THE ANATOMY OF THE BRITISH SPECIES OF THE GENUS SOLEN. Pt. i.

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(Plates ii-iii.)

In working at the anatomy of the various British species of the genus Solen, I was somewhat surprised to find that, while S. ensis and S. siliqua are in their structure very similar to each other, they differ very materially from S. marginatus, the latter exhibiting many points of interest. Apart from this, Solen also presents many interesting features when compared with other types of the Pelecypoda. Further, on looking through the literature, I have failed to find any work dealing fully with the anatomy of the genus. Menegaux¹ has described at length the circulatory system, and Pelseneer, Barrois, Lang, Faussek⁵ and others, have made reference to other portions of the anatomy, but have not dealt systematically with it.

There are four species of *Solen* recognised as British, viz., *S. ensis*, L., *S. siliqua*, L., (*S. marginatus*, Pult. and Don. or *S. vagina*, L.), and *S. pellucidus*, Penn. In the latest classification, *ensis* and *siliqua* are placed in the genus *Ensis*, Schum., *pellucidus* in the genus *Cultellus*, Schum., leaving only one species, *marginatus* or *vagina*, in Linné's genus *Solen*. I purpose dealing with this question in a later paper.

It is my intention in the present paper to deal with the external characters, the musculature, and the alimentary canal of the first three species, and in a future contribution to complete the anatomy of the same, and the whole of the anatomy of *S. pellucidus*.

I desire to express my thanks to the Council of the Birmingham Natural History and Philosophical Society for the grant they have made me towards defraying the expenses in connection with this work; also to Mr. Walter E. Collinge for the kindly advice he has extended to me.

EXTERNAL CHARACTERS.

Solen ensis, L. (Pl. ii, fig. 2).

S. ensis is an elongated animal, measuring in length from six to seven times the measurement from the dorsal to the ventral surface at

^{1.} Recherches sur la circulation des Lamellibranches Marins, pp. 170, Besançon, 1890.

^{2.} Introduction à l'étude des Mollusques, 1894.

^{3.} Revue biol. du Nord de la France, 1890, T. ii, pp. 209-229, 299-311, 351, 356.

^{4.} Text book of Comparative Anatomy, 1896, pt. ii.

^{5.} Trudui St Peterb. Obshch., xxviii, pp. 213-270, 2 pls.

its widest part. It curves a little dorsally, is bilaterally symmetrical, and is enclosed ventrally by the concrescence of the edges of the mantle lobes, with the exception of the apertures at the anterior and posterior ends, and a fourth aperture situated nearly at the centre of the ventral surface.

The periostracum passes from the outside of the shell to the edges of the mantle lobes, to which it adheres.

The pallial muscles form a deep band along the margin of the mantle lobes, and at the anterior end, surround the pedal aperture, through which the foot is protruded. At the posterior end the muscles assume a more circular condition, and give rise to the siphon containing the afferent and efferent chambers.

On separating and turning back the left mantle lobe, it is seen that the foot projects from nearly the centre of the ventral surface of the animal and proceeds in an anterior direction. A little anterior to the foot is the mouth, and in the front of the mouth the broad anterior adductor muscle (Pl. ii, fig. 2, A.A.). On each side of the viscero-pedal mass are the labial palps, and commencing between and passing posterior to them, are the two pairs of gills which extend to the siphon. The anus opens into the cloacal chamber from a free portion of the rectum, behind the posterior adductor muscle.

The siphon consists of two separate chambers, the upper one the exhalent, the lower one the inhalent. The free portions of the siphonal chambers are short, and separate from each other, both are encircled with a fringe of pale tentacles, and at the distal end of each chamber are two flaps forming the valve.

The fourth aperture is an elliptical opening which narrows very much at the inside edge of the mantle lobes; around the inside of it, but near the outer edge, is a row of tentacles, those on the one side alternating with those on the opposite side. The tentacles and surface of the lobes bordering the opening are of a lighter or paler colour. On the inside of each mantle lobe is a groove passing dorsally from this aperture towards the foot, and in it lie the distal portions of the labial palps.

Solen siliqua, L. (Pl. ii, fig. 3).

This species very closely resembles S. ensis in its external characters, only it is larger, and quite straight along its dorsal surface.

Solen marginatus, Pult. and Don. (Pl. ii, fig. 4).

Externally this species exhibits many points of difference when compared with *S. ensis*. It is shorter, and, like *S. siliqua*, straight along its dorsal surface. The pallial muscles are more strongly developed, while at its anterior end in the muscular part of the mantle

lobes which encircle the pedal aperture, is a groove, in which the constricted part of the shell lies, from which character arises the name of the species. The most important feature, however, appears to be the non-existence of the fourth aperture, and of the labial grooves on the inside of the mantle lobes. The diminution in the length of the animal, when compared with *S. ensis* and *S. siliqua*, is seen to be in the portion anterior to the foot. Just in front of the mouth, the muscular portion of the ventral integument terminates abruptly, and with the lips formed by the fusion of the labial palps, projects anteriorly. The anterior adductor is not so broad as in the two preceding species. It is also observable through the transparent ventral integument, that the liver does not project anterior to the mouth. The foot is larger, and has a more massive appearance.

The siphon is much longer than in *S. ensis*, and in one piece, though it shows clearly that at one time it was two distinct siphons. Both internally and externally, the chambers exhibit a transverse and longitudinal ribbing, and the free end of each is encircled with a row of tentacles.

The periostracum passes from the outside of the shell to the mantle lobe, to which it firmly adheres, and then forms a free border, particularly so at the anterior and posterior ends.

The bases of the two inner gills are joined and enclose the cloacal chamber for the greater portion of its length, whereas in *S. ensis* and *S. siliqua*, I have found in the course of examination of a large number of specimens, they are not so connected.

MUSCULATURE.

Solen ensis, L. (Pl. ii, fig. 1 and Pl. iii, fig. 5).

i. The Pallial Muscles.—The muscles along the edge of the mantle lobe, or the muscles of the pallial edge (Pl. ii, fig. 1, Pal. M'.), form a deep and thick band. They are composed of closely arranged bundles, running in a ventral direction, at right angles to the mantle edge, and become closer as they approach the line of concrescence of the two lobes, where the thickness is further increased by another band of muscles traversing each lobe parallel to the pallial edge. The mantle lobe attains its maximum thickness just ventral to the line of its adherence to the shell. At the anterior end, the pallial muscles form a circular growth enclosing the pedal aperture (Pl. ii, fig. 1, Pal. M.), and have two lateral portions, which are free and to a considerable extent close the aperture on the withdrawal of the foot. The circular muscular arrangement is the same at the posterior end, where, how-

ever, its continuity is more complete, and it is also more developed, forming the proximal end of the siphon.

Along the whole dorsal surface of the animal is a muscular integument (Pl. ii, fig. 1, Int. D.), consisting of transversely crossed muscles; these are further crossed and intertwined with longitudinal muscles of the raised and fluted portion along the median line. The integument is joined to the pallial muscles of the anterior and posterior ends, and is also connected with the posterior adductor and retractor muscles, the dorsal portion of the foot, and the teeth of the hinge of the shell valves. Behind the posterior adductor muscle it is much more developed and is attached laterally to the valves, in consequence of which it appears as a continuation of the posterior adductor muscle.

The anterior adductor muscle (Pl. ii, fig. r, A.A.), is an extremely broad plate of muscles, extending from a position a little anterior to the mouth to the pallial muscles, bordering the pedal aperture, to which it is united.

The posterior adductor muscle (Pl. ii, fig. 1, P.A.), is also plateshaped, but is not nearly so wide as the anterior adductor. It is connected on its anterior side with the retractor pedis posterior (Pl. ii, fig. 1, P.R.P.), while on the opposite side it joins the circular muscular growth supporting the siphon. Over and connected with it, runs the dorsal muscular integument.

ii. The Pedal Muscles.—The foot is a narrow and elongated body, somewhat flattened laterally with a tendency to be keeled ventrally and grooved dorsally. In it are three kinds of muscles. The first consisting of longitudinal, the second of circular and semicircular, and the third of transverse and oblique muscles, the whole being enclosed in a muscular integument. When examined in detail, there are seen on each lateral side two groups of longitudinal muscles (Pl. ii, fig. 1, and Pl. iii, fig. 5, Lo.M.) which traverse the whole length of foot, and between each of these groups is a semicircular band, passing from the dorsal to the ventral surface (Pl. ii, fig. 5, Sem. M.). Bordering the dorsal and ventral surfaces of the pedal cavity, are two rows of bundles of transverse muscles (Pl. ii, fig. 1, and Pl. iii, fig. 5). The ends of these bundles spread out and their fibres pass between the inner longitudinal muscles, to the inner sides of the bands of semicircular muscles, while from the outer sides of these bands, muscular fibres or oblique muscles (Pl. iii, fig. 5, Ob.M.) pass in greater numbers, between the outer longitudinal muscles to the muscular integument. Towards the distal end of the foot these semicircular muscles gradually come together, first ventrally, then dorsally, and eventually form

a continuous circ

a continuous circular band. Afterwards they and the transverse muscles, which become irregular in their distribution, fray out, and the whole form a network of muscular fibres.

At the proximal and posterior end of the foot is the retractor pedis posterior muscle (Pl. ii, fig. 1, P.R.P.), which, prior to its attachment to the valves of the shell, bifurcates and forms the right and left muscles.

At the anterior end of the proximal portion of the foot are the retractor pedis anterior muscles (Pl. iii, fig. 1, P.R.A., P.R.A'.). Each of these is a long rounded muscle passing from the foot along the ventral integument, and on leaving this, the muscle bifurcates, the two portions then passing through the liver and dorsal integument to the shell. The posterior bifurcation is the shorter one and it passes directly to the valve. The anterior one is much longer, and passes in an oblique direction over part of the anterior adductor muscle to the valve. At its junction with the foot, the fibres spread out and pass directly on the inside of the longitudinal muscles to the ventral and ventrolateral surfaces.

On each side of the foot a muscular band (Pl. ii, fig. 1, P.P.) runs along the anterior ventral integument, in close proximity to the anterior retractor pedis, to the anterior adductor muscle to which it is attached, but has no connection with the shell. Possibly this represents the protractor pedis anterior, as I have been unable to trace any other muscle likely to correspond to it.

The dorsal part of the foot has also on each side, a slight muscular connection (Pl. ii, fig. 1, *P.El.*) with the muscular dorsal integument, but it has no attachment to the shell, and so far as I have been able to ascertain, this is all that remains of the muscle representing the elevator pedis.

Solen siliqua, L.

The muscular system in every way resembles that of *S. ensis*, and does not call for any special comment.

Solen marginatus, Pult. and Don. (Pl. ii, fig. 4).

In comparison with S. ensis, the muscles in this species are much more powerfully developed. The pallial muscles are wider and thicker, and at the posterior end, the circular portion carrying the siphon is considerably wider and more strongly built. The anterior adductor muscle is not nearly so broad, while the posterior adductor is normal. The free portion of the retractor pedis anterior is much shorter, the bifurcated parts lie much closer together, and the fibres crossing the foot pursue a more posterior direction, and pass underneath instead of over the longitudinal muscles, and are embedded in the muscular

integument of the foot. On the ventral integument there is only a very slight trace of the muscle connecting the foot with the anterior adductor muscle.

The arrangement of the muscles of the foot is similar to that in *S. ensis*, only they are much more powerfully developed, and passing posteriorly, spread out sooner into the muscular network, as noticed in the distal portion of the foot of *S. ensis*.

THE ALIMENTARY CANAL.

Solen ensis, L.

The fore-gut and the greater portion of the mid-gut and liver lie anterior to the viscero-pedal mass, which, in its distal portion, contains the caecum of the crystalline style, and the posterior portion of the left lobe of the liver.

The mouth (Pl. ii, fig. 2, M.) opens externally as a transverse slit of the body integument on its ventral surface. Its situation is anterior to the foot, but posterior to the anterior adductor muscle, and between the lips formed by the fusion of the labial palps. The outer palps give rise to the anterior or upper lip, and the inner ones to the posterior or lower lip. (Pl. ii, fig. 2, A.L., P.L.).

The oesophagus (Pl. ii, fig. 2, Oe.) is short, slightly curved, and soon widens into the stomach on its anterio-ventral surface.

The stomach is an irregularly shaped sac, divided into several parts, while the right lateral half differs from the left half.

For the sake of convenience, it is proposed to use the following terms for the different divisions: oesophagael—for the anterio-ventral portion, cardiac—for the portion dorsal to the oesophagael, and pyloric—for the posterior portion.

The left oesophagael portion (Pl. iii, fig. 6, Oe. St.) is somewhat muscular, with a few slight folds of its walls, and is bordered by a muscular ridge (Pl. iii, fig. 6, M.R.C.), culminating at the posterio-dorsal edge with a more muscular papilla (Pl. iii, figs. 6 and 11, M.P.). From the base of this papilla two other muscular ridges diverge, dividing the remaining portion of the side into three parts. The middle portion occupies a ventro-lateral position, adjoining the oesophagael part, and in a narrow and deep cavity. (Pl. iii, fig. 6, Cav.). At its distal end it receives the small bile duct (Pl. iii, figs. 6 and 11, Cav.). It is separated from the pyloric portion by the muscular ridge passing ventrally (Pl. iii, fig. 6, M.R.P.), whereas the ridge running in a dorsal direction (Pl. iii, fig. 6, M.R.C.) divides the cardiac from the pyloric portion. The former is a large, deep, pocket-shaped lobe lying dorsal

to the oesophagael part, and projecting anteriorly to it. The pyloric portion is not so deep, or so large, and rises at its posterior end.

The right side of the oesophagael portion is smaller than the left side, but is likewise bordered by a slight muscular ridge (Pl. iii, fig. 7, M.R.O.). The remaining portion of this side is large, but is not divided in the same manner as the left half into cardiac and pyloric portions. At the anterior lateral end, just above the cardio-oesophagael ridge, it receives the large bile duct (Pl. iii, fig. 7, B.Dt.), and, at its posterior end on its ventral side, the intestine leaves it (Pl. iii, fig. 7, In.). The posterior end of the pyloric portion of the stomach contracts to form the caecum (Pl. iii, fig. 7, C.C.) containing the crystalline style. The caecum is of considerable length extending in a posterio-ventral direction through the proximal portion of the foot.

The crystalline style (Pl. iii, fig. 7, C.S.) is a long rod of a light brown colour, traversing the whole of the caecum and the centre of the stomach, in a course tending from the left to the right side, to the anterior wall of the cardiac portion, where it generally has a hooked termination.

A transverse section of S. siliqua shows the epithelium (Pl. iii, fig. 10, Ep.C.) of the caecum to be very characteristic, and in marked contrast to that of the adjoining intestine. It consists of long regular columnar cells, with the nuclei generally situated nearer to the free end than the proximal one. The nuclei are so regularly placed that they appear to form a continuous ring around it. The cells stain deeply at the free end, and carry a dense mass of long cilia. A section through the anterior part of the caecum shows a curious growth in the end lying near the intestine, where there is a fibrous mass (Pl. iii, fig. 10, x) coming from the caecal wall; this afterwards gradually disappears.

After the intestine leaves the stomach, it proceeds to the foot where it makes a large number of closely lying convolutions (Pl. ii, fig. 2, C.In.), then describing a semi-circular course round the base of the caecum, containing the crystalline style, and between the transverse pedal muscles (Pl. ii, fig. 2, T.P.M.), it passes along the dorsal side of the caecum, on which it forms three large loops, and shortly afterwards another one, then at the posterio-dorsal part of the stomach, it turns, and as the rectum (Pl. ii, fig. 2, R) pursues a straight posterior course, passing through the pericardium, and encircled by the ventricle. (Pl. ii, fig. 2, V.) It continues over the posterior adductor muscle (Pl. ii, fig. 2, P.R.P.), and enters the cloacal cavity, where, having become free, it terminates at the bi-lobed anus. (Pl. ii, fig. 2, A.)

The folding and exact position of the folds vary somewhat in different specimens, but this is probably due to the extent of the contraction or distension of the proximal part of the foot.

When the intestine leaves the stomach, the wall on the one side is invaginated, and forms the typhlosole, which extends along the convoluted part of the intestine (Pl. ii, fig. 2, C.In.) near to where it passes the distal end of the caecum containing the crystalline style.

The typhlosole commences with a slight invagination of the wall of the intestine, this gradually increases in size and flattens out (Pl. iii, fig. 8, Ty.); at the same time, its walls become folded, and the width across the base is diminished. Towards its termination, it decreases in size and ends in the folded walls of the intestine.

The typhlosole is lined with ciliated epithelium, and the inside of it is filled with connective tissue. A transverse section of S. siliqua (Pl. iii, fig. 9, Ty.) across one of the first convolutions show the typhlosole of the one fold to be joined by connective tissue to the typhlosole of the opposite fold, without any divisional wall.

The tricuspid body, or the flêche tricuspide, in the specimens examined, occupied the posterior portion of the stomach, with branches radiating from the muscular papilla into the lobes, and undoubtedly reminds one of what Fischer 6 described as a body shaped like the screw propeller of a boat.

The digestive gland or liver (Pl. ii, fig. 2) is a large organ lying around the stomach, and covering the greater portion of it. The right lobe (Pl. iii, fig. 12, R.L.) spreads over the right and anterior sides, and projects over the anterior adductor muscle, while the left lobe (Pl. iii, fig. 12, L.L.) covers the left and ventral sides and projects posteriorly for some distance under the caecum of the crystalline style. The large bile duct, with branches ramifying the right lobe (Pl. iii, fig. 12, B.Dt.), enters the cardiac part of the stomach on the right anterio-lateral side, and the small bile duct, though of no inconsiderable size, ramifies the left lobe (Pl. iii, fig. 12, B.Dt'.), and enters the small middle cavity situated between the cardiac and pyloric portions.

Solen siliqua, L.

The alimentary canal (Pl. ii, fig. 3.) is in all its important points similar to that of S. ensis, but differs somewhat from it in detail.

The oesophagus is straighter. The stomach is similar to that in S. ensis, but the divisions are more pronounced. The cardiac portion (Pl. iii, figs. 13 and 14, C.St.) does not project so far anteriorly, nor does the posterior end of the pyloric portion rise so much dorsally. The muscular papilla is more central, and the folds of the stomach are more distinct. (Pl. iii, fig. 13).

The intestine leaves the pyloric portion more posteriorly, and is joined for some distance to the caecum of the crystalline style by connective tissue. This, however, appears to be subject, in some specimens, to some slight variation where a small portion of the liver interposes between them. The intestine after it has passed round the distal end of the caecum of the crystalline style, assumes a larger number of folds, and in some specimens it presents a very folded condition. (Pl. ii, fig. 3).

Solen marginatus, Pult. and Don.

The alimentary canal of S. marginatus (Pl. ii, fig. 4), presents many points of difference when compared with either S. ensis or S. siliqua.

The mouth (Pl. ii, fig. 4, M.) is situated some distance anterior to the stomach, and not ventrally as in the before-mentioned species. The lips formed by the labial palps are directed forwardly (Pl. ii, fig. 4, A.L., P.L.). The oesophagus is longer and proceeds posteriorly to the oesophagael portion of the stomach (Pl. iii, figs. 15 and 16). The stomach (Pl. ii, fig. 4, St.) lies in a more posterior position over the distal end of the foot, and whilst retaining the characteristic divisions as described in S. ensis, presents several striking modifications. The muscular wall (Figs. 15 and 16, M.R.O.), dividing the oesophagael from the cardiac portion, is much more developed and very muscular, and projects a considerable distance into the stomach, thus separating the anterior part of these divisions from each other. The caecum of the crystalline style, which is or greater length, leaves the pyloric portion on its ventral surface, curves and passes in an anterior direction near the ventral wall of the pedal cavity. (Pl. ii, fig. 4, C.C.).

The intestine (Fig. 4, C.In. and In.) pursues a course similar to that of S. ensis, and is for a long distance joined with connective tissue to the caecum of the crystalline style, both in going, and in returning along it, and afterwards forms only two or three small folds on the dorsal surface of the caecum, before passing into the rectum.

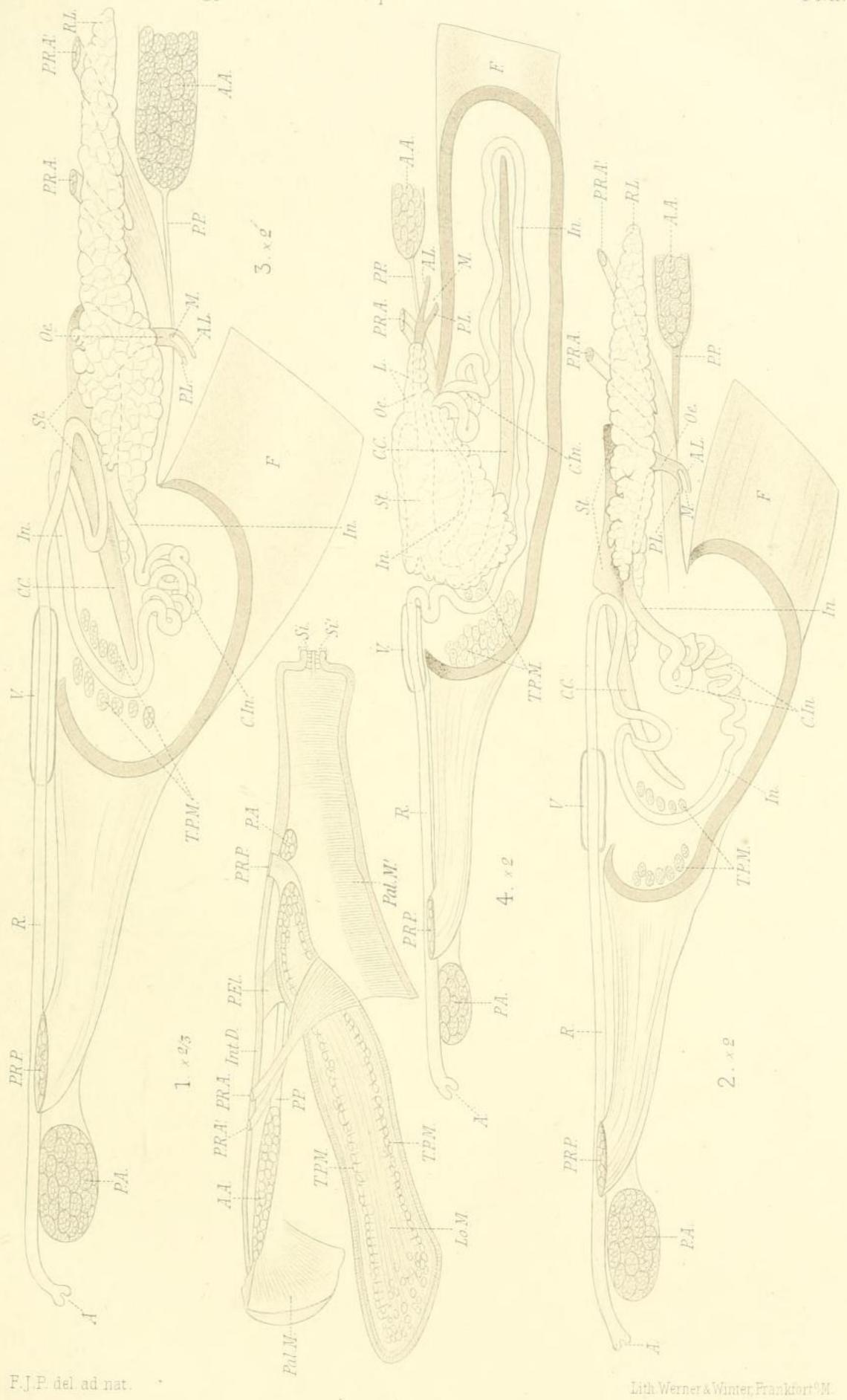
The liver surrounds the stomach and oesophagus, but a large part of it is situated ventrally to the stomach, and extending backwards, encloses a portion of the proximal parts of the intestine and caecum of the crystalline style. (Pl. ii, fig. 4).

REFERENCE LETTERS.

A.	Anus.	Ob. M.	Oblique Muscles.
A. A.	Anterior adductor muscle.		Oesophagus.
A. Ao.	Anterior aorta.	Oe. St.	Oesophagael portio
A. L.	Anterior lip.		of stomach.
	Large bile duct.	P. A.	Posterior abductor
B. Dt.	Small bile duct.		muscle.
Car.	Small cavity receiving the	P. El.	Muscle representin
	small bile duct.	1000-200	elevator pedis.
C. C.	Caecum of crystalline style.	P. L.	Posterior lip.
	Convoluted portion of intes-		Pallial muscles.
	tine.	Pal. M.	Muscles of pallia
Ce. P.	Cerebro-pedal connective.		edge enclosing pe
Ce. V.	Cerebro-visceral connective.		dal aperture.
Con. T.	Connective tissue.	P. P.	Muscle representin
C. S.	Crystalline style.		protractor pedis.
C. St.	Cardiac portion of stomach.	P. St.	Pyloric portion of
Εp.	Epithelium.		stomach.
	Ciliated epithelium.	P.R.A. P.R.A!	Bifurcated parts of
Ep. Col.	Columnar epithelium.		retractor pedis ar
F.	Foot.		terior.
	Intestine.	P. R. P.	Bifurcated parts of
	Dorsal integument.		retractor pedis pos
L.			terior.
	Left lobe of liver.		Rectum.
	Longitudinal muscles.	Sem. M.	Semicircular muscles
M.	Mouth.	Si.	Exhalent chamber of
	Muscular papilla.		siphon.
M. R. O.	Muscular ridge separating	Si.'	Inhalent chamber of
	the oesophagael from the		siphon.
	cardiac portion of the	St.	Stomach.
	stomach.	T. P. M.	Transverse pedal
M. R. C.	Muscular ridge separating the		muscles.
	cardiac from the pyloric		Typhlosole.
	portion of the stomach.		Ventricle.
M. R. P.	Muscular ridge separating the	X.	Fibrous mass of th
	small cavity receiving		caecum of th
	small bile duct, from		crystalline style.
	pyloric portion.		

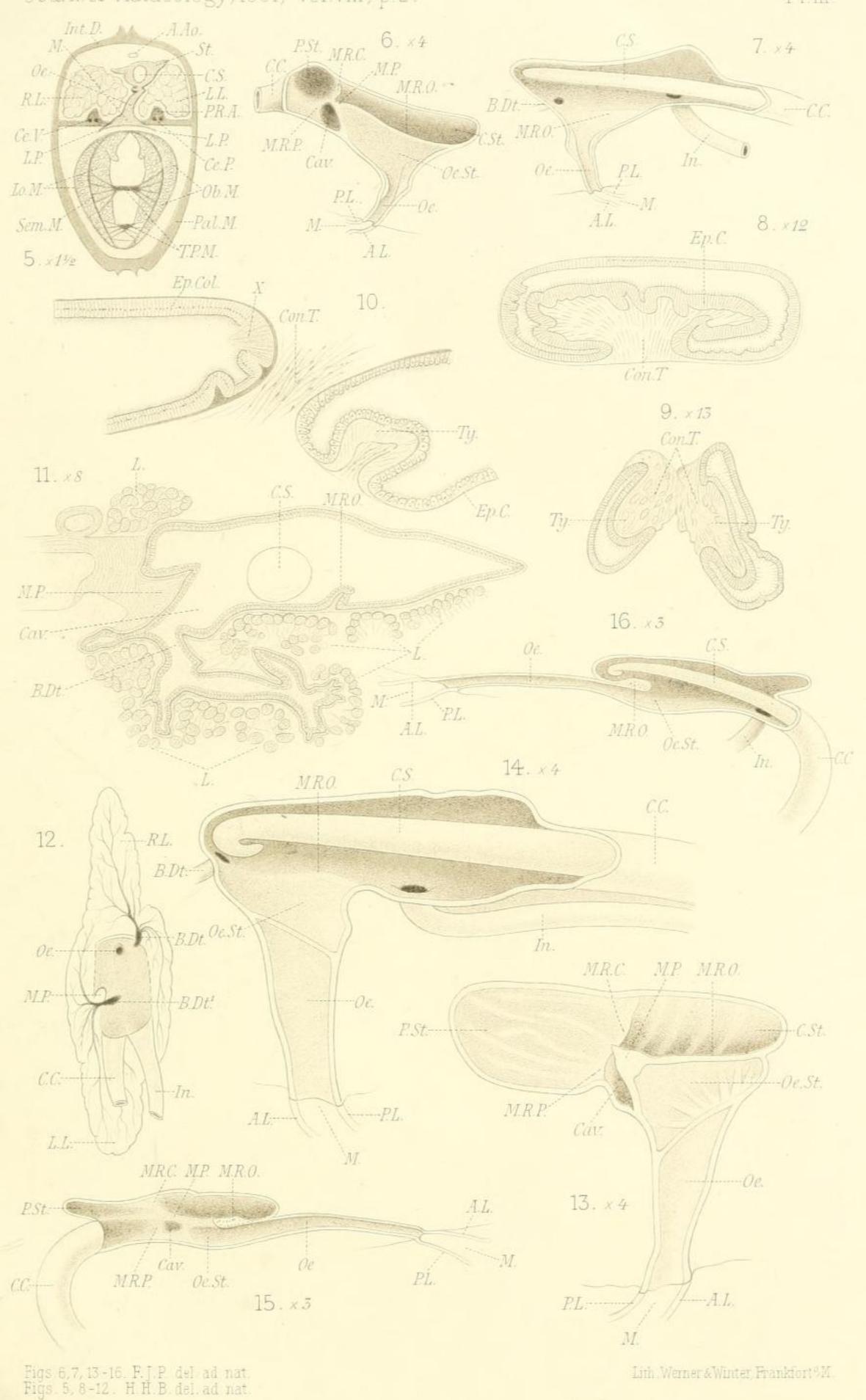
EXPLANATION OF PLATES II AND III.

Fig.	I.	Solen ensis.	Muscular system. $\times \frac{2}{3}$.
Fig.	2.	do.	View from the right side showing alimentary canal, &c. × 2.
Fig.	3.	Solen siliqua.	View from the right side showing alimentary canal,
Fig.	4.	Solen marginatus.	View from the right side showing alimentary canal, &c. × 2.
Fig.	5.	Solen ensis.	Transverse section of the animal showing the liver, stomach, oesophagus, musculature of the foot, &c. × 1½.
Fig.	6.	do.	Longitudinal section of the stomach, showing the internal structure of the left side. ×4.
Fig.	7.	do.	Longitudinal section of the stomach, showing the internal structure of the right side. ×4.
Fig.	8.	Solen siliqua.	Transverse section through intestine, showing the posterior portion of the typhlosole. × 12.
Fig.	9.	do.	Transverse section through a convolution of the intestine showing the fold of the typhlosole. × 13.
Fig.	10.	do.	Transverse section through the anterior portion of the caecum of the crystalline style and intestine, showing the columnar epithelial lining of the former, and the ciliated epithelial lining of the latter. × 45.
Fig.	II.	do.	Transverse section of the stomach passing through the muscular papilla and small bile-duct. × 8.
Fig.	12.	Solen ensis.	Semi-diagrammatic view of the ventral portion of stomach, showing bile-ducts and their ramifica- tions in the lobes of the liver.
Fig.	13.	Solen siliqua.	Longitudinal section of the stomach showing the internal structure of the left side. × 4.
Fig.	14.	do.	Longitudinal section of the stomach showing the internal structure of the right side. × 4.
Fig.	15.	Solen marginatus.	Longitudinal section of the stomach showing the internal structure of the left side. × 3.
Fig.	16.	do.	Longitudinal section of the stomach showing the internal structure of the right side. $\times 3$.



ANATOMY OF SOLEN.





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