of the intestine; *ft.*, foot; *h.*, heart; *h.m.*, hermaphrodite gland; *i.*, intestine; *k.*, kidney; *l.*, liver; *m.*, mantle-edge; *oe.*, oesophagus; *og.*, 'Organ de la glaire'; *p.c.*, palleal cavity; *pr.*, prostate; *s.*, stomach; *s.v.*, spermatheca.

The foot is ventral, leaf-shaped, broadly rounded in front and tapering behind.

The neck is a somewhat elongated cylindrical structure stretching obliquely backwards above the head.

The edge of the mantle is slightly thickened and does not extend beyond the margin of the aperture. At the base of the neck and on its left is a small rounded aperture through which bubbles of air may be seen to escape. This is the opening of the pulmonary siphon. Close to the narrower side of the aperture and projecting from below the mantle is a broad roughly triangular lobe with transverse folds on its upper and lower surfaces, and with its free extremity often curled up.

This is the branchial process or pseudobranch.[1] Between the pulmonary siphon and the base of the pseudobranch is the circular anal aperture. This is not clearly seen as a rule, but its position can be made out in the living animal by the occasional ejection of long threads of fæcal matter consisting of mud and sand grains.

The animal as a whole is capable of great contraction, and when disturbed withdraws itself to the inner extremity of the body-whorl. In the fully expanded animal the head, foot, and neck with the associated structures mentioned above are alone to be seen, the remaining organs of the body being confined to the inner whorls of the shell.

The body on removal from the shell may be seen to consist roughly of three regions. The anterior region includes the head, neck and foot; the middle the pallial cavity (with the pulmonary siphon and the pseudobranch), the œsophagus, the columellar muscle, the kidney and heart,

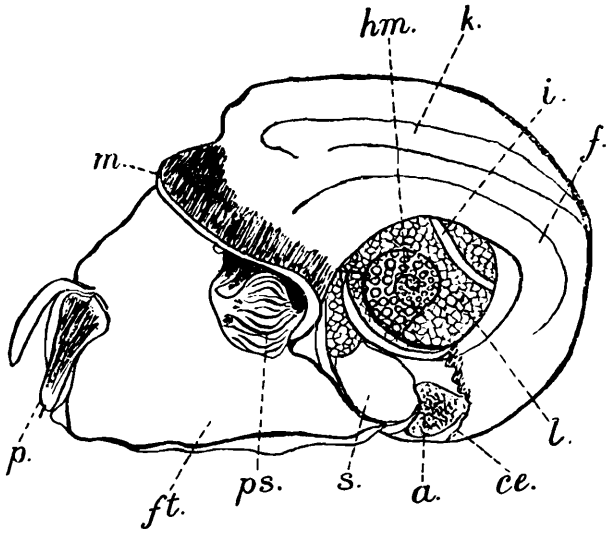

Fig. 2.—*Indoplanorbis exustus*: Viewed from the left. The thin membrane covering the inner whorls has been removed. *a.*, auricle; *ce.*, cut edge of thin membrane covering the internal organs; *f.*, fold hanging from the roof of the pallcal cavity; *ft.*, foot; *hm.*, hermaphrodite gland; *i.*, intestine; *k.*, kidney; *l.*, liver; *m.*, mantle-edge; *p.*, everted penis; *ps.*, pseudobranch; *s.*, stomach.

part of the genitalia, and the rectum; and the posterior the stomach, the intestine and liver, and the rest of the genitalia. A thin membrane covers the middle and posterior regions. It is pigmented black on the middle region, and is transparent on the posterior, but the depth of colour varies in different parts of the regions, and in different individuals. On removing this thin membrane the disposition of most of the internal structures can be made out with great facility.

On the right side, the middle region has the pulmonary cavity roofed over by the tabular part of the kidney in the middle. On slitting open the pulmonary cavity on this side, part of the genitalia and the œsophagus lying above the columellar muscle may be seen. The stomach, the liver and intestine may be seen in the posterior region.

On the left side, a small portion of the pulmonary cavity with the rectum below may be seen in the middle region, while a portion of the

[1] The term 'pseudobranch' has been proposed by Dr. Annandale for this process, as it is quite different in structure from the typical molluscan branchiæ. I adopt this term throughout in the present description.

liver and intestine, and the entire hermaphrodite gland occupy the posterior region.

The mantle is thin and vascular over the pulmonary cavity, and is attached anteriorly to the neck of the animal on the right of the pulmonary siphon. Its free margin is slightly thickened, smooth, vascular, and has short longitudinal muscle fibres.

On cutting the mantle above the pseudobranch along the length of the pulmonary cavity and reflecting it to the right, it may be seen that the pulmonary siphon is formed by the broad superior pallial lobe. On its left separated by a short space lies the pseudobranch, which is the modified inferior pallial lobe. Between the two, but close to the base of the pseudobranch is the circular anal aperture. The female opening is a small round aperture at the base of the neck, and a little below the right side of the siphon. The floor of the pulmonary cavity is lined by a thin membrane which shuts off the underlying structures. This membrane is continued upwards over the posterior part of the cavity separating the structures of the posterior region from it. There are two vascular folds lying parallel to and above the rectum. From the roof of the pulmonary cavity depend two vascular folds, a large one close to the kidney, and a small a little to the left. The kidney is an elongated tubular structure running obliquely from the posterior to the anterior end of the roof of the pulmonary cavity. It will thus be seen that the latter is an incompletely closed chamber communicating with the outside by means of the siphon. In the living animal it is filled with air which may be expelled when required through the siphon. The air, however, never seems to be completely expelled, a small residue being always left even in individuals killed in a contracted state.

The colour varies to some extent in different examples of the species from different localities. The head, foot, and neck are deep reddish brown, or dark grey speckled with minute yellow dots. The margin of the foot is yellowish brown. In the living condition the red blood of the spacious sinuses is responsible for the deep reddish colour, which fades frequently with the rushing back of the blood into the upper parts of the body. In preserved examples the colour is dark brown fading to a deep slaty gray. The sole of the foot is paler than the rest of the foot. The tentacles have dark spots or transverse bands, and are minutely dotted yellow. A small mass of dark pigment is sometimes found at the tip of the tentacle, and has the appearance of an eye. The mantle has a layer of black pigment above, traces of which may be seen on the membrane covering the upper whorls of the animal.

The Alimentary System.—The mouth, as has already been described, is a narrow Y-shaped slit. But it may also be T-shaped when tightly closed. When the animal feeds, or hangs upside down from the surface-film the aperture of the mouth is oval, and frequently opened and closed. A little behind the aperture are to be found the chitinous jaws, which consist of a transverse and two vertical pieces. The former is a strongly chitinised semicircular piece of a dark brown colour, which has its inferior margin uneven. The latter are less strongly chitinised, slightly curved, narrow strips of a yellowish colour, and are placed one on each side close to the outer and inferior margins of the transverse piece with the concave

side directed outwards and the inner convex sides often meeting in the middle. Under a low power of the microscope they are seen to be indistinctly divided into numerous, narrow, transverse segments. Close to each of the vertical pieces on the inner side is often found a thin, yellow strip of chitinous structure which is divided into a number of club-shaped filaments directed towards the buccal cavity.

In *P. corneus* and in some species of *Gyraulus* the jaw is of the same type, whereas in other species of *Gyraulus* and in species of the genera *Segmentina* and *Intha* it is a single, narrow, chitinous strip of a yellowish brown colour bent in the form of an inverted U, and is distinctly segmented.

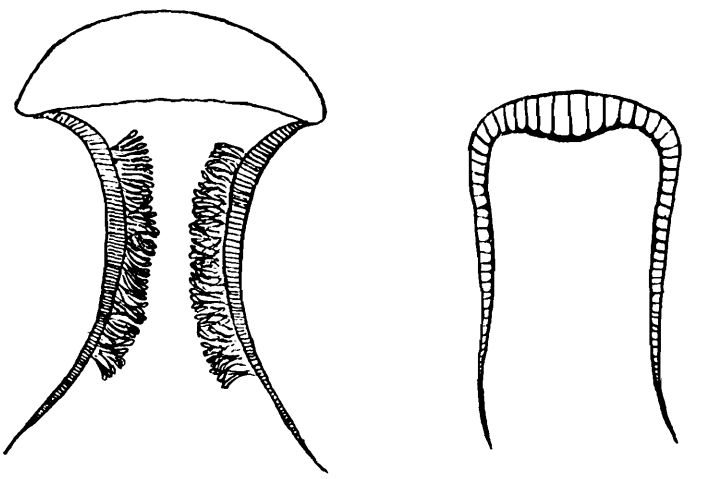

Fig. 3.—*a.*, jaw of *Indoplanorbis exustus*; *b.*, jaw of *Gyraulus* sp.

The mouth leads upwards and backwards into the narrow buccal cavity, the roof and sides of which have muscular walls, while the floor is formed by the odontophore. The latter consists of a soft but thick and tough, saddle-shaped structure supported by a pair of vertical muscle-pads. The radula lies over this structure, and stretches downwards and backwards into the radular sac, which is a short digitiform process projecting from below the posterior end of the buccal mass. When the animal actively feeds, or floats upside down from the surface-film of water, the radula is worked upwards, forwards and backwards. It is a broad chitinous ribbon with several rows of teeth, usually 77 to 83 longitudinal rows of teeth in the broadest portion of the radula, with the approximate dental formula 26·12·1·12·26. Each tooth consists of a broad basal part and an overhanging flap above bearing triangular or conical cusps on its free margin. The cusps are worn out and consequently blunt in some of the anterior rows of teeth. The marginals vary in number to some extent, while the central and laterals are always constant. The outermost lateral, which has traces of a division of the entocone into small secondary cusps, may be considered as the first marginal, and all the teeth centrad of it with only three cusps on each as the laterals. The central is small and has only two cusps slightly unequal in size. A minute cusp is sometimes seen at the base between the two. In the laterals the mesocone is the largest cusp, and

the ectocone small and shorter than the rest. In the first marginal the entocone is usually divided into smaller secondary cusps, while the base of the ectocone and the outer margin of the flap bear very minute cusps. In the second and third marginals generally the innermost cusp of the entocone has its inner base somewhat deeply divided. In the next few marginals the cusps of the entocone and the mesocone stand out in a single, more or less, transverse row with the ectocone much below the base of the mesocone. The ectocone may often be divided into two nearly equal cusps with several minute ones at its base. In all these marginals the mesocone remains unchanged and is the largest cusp. In the next few marginals the mesocone gradually becomes smaller and smaller until it is of the same size as the secondary cusps of the entocone. Some of these latter are entirely suppressed so that there are fewer cusps on an elongated, narrow body. The cusps themselves become blunt and rounded. The ectocone is also gradually reduced until it disappears. In the last few marginals the cusps are all gradually reduced until the last marginal loses all traces of them and becomes a narrow strip of chitin with its free extremity blunt and rounded.

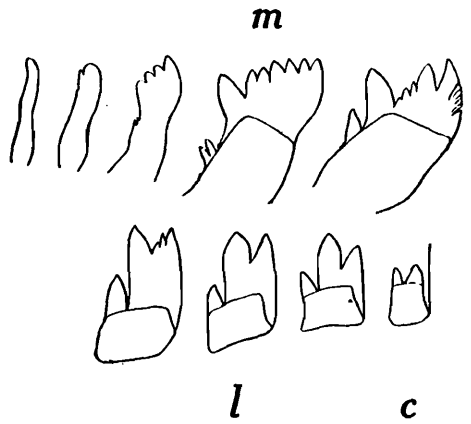

FIG. 4.—*Indoplanorbis exustus* Radular teeth. *c.*, central; *l.*, laterals; *m.*, marginals.

A pair of salivary glands lies above, or in close relation with the male genital duct, and passes close to the inner side of the cerebro-pleural commissure to open into the buccal cavity one on each side of the commencement of the œsophagus. Each gland is a long tube which may, for convenience, be divided into three regions. The posterior region lies behind the nerve collar and has small diverticula. It gradually narrows to a fine tube which crosses the nerve collar, and enlarges into a wide lobed sac lying on the posterior face of the buccal mass. This is the middle region. The posterior and the middle regions form the gland proper, while the anterior which is a short fine tube commencing from the sac, is the duct. At the posterior extremity the glands of the two sides are united by a very short narrow connective.

In *P. corneus* the salivary glands are of the same type with slight differences. The saccular middle region is much larger, and is in the form of a mushroom with a large number of thin finger-shaped diverticula, while the posterior tubular region is much longer with prominent diverticula on them.

In the smaller Planorbids belonging to the genera *Gyraulus*, *Segmentina*, and *Intha* the salivary glands are much simpler and almost uniformly tubular.

The buccal cavity leads backwards and upwards to the œsophagus which commences as a median narrow tube from the top of the buccal mass near its posterior end. On leaving the buccal mass the œsophagus descends to pass through the nerve collar, and runs parallel to and on the right margin of the columellar muscle as a narrow compressed tube. It passes below the albumen gland on its right and enters the stomach. It is pigmented dull gray, and has longitudinal folds in its lumen which give it a striated appearance externally. The stomach is roughly barrel-shaped with both ends gradually tapering. The wide central part is smooth, and provided with thick, shining, transverse muscle-fibres. It has a spacious lumen filled with small grains of sand. The anterior and posterior tapering portions have longitudinal folds in the lumen.

The colour of the stomach is usually reddish pink. The intestine is a long cylindrical tube with smooth walls, and commences from the posterior end of the stomach. It turns sharply to the right and passes parallel to the stomach up to the anterior end, and then to the left bordering the anterior part of the stomach. It runs obliquely backwards in a groove on the liver towards the right side and surrounds the entire liver in a wide loop. On passing obliquely forwards nearly touching the first loop it slightly descends to emerge from the hind end of the pallial cavity as the rectum. The latter has a straight course to the anus and is roofed over by two parallel vascular folds about which mention has already been made. The intestine is usually of a dull pink colour which deepens on the rectum. A small finger-shaped cæcum is present at the commencement of the intestine in the bend formed between the latter and the stomach. Its lumen has minute longitudinal folds. The ducts of the liver which are usually four in number open into the stomach at the base of the cæcum.

The disposition of the alimentary tract is essentially the same in *P. corneus* and the smaller Planorbids, but some variations in the length and nature of the intestinal loop, and in the size of the cæcum occur in the latter. In some species of *Gyraulus*, as for instance *G. euphraticus* Mousson, the intestinal loop round the liver is either very short or totally absent, the intestine in the latter case proceeding forwards straight from the stomach instead of coiling round the liver; and the cæcum is well developed. In other species of *Gyraulus* and in *Segmentina taia* Annandale and *Intha capitis* Annandale the intestine is long and surrounds the liver more or less completely. The cæcum in these is very small, and is often overlooked.

The liver is a large brownish mass extending from the posterior end of the albumen gland up to the base of the hermaphrodite gland. It is often heavily infected with cercariæ of a parasitic trematode. Most of the individuals that I examined from Calcutta and Nagpur had the liver disintegrated to a slight extent on account of the infection. The hermaphrodite gland, being close to the liver, is also frequently affected.

The pallial cavity.—The pulmonary chamber occupies a greater portion of the body whorl, and is about a third of the length of the whole

animal. The sides and roof are formed by the mantle, while the hind end is shut off from the structures of the upper whorls by a membranous partition which also paves the floor of the chamber, separating off the underlying organs, while the front end is shut off from the head by the union of the mantle with the neck. It communicates with the outside by means of the pulmonary siphon. The mantle is highly vascular over the roof and sides of the chamber, and branching lacunæ may be seen through the pigmented membranous covering. The respiratory surface of the interior of the chamber is increased by the presence of longitudinal vascular folds projecting into it from the roof and the floor. A comparatively large thick fold commencing from about the level of the heart extends along the left margin of the kidney to the front end of the chamber, and hangs down as a vertical flap just above

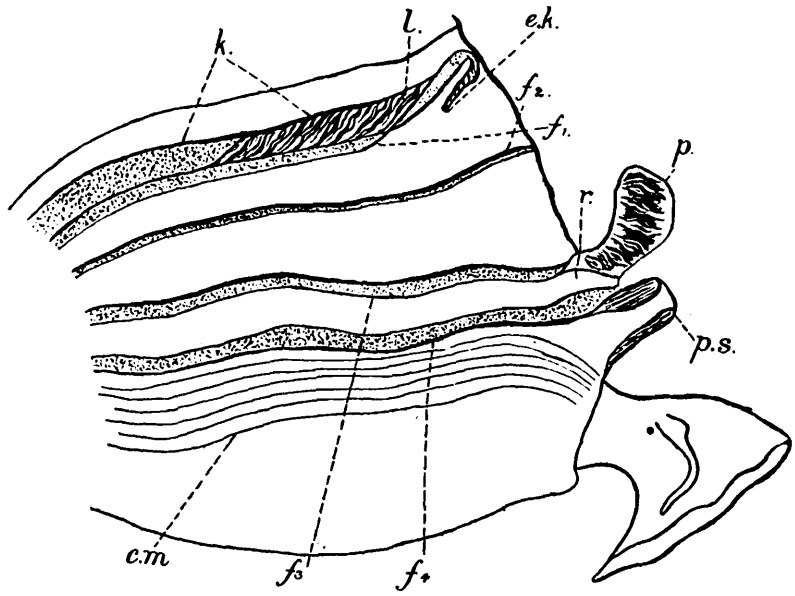

FIG. 5.—*Indoplanorbis exustus*: Mantle cut open longitudinally on the right side and reflexed to the left showing the folds of the palleal cavity. The kidney is partly opened from below to show the internal folds. *c.m.*, columellar muscle; *ek.*, external opening of kidney; *f.1*, *f.2*, folds on the roof of the palleal cavity *f.3*, *f.4*, rectal folds of the palleal cavity; *l.*, folds in the lumen of the kidney; *k.*, kidney; *p.*, pseudobranch; *p.s.*, pulmonary siphon; *r.*, rectum.

the rectum roughly dividing the cavity into two chambers. It seems probable that in life, when the pulmonary chamber is distended, even this temporary division does not take place. A little to the left of the large fold is another small one lying parallel to the kidney from the hind end of the chamber to a little behind the margin of the mantle. Above the rectum and parallel to it on each side runs a prominent, thin, vascular fold, the right continuous with the left margin of the siphon, and the left with the right margin of the pseudobranch. So far as I have been able to make out in the examples of *P. corneus* before me the right fold is absent,[1] but in its place there is a broad convex ridge.

In the smaller Planorbids the vascular folds are very minute, and are found in the same positions.

[1] Pelseneer has figured two folds above the rectum in *P. corneus*. Vide *Arch. de Biol.*, XIV, pl. xvii, fig. 27 (1895-96).

Running close to the base of the renal and rectal folds are two principal veins which may be observed on removing them. Spherical calcareous concretions are found in great numbers on all the folds. They are also found on other structures of the pallial cavity and on the walls of the vascular sinuses.

The air in the pulmonary chamber is often expelled in small bubbles through the siphon, and this act is probably an expulsion of impure air. When the animal is disturbed at the surface of the water it usually discharges a few bubbles of air with a simultaneous contraction of the body to a slight extent, and drops to the bottom. It does not rise up to the surface directly from the bottom, but crawls over weeds and other supports to the surface of water. It seems to me therefore that the pulmonary chamber is not, strictly speaking, a hydrostatic organ as well.

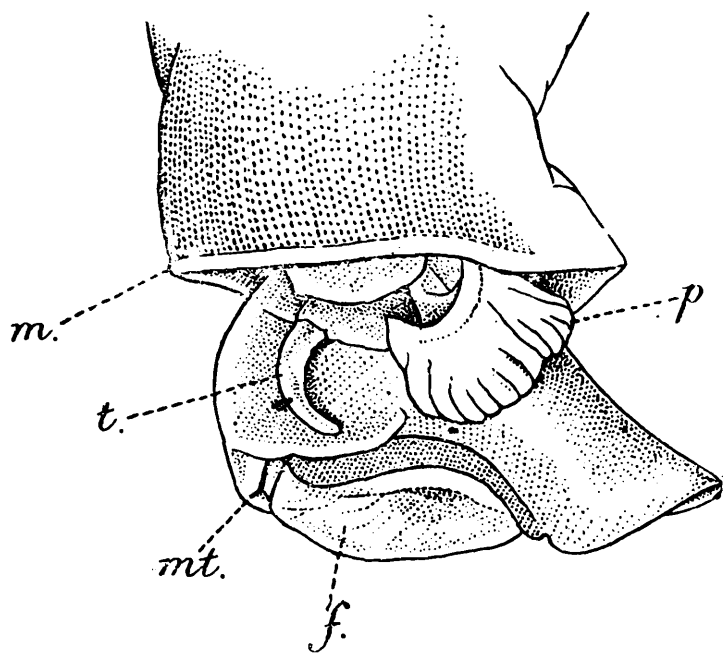

Fig. 6.—*Indoplanorbis exustus*: Left view of the anterior region showing the pseudobranch. *f.*, foot; *m.*, mantle; *mt.*, mouth; *p.*, pseudobranch; *t.*, tentacle.

The siphon is a broad thin lobe, deeply emarginate in the middle of the anterior margin, and when the sides of the lobe overlap above, a temporary tube is formed, through which the air in the pulmonary chamber escapes to the outside. Usually the whole siphon is well within the margin of the mantle, but at the time of expulsion of the air it is slowly protruded slightly beyond the edge of the mantle with its extremity expanded into a funnel. As soon as a bubble has been discharged the extremity of the siphon is flattened and is the first to touch the surface film of water. It then suddenly contracts so that the wide funnel-shaped opening is reduced to a small circular aperture, through which water does not pass into the pulmonary chamber.

In *P. corneus* the siphon is short, broad, thick and prominent. In the smaller Planorbids it is always present,[1] but varies in form and size.

[1] Drs. Annandale and Prashad have observed a spirally coiled, epipodial siphon in *Camptoceras lineatum* Blanford (*Rec. Ind. Mus.*, XXII, p. 586). A similar siphon in *C. hirasei* Walker from Japan is figured by Walker in *Occ. Papers Mus. Zool. Univ. Michigan*, no. 64, pl. 1 (1919).

In some species of *Gyraulus* it is short and broad while in others long and narrow ; and in *Segmentina taia* and *Intha capitis* it is small and less conspicuous.

The pseudobranch is a broad leaf-shaped lobe attached by its broader end below the anal opening on its left. The upper and lower surfaces are thrown out into a number of prominent pleats or folds, three or four of which are grouped together. Each group of folds is separated one from the other by a short deep gap. The free margins of the pseudobranch are not involved in the folding, but form a border to the central folded area. The colour is a dull brown or slaty gray speckled with yellow dots. In the expanded animal the free terminal portion is curled up against the edge of the mantle, or rarely of the shell. In this position the folds of the upper surface are not visible, and even when uncurled appear much less prominent than those of the lower surface. They are very complex as may be seen in transverse and longitudinal sections

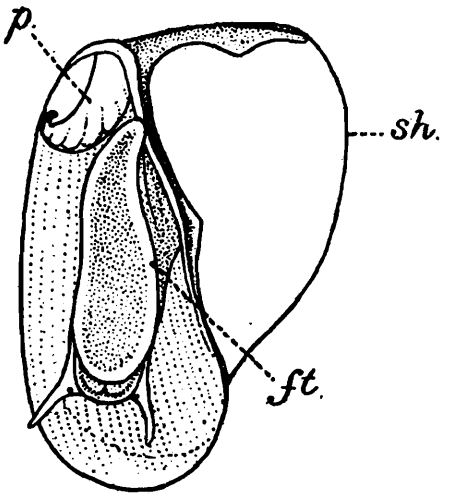

FIG. 7.—*Indoplanorbis exustus*: Ventral view of a living young specimen. *ft.*, foot ; *p.*, pseudobranch ; *sh.*, shell.

of the pseudobranch. In several living examples that I observed the pseudobranch had its free extremity always curled up both in the expanded and contracted state.[1] It is vascular and has well developed efferent and afferent veins, and has a supply of muscle-fibres and nerves. In young individuals it has the same structure and disposition as in the adult. From its position and structure the pseudobranch appears to be an accessory respiratory organ.

In *P. corneus* the pseudobranch is a simple leaf-shaped lobe without the folds of *I. exustus*. In the examples before me it is very much contracted and hardly distinguishable as a distinct lobe owing to the effect of spirit in which they were killed and preserved. The figures of Simorth[2] and Pelseneer,[3] however, show clearly the position, form, and extent to which it can be extended. One of the chief

[1] Dr. Annandale informs me that he has observed the pseudobranch in a straight condition in living examples on the Barkuda Island under certain abnormal conditions such as foulness or salinity of the water in which they live.

[2] Simroth, in Bronn's *Tier-Reich*, III, 3, p. 453, text-fig. 152c.

[3] Pelseneer, *Arch. de Biol.*, XIV, pl. xvii, figs. 23, 24, 26 (1895-96).

general differences between *I. exustus* and *P. corneus*, therefore, lies in the nature of the pseudobranch.

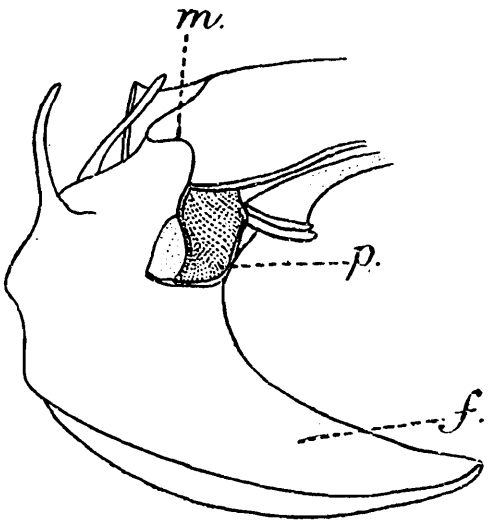

Fig. 8.—*Gyraulus euphraticus* : *f.*, foot ; *m.*, mantle edge; *p.*, pseudobranch.

In *Pulmobranchia lamellata*[1] Pelseneer the pseudobranch is remarkably of the same type as in *I. exustus*, and in some respects the anatomy of the latter resembles more closely that of the former than *P. corneus*.

Fig. 9.—*Indoplanorbis exustus* ; Transverse section of pseudobranch through the anterior part.

In species of *Gyraulus* the pseudobranch is a simple, thin, leaf-shaped vascular lobe without the transverse folds. There is, however, an oblique

[1] Probably a species of *Physastra* (*cf.* Prashad, *Rec. Ind. Mus.* XXII, p. 475).

vertical fold on the upper surface extending from the base to the free extremity. Faint transverse striations may often be seen on either side of the fold. Slight variations in the size and shape of the pseudobranch may also occur. The presence of the vertical fold apparently distinguishes the structure of the pseudobranch from that of *Planorbis* s.s.

It is curious that there is no trace of a pseudobranch in *Segmentina taia* and another unnamed species of the same genus or in *Intha capitis*. If this structure is proved to be absent in all other species of these genera it would afford an important generic distinction between them and the larger Planorbids, and indicate the close relationship of the genera *Segmentina* and *Intha*. As will be seen later these latter are closely related in anatomical characters.

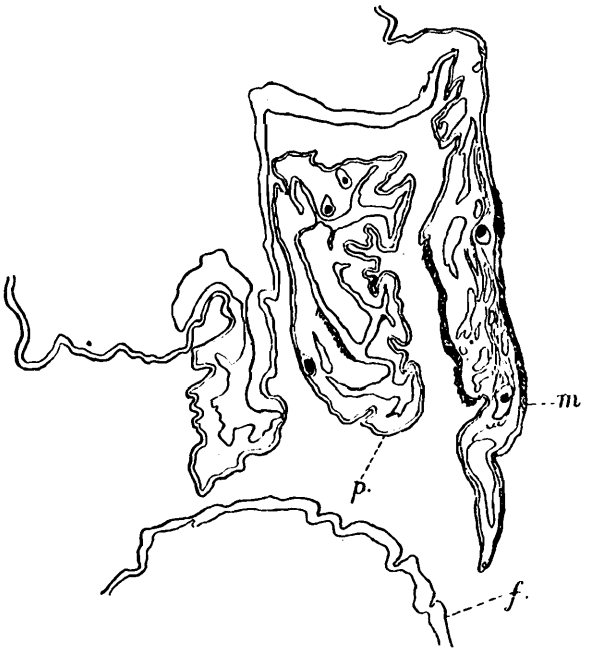

FIG. 10.—*Indoplanorbis exustus*: Longitudinal section of pseudobranch and mantle.

The vascular system.—This consists of the heart enclosed within a pericardial chamber, the thin-walled vessels carrying blood to the various organs, the so-called veins with no definite walls taking blood to the respiratory organs, and the large sinuses which place the two systems in communication. The latter are very numerous in the foot, mantle, head, pseudobranch, and folds of the pallial cavity. In preserved examples the veinous vessels have a wide lumen filled with a whitish cheese-like mass, while the others have thin, collapsed, pigmented walls with numerous calcareous concretions. The heart lies at the extremity of the pallial cavity on the right side and may be seen through the pigmented membrane of the mantle as a whitish triangular structure. The pericardial membrane is extremely thin and closely adherent to the lower surface of the mantle. The heart has the kidney on its left below and in front, and posteriorly the albumen gland and a portion of the alimentary tract. It consists of an anterior elongated roughly triangular auricle with thin spongy walls and a posterior broad pear-

shaped ventricle with somewhat thicker walls having a reticulate appearance.

From the ventricle arises a short vessel from which branches are given off to the various organs of the posterior region. The chief of these may here be mentioned. Immediately on starting from the ventricle a short branch is given off to the kidney, and a little behind, the main vessel passes over the anterior loop of the intestine, and at this point gives off a large branch which immediately divides into right and left branches. The left is a short, narrow vessel supplying the intestine, and the right on crossing the stomach gives off a short branch passing downwards between the œsophagus and the cæcum and supplying the

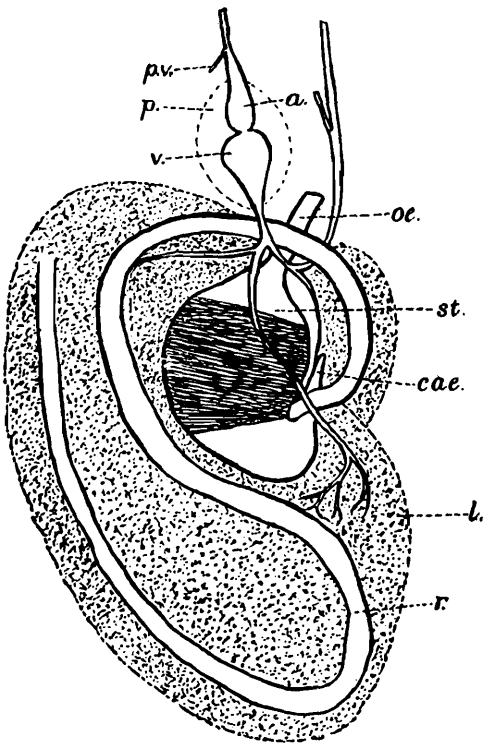

Fig. 11.—*Indoplanorbis exustus* : Circulation in the region of the stomach, *a.*, auricle ; *cae.*, cæcum ; *l.*, liver ; *oe.*, œsophagus ; *p.*, pericardium ; *p.v.*, pericardial vein ; *r.*; rectum ; *st.*, stomach ; *v.*, ventricle.

stomach. It is continued on as a long narrow vessel and crosses the intestine to enter the liver, immediately dividing into smaller branches. The main vessel after giving off the branch to the intestine curves round underneath the anterior loop of the latter and proceeds straight in front below the genitalia. A small branch is given off to the cæcum from the bend of the main vessel. About the level of the albumen gland a large branch arises from the main vessel and soon breaks up into smaller vessels distributing blood to the various parts of the genitalia. The main vessel is continued below the oviduct and close to the columellar muscle below the œsophagus finally crossing the pedal commissure. Various small branches arise from it in its course to the brain. It gradually widens until it enlarges to form an elliptical sinus below the buccal mass. From the front and lower sides of this sinus fine branches reach the foot and the anterior part of the head. A small vessel from the sinus supplies the penis-sheath closely following the course of the nerve.

The veinous circulation is difficult to make out satisfactorily in freshly killed examples, and even in well-preserved individuals the thin-walled veins are usually damaged. The course of the veins can, however, be traced by the presence of a whitish, coagulated, cheese-like mass in them. So far as my observation goes the veinous circulation closely resembles that of *Pulmobranchia lamellata*.[1]

On the right margin of the kidney, commencing from the anterior end, lies the renal efferent vein which is in close relation with the highly vascular roof of the pulmonary chamber on its right. This vein at its posterior extremity opens into the auricle and at its junction with the latter, a small short branch is given off to the pericardial membrane on the right side. On the left margin of the kidney lies the renal afferent vein, which breaks up into several minute capillary-like vessels below the transverse folds of the kidney. The blood is distributed to the renal efferent vein by means of a similar set of vessels on the right margin of the kidney.

The renal afferent vein has its origin in a closed sinus in the mantle at its junction with the neck of the animal. The right pallial vein, running parallel to the edge of the mantle a little behind it, and the efferent pseudobranchial vein, which runs along the right border of the pseudobranch and then below the base of the siphon, empty themselves into the closed sinus. The rectal vein which runs close to the rectum on its left is joined by the left pallial vein at the base of the pseudobranch and enters the left border of the latter as the pseudobranchial afferent vein, which breaks up into smaller branches among the folds of the pseudobranch. I have been unable to make out the course of the sub-intestinal vein, which runs parallel to the rectum on its right. It probably joins the left pallial vein at some point above the pseudobranch or breaks up into sinuses in the mantle.

It will thus be seen that the pseudobranch is an important organ of respiration. It receives veinous blood from the left side of the animal and, after aërating it, sends it on to the large dorsal sinus, which receives aërated blood from the mantle and the vascular roof of the pulmonary chamber.

The renal system.—This organ consists of a posterior saccular and an anterior tubular region. The former is a pear-shaped body lying immediately above the albumen gland and separated from the latter by a thin membrane. On its right a little in front lies the heart on a slightly higher level, while on its left the hind extremity of the pulmonary chamber. It has the liver on its posterior side. Its lumen is narrow on account of the presence of a number of longitudinal folds, which are yellow in colour in the freshly killed animal. The tubular region of the kidney commences from the neck of the saccular part, and extends obliquely forwards on the roof of the pulmonary chamber, as a broad compressed tube up to the junction of the mantle with the neck. It then curves sharply to the left as a short narrow arm directed backwards, and carries at its extremity the minute renal aperture. In some preserved individuals the renal aperture is distinctly slit-like and

[1] Pelseneer, *Arch. de Biol.* XIV, pl. xv, fig. 14 ; pl. xvi, fig. 22.

provided with a pair of tumid lips. In *P. corneus* the external opening of the kidney is a circular aperture on a prominent papilla.

The floor and roof of the tubular part of the kidney are raised into a number of short digitiform processes or vertical folds arranged in more or less equidistant transverse rows. These folds are lined by cubical cells which give them a moniliform appearance in sections.

The reno-pericardial opening is minute, and is found as a very short, backwardly directed, tubular passage at the neck of the saccular portion of the kidney on its right.

The Reproductive system.—The male and female ducts are separate, each having a distinct opening to the outside. The position of these openings has been described in connection with the external features.

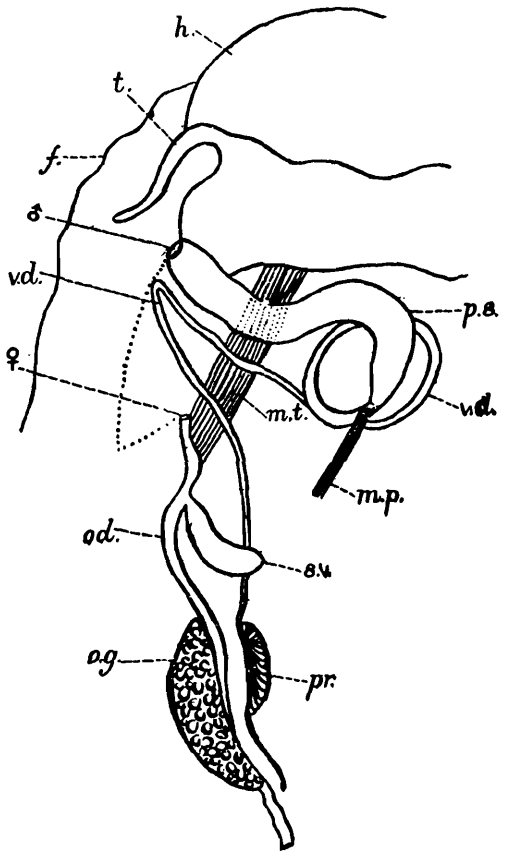

FIG. 12.—*Indoplanorbis exustus*: Anterior part of the genitalia, *f.*, foot; *h.*, head; *mt.*, retractor muscle of the tentacle; *m.p.*, retractor muscle of the penis; *od.*, oviduct; *og.*, 'Organe de la glaire'; *pr.*, prostate; *ps.*, penis sac.; *sv.*, spermatheca; *vd.*, vas deferens.

The various parts of the reproductive system are essentially the same as in *P. corneus*.[1] But differences of considerable taxonomic value occur in the structure of the terminal portion of the male duct.

The hermaphrodite gland is an elongate triangular body lying coiled at the apex of the spire, when viewed from the left. The colour is a bright orange or yellowish brown in the freshly killed individual. The apex of the gland is tightly coiled and occupies the top of the spire, while its base is in close contact with the posterior extremity of the liver. The gland consists of a number of small finger-shaped processes

[1] A good description of the reproductive system of *P. corneus* with an excellent plate is given by Baudelot in *Ann. Sci. Nat.* XIX, pp. 197—203, pl. iv, figs. 2—5 (1863).

opening into a median, narrow, hermaphrodite duct below. A few small ovate eggs with a single, rounded nucleus in the centre are often found in sections of the gland. Clusters of spermatozoa with long tails are often found in the spaces between the ova. They are more deeply stained than the latter. The hermaphrodite duct, on leaving the gland, is continued obliquely forwards below the liver, and at the level of the stomach passes upwards to the albumen gland situated just in front of the former. The proximal portion of the duct has very small diverticula opening into it.

The hermaphrodite duct joins a short duct from the albumen gland. A little in front of the junction of the two ducts the male and female ducts can be distinguished. The albumen gland is a dark gray fan-shaped body convex above and concave below. It has its posterior border broadly rounded while its anterior is deeply concave. The two ducts arise from below this concavity and run close together parallel to the œsophagus on its left. The ducts and the associated glands lie on the right half of and below the pulmonary chamber separated from the latter by a thin membrane. The male duct is narrow and lies below the oviduct and in close contact with it. The female duct is large and has thin walls. It passes below a large oval gland in front, called the 'Organe de la glaire' 'the gelatinous secretion of which appears to serve the purpose of preserving the ova from contact with water.' It is broad and flattened, and has a striated appearance. There is no definite duct by which the products of the 'Organe de la glaire' are led into the oviduct, apparently the gland opens into it by means of numerous small pores. The oviduct on emerging from below the gland is slightly enlarged, but soon becomes narrowed into a short, cylindrical tube into which opens a pear-shaped sac by means of a short duct. This sac is called variously the copulatory pouch, the seminal vesicle, or the receptaculum seminis. It has thin walls, and is usually filled with an orange-colour fluid. The duct of the seminal vesicle varies in length. In not a few individuals it is very short, but occasionally examples with long ducts are also to be met with. Baudelot's figure of the genitilia of *P. corneus* shows the duct to be long, but he does not mention whether any variation occurs in this species. The oviduct in front of the junction of the seminal vesicle with it is a short duct with fairly thick walls and opens to the outside a little below the pulmonary siphon.

The male duct, as has been described above, passes close below the oviduct and to the right margin of the 'organe de la glaire,' and near the anterior end of the latter receives the flattened, elliptical prostrate gland, which is closely pressed to the right anterior margin of that organ. The male duct passes below the prostrate, receiving its products, and is continued forwards as a very fine rounded tube. The prostrate gland consists of a large number of diverticula closely bound together and hardly distinguishable as such. It has no definite duct, and probably like the 'organe de la glaire' opens by means of minute pores into the flattened male duct below. The vas deferens is long and coiled, and on leaving the prostrate runs nearly parallel to the oviduct, and passing close to the female opening proceeds in front to the integument near the male opening. It then curves sharply backwards as a somewhat

wider tube. It crosses the tentacular retractor muscle, and running parallel to the penis-sheath lies coiled up behind the buccal mass, and finally joins the penis-sheath. A single retractor muscle[1] arises from the left half of the columellar muscle, and running between the coils of the vas deferens joins the terminal portion of the latter just before it reaches the penis-sheath. It is usually smooth and shining but may be dark gray owing to the presence of a small blood-vessel which is frequently pulled off in cleaning the muscle.

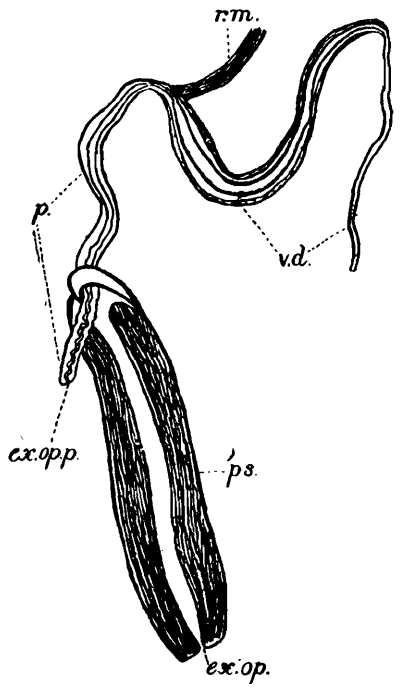

Fig. 13.—*Indoplanorbis exustus :* Male genitalia. The penis-sac and the vas deferens are cut open. *ex. op.*, external opening of penis-sac ; *ex. op. p.*, external opening of penis ; *p.*, penis ; *ps.*, penis-sac ; *r. m.*, retractor muscle of the penis ; *v. d.*, vas deferens.

The penis-sheath is a long, stout, cylindrical, muscular organ lying close to the integument posterior to the left tentacle. It is covered over by a thin, black membrane, and is held in position by short, thin muscles and shredded membranes above and below. The lumen of the sheath is somewhat compressed, and has on each side an elongated muscular pad. Between these pads hangs the long tubular penis, which is often broken or else extremely contracted in preserved examples. Though contracted into the upper part of the sheath it maintains a cylindrical form. It has thin walls and is continous with the thin zig-zag tube in the lumen of the vas deferens. It is often as long as the sheath itself, and has at its free end a minute circular opening. The outer wall of the penis is continuous with the tube inside it at the external opening. In preserved individuals the penis-sheath undergoes great contraction and is consequently stout and bulbous with part of the vas deferens everted into it ; or it may be completely protruded inside out from the external opening with the penis at its extremity ; or everted

[1] Drs. Annandale and Prashad evidently overlooked this muscle. In a later paper the former mentions two retractor muscles, but it is probable that the small blood-vessel and nerve supplying the penis-sheath, and reaching the same point on the vas deferens as the retractor muscle, were mistaken for a second muscle.

with the pads curled out on each side of the external opening with even a part of the vas deferens protruded in the centre.

In *P. corneus* the penis-sheath is short and stout, and the penis appears to be developed as a stout invaginated process from the walls of the sheath and has an open groove-like duct opening on a gland-like apical structure. There are two well developed retractor muscles divided terminally into two or three short branches. One of them is attached to the sheath, while the other to the terminal part of the vas dèferens, a branch of which goes to the penis-sheath.

It will be seen, therefore, that the essential differences in the genitalia between *I. exustus* and *P. corneus* lie in the form and structure of the penis, and in the number and arrangement of the retractor muscles.

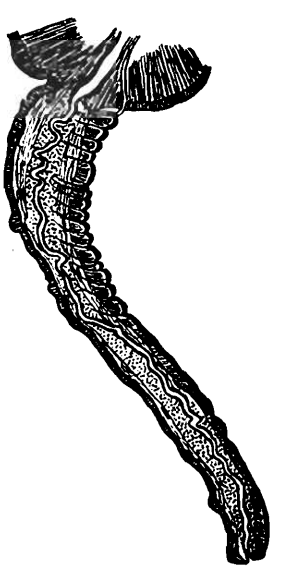

Fig. 14.—*Indoplanorbis exustus*: Penis (Highly magnified).

Buchner[1] recognises four types of penis in the Planorbidae. It is evident that the type in *I. exustus* is not identical with any of Buchner's, though closely allied to his third type. I agree, therefore, with Dr. Annandale[2] in recognising a fifth type represented by the penis of *I. exustus*.

The reproductive organs of the smaller Indian Planorbids (*Gyraulus*, *Segmentina* and *Intha*) have the same arrangement as in the larger forms but differ in some respects, chiefly in the structure of the genital glands and the penis. In these forms the hermaphrodite gland is usually long, and consists of longer and more distinct digitiform processes than in the larger Planorbids. The albumen gland has an irregular outline, and is much less compact than that of *I. exustus* or *P. corneus*. It has long diverticula, and is of a pale white colour. The prostrate gland is remarkably different. It is an elongated, flattened structure consisting of a few, usually eighteen to twenty, long club-shaped processes arranged

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[1] Buchner, *Jahreshefte d. Vereins f. Vaterl. naturkunde in Württemburg*, XLVII, pp. 68-69, pl. vi (1891).

The figures are reproduced by Simroth in Bronn's *Tier-Reich*, III, 3, p. 502. I am indebted to Dr. Prashad for drawing my attention to the first named reference.

[2] Annandale, *Rec. Ind. Mus.* XXIV, p. 359 (1922).

in a linear row alongside the vas deferens, each opening individually into the latter. The penis-sheath is not covered by a pigmented membrane, but is more or less transparent. It is broad posteriorly and gradually narrows anteriorly, where it has a bulbous swelling, which is continued as a short cylindrical tube to the external opening. The penis is long, and in *Gyraulus* bears at its free end a reddish brown chitinous stylet. There is only a single retractor muscle attached to the penis-sheath near the bulbous swelling. In *Segmentina taia* and *Intha capitis* both the bulbous swelling and the penial stylet are absent. The structure and arrangement of the rest of the genitalia are the same as in *Gyraulus*.

The muscular system.—This consists of the columellar system extending antero-posteriorly on the ventral surface of the animal, and the muscles of the buccal region. The former is a broad sheet of muscle consisting of thin and thick fibres, and gradually narrowing towards the posterior end near the apex of the spire. Anteriorly the fibres are very closely arranged. On the ventral side of the greater part of the body-whorl the columellar muscle can be divided into a broad, median, almost transparent region consisting of thin fibres, and a narrow whitish, shining region on each side of the former consisting of thick fibres. From the columellar muscle arise two pairs of muscles, namely, the retractors of the foot, and of the buccal mass. The single retractor muscle of the penis takes its origin from the left side of the columellar muscle. Each retractor of the foot consists of thick fibres and comes off from the lateral region of the columellar muscle. It is closely adherent to the integument, somewhat narrow at its origin but gradually widening towards the antero-lateral part of the foot, which it supplies. A few fibres from the left retractor of the foot pass obliquely towards the left, close to the base of the pulmonary siphon and supply the pseudobranch. A broad sheet of thin fibres extends from the retractor of the foot on each side to the base of the tentacles. This is the tentacular retractor muscle. Two long narrow strips of shining muscle have their origin at about the middle of the columellar muscle one on each side of the central transparent region, and proceed forwards parallel to the visceral nerves. They pass through the circum-œsophageal nerve-ring close to its sides, and reach the ventro-lateral surface of the middle of the buccal mass. These are the buccal retractors. The penial retractor muscle is a slender muscle with minute fibres and has its origin at the junction of the median and lateral areas of the columellar muscle on the left side. It proceeds forwards and upwards between the coils of the vas deferens, and is attached to the terminal portion of the latter.

The buccal mass is also supplied with intrinsic muscles, the chief of which may be mentioned. Posteriorly, near the ventral surface of the buccal mass a fan-shaped muscle take its origin, and passes obliquely forwards and upwards widening gradually in its course to the top of the buccal mass, and joins with its fellow of the opposite side in a broad, transverse band of muscle fibres across the anterior half of the buccal mass. Below this fan-shaped muscle is a broad band with fibres running concentrically round the buccal mass. It extends behind the fan-shaped muscle, and is tucked in to form a groove in the median ventral surface.

A small band of muscle from the sides of the buccal mass a little behind the buccal ganglion passes forwards to the anterior end. Besides these larger muscles there are fine strands arising from above and below the buccal mass, which are attached to the integument of the snout and head above, and to the foot below.

The nervous system.—A full account of the nervous system of *P. corneus* has been given by Lacaze Duthiers.[1] So far as I have been able to ascertain, the nervous system of *I. exustus* agrees in every particular with that of *P. corneus*. The cerebral, pleural, and pedal ganglia form the circum-œsophageal nerve-ring behind the buccal mass near its ventral surface. The visceral ganglia are also found close together and united with the pleural ganglia. They present a granular appearance, and are usually of a pink or yellowish brown colour in the freshly killed individuals. The buccal ganglia are a pair of small, roughly triangular bodies placed close to the sides of the œsophagus at its commencement from the buccal mass, and connected by a short nerve-commissure below the œsophagus. From each of the buccal ganglia arise five nerves. From the outer angle in front is given off a small nerve to the salivary gland, and from the inner angle close to the beginning of the buccal commissure is given off a short fine nerve to the posterior face of the buccal mass. From the outer angle below arise three nerves of which two pass close to the sides of the buccal mass, while the third proceeds backwards to join the anterior ventral surface of the cerebral ganglion. The cerebral ganglia are somewhat elongated triangular bodies united by a short commisure above the œsophagus, the two together forming a horse-shoe shaped structure. They are broader near the middle and slightly taper towards the sides. From these arise the nerves to the tentacles, eyes, otocysts, skin and muscles of the head and snout. The tentacular and optic nerves together with those supplying the skin and muscles of the head and snout are given off from the lower outer angle of the cerebral ganglia. At the base of the tentacle a few small branches from the tentacular nerve supply the semicircular expansions on the outer side. The optic nerve is fine and is united with the tentacular nerve for some distance. The eye is simple in structure, and has a central spherical lens surrounded by a thick layer of black pigment. The nerve to the otocyst is very short and minute and recognised only in balsam mounts. It starts from the posterior face of the cerebral ganglion and proceeds parallel to it until at its outer angle it sharply turns downwards to join the otocyst. The otocyst is a minute, whitish, spherical mass at the posterior outer angle of each pedal ganglion. Its cavity is filled with numerous elliptical otoliths. From the outer extremity of the left cerebral ganglion arises a long thin nerve which runs backwards to supply the penis-sheath. The pleural ganglia are small squarish bodies placed ventral to the cerebral ganglia. The pleuro-pedal and the cerebro-pedal commissures may be seen in front of the pedal ganglia at their outer angle. There are three visceral ganglia somewhat un-

[1] Lacaze Duthiers, *Arch. Zool. Exp.* I, pp. 476—482 and 484—487, pl. xx; also pp. 155—156, pl. iii, figs. 9—10 (1872).

equal in size and arranged in the form of a U. They are roughly four-sided bodies placed close together dorsal to the pedal ganglia and behind the cerebral. From the left visceral ganglion is given off a fairly stout nerve from which branches arise supplying the pulmonary siphon, the pseudobranch, and the left side of the mantle. A little above the origin of this nerve a small branch proceeds upwards in the mantle where it joins the neck of the animal, and supplies the osphradium situated next to the right border of the siphon. The osphradium, also known as the organ of Spengel or Lacaze Duthier's new organ of innervation, is a flask-shaped structure of whitish colour opening by means of a broad, funnel-shaped aperture to the outside. The nerve supplying it enters the broad end of the structure. From the middle visceral are given off three nerves, branches of which supply the floor and roof of the pallial cavity. A long nerve passes over the 'organe de la glaire' supplying the genital organs and the pericardium. From the right visceral are given off two nerves, a small nerve to the œsophagus and a stout one to the right side of the mantle. The pedal ganglia are flattened quadrilateral bodies rounded posteriorly, and give off three or four stout nerves with several branches supplying the foot. A short commissure connects the left visceral ganglion with the pallial nerve from the middle visceral.

In spite of the greater development of the pseudobranch in *I. exustus* its nerve does not seem to be any better developed than in *P. corneus*.