Notes on some specimens of the genus Atopos (Mollusca Pulmonata) with microphotographs illustrating points in the anatomy of the genus

By F. F. LAIDLAW

PLATES XXX–XXXIII

This account is based on specimens sent me from the Raffles Museum, Singapore, and on a fine example of *maximus* Collinge lent me by Mr. Forster-Cooper, then Curator of the University Museum of Zoology at Cambridge.

Material.—Two individuals "from limestone hill, near Baling, Kedah". These are similar to the form described as *sarasini* Collinge 1902.

The larger specimen is 70 mm. in length, the smaller 50 mm. Sections were cut from the smaller specimen. Sent from the Raffles Museum.

One specimen from the Cameron Highlands, Pahang. 40 mm. in length. Not unlike the above, but grey-black, rather than blue, and with the foot-sole pigmented, of the same colour as the rest of the body, but rather paler. Sent from the Raffles Museum.

One specimen from Gunong Pulai, Johore. Length 50 mm., greatest height 8 mm. breadth 6 mm. Very like the type of *laidlawi* Collinge 1902 but without a dark, dorsal band. Sent from the Raffles Museum.

One specimen from Bukit Besar in Jalor. Coll. N. Annandale. This is an example of *maximus* Collinge 1903*a*. From the University Museum of Zoology, Cambridge.

I wish to give my best thanks to the Director of the Raffles Museum and to Mr. Forster-Cooper for allowing me to examine these very interesting creatures.

I have to thank Col. Peile for notes on the radula of one of the specimens, which he was good enough to mount for me, and for photographs and figures of the same.

I am also indebted to Mr. J. T. Wadsworth of the Zoological Dept. of the University of Manchester for sections. These were cut serially, in a plane transverse to the long axis of the body, from a specimen embedded in collodion, and are 90 μ thick.

Unfortunately the front end of the specimen is strongly ventriflexed, as is so often the case in preserved specimens, so

that the plane of the sections varies towards the front of the body, making any reconstruction very difficult. In addition the radula is partly protruded.

The sections were stained with borax-carmine.

I have retained the generic name *Atopos* as a matter of convenience; to judge from Rathouis' account and figures there is little of generic value to distinguish Heude's *Rathouisia leonina* from species of *Atopos*.

The family name must stand as *Rathouisiidae*, as *Rathouisia* was the first genus to be distinguished (Heude 1884).

Its distribution is interesting. Species have been recorded from South China, Burma, Siam, Malaya, and all through the Sunda Archipelago to New Guinea and N. Australia. No representative has been recorded from any other Zoogeographical Region.

Certain sub-genera (or genera) have been defined for species of the genus.

These are:—

Prisma Simroth 1891.
Padangia Babor 1900. (=*Podangia* Ghosh 1913).
Parapodangia Ghosh 1915.

I agree with Hoffmann in thinking that the single genus *Atopos* (or *Rathouisia*?) may include all the known forms.

Hoffmann has also put down a number of the described species as synonyms. I cannot give an opinion of any value on this matter.

The present paper records specimens of *Atopos* from Pahang, Johore and Kedah for the first time.

From Kedah and Jalor I am able to record *sarasini* Collinge. Hoffmann regards *harmeri* Collinge as synonymous, and further looks on both as identical with *tourannensis* (Soul.) from Cochin-China. The small specimen from the Cameron Highlands (Pahang) whilst showing some differences, is in general very similar.

Collinge's species *laidlawi* is known from Jalor and Johore and is looked on by Hoffmann as the same species as *pulverulentus* (Benson) and *sanguinolentus* (Stol. MS.) Ghosh. both from Penang. Here too *fide* Hoffmann is to be referred *strubelli* Collinge (nec Simroth), from Jalor.

Both *maximus* Collinge and *rugosus* Collinge are admitted by Hoffmann; both are from Jalor.

Lastly *punctatus* Collinge from Jalor is said to be a synonym for *cristagalli* Saras. from Celebes.

There are therefore some five distinct forms of this genus in Malaya, possibly more, and it is evident that they are widely if sparingly distributed. A knowledge of their habits may show that they are not so rare after all.

Rathouis (1884) has given a graphic account of the habits of the species discovered by him in the Yang-tze valley and named *leonina* by Heude (1884). He found that it hid itself when the weather was dry or cold, but did not choose very damp situations; it was found most abundantly in crannies of old brick walls. "It preys on other molluscs, for choice a *Succinea*. It worries "its victim until it induces it to withdraw into its shell, where-"upon it proceeds first to suck away any mucus secreted by it, "and then to absorb little by little the tissues of its victim through "its proboscis, the whole process taking from 20 minutes up to "two hours or even longer, according to the size of the animal "attacked".

Rathouis writes that he has found the entire body of a snail so devoured in the stomach of *Rathouisia*. Such a meal is sufficient for two or three days. He has detected the radula and jaws of the prey in the fæcal bolus of the slug, along with small living nematodes.

He describes also the mating of *leonina*. This takes place at the end of April or early in May. For some time before pairing less food is taken. (This observation bears on the condition of the specimen of *maximus* that I have examined, where the great enlargement of the albumin gland has compressed the liver and almost obliterated the cavity of the stomach).

Whilst mating the two individuals take a position almost foot to foot, ("un peu rétournes et presque pied a pied. Il ne parait rien en dehors; les pénis seuls sortent pour pénétrer directement dans les vagins).

Pairing begins early in the morning and lasts most of the day. The eggs are laid about a month later, usually in one or two "paquets". The young slugs emerge from the eggs after some three weeks; they feed first on "albumine sécrétée par les microphytes" and on mucus from the tracks of other molluscs.

Rathouis states that so far as possible he observed the slugs in their natural surroundings, but that he had further reared and fed slugs in glass cages.

Similar study of the methods of obtaining a livelihood employed by Malayan species would be sure to be full of interest.

The big foot-sole of *Atopos* (and of *Rathouisia* suggests that the the animal is an active crawler. Most preserved specimens show some degree of ventriflexion, I have not seen any that have lateral flexion. Perhaps the power of lateral bending is not much developed in the living animal.

The colouring and texture of the body have been compared to that of *Peripatus* (Annandale, in Collinge 1903) with justice, and the shading off of the colour on the edge of the notal flap

as for example in *maximus* may give some resemblance to the legs of *Peripatus* especially when the animal is moving.

Annandale (loc. cit.) has noted that the Malays call these slugs by the same name as they use for *Peripatus,* and regard them as very poisonous. (See also Gimlette: Malay Poisons and Charm Cures).

Two specimens of Atopos were recovered from the stomach of the snake *Boiga dendrophila* (Boie) by Annandale.

The Rathouisiidæ may be reckoned as one of the groups of very primitive creatures that have survived in Malaya and neighbouring lands. With the Onchidiidæ and Veronicellidæ they form a distinct group remote from all other Pulmonata. In certain important respects they are more primitive than the two families associated with them. The position of the opening of the cloaca, and the presence of paired head glands (Simroth glands) give the Rathouisiidæ a right to stand apart from the others, whilst the proboscis and lack of jaw are specializations in accordance with the carnivorous habits of the animals.

(The curious white head and tail of *laidlawi* may serve to break the outline of the body, and give it some resemblance to a bit of stick or some other jungle debris).

External characters.—The body is long, pointed at both ends, and triangular in cross-section. The apex of the triangle is made by a keel which runs the whole length of the dorsum, the base by the foot-sole. The sides are formed by the 'notum' which slopes down on either side from the keel. The foot is separated from the notum by a deep groove on either side, the free edges of the notum making a flap which hides the foot when the animal is crawling in a natural position.

The foot is wrinkled transversely and extends for the whole length of the body, except for a small pyramidal space at the front, into which the head can be withdrawn.

The head itself is small, the tentacles non-retractile. The upper pair are finger shaped, each carries a well-developed eye (pl. xxxiii, 2). The lower pair are bilobed, flattened laterally, lie somewhat obliquely, and are well supplied with sensory organs.

Integument.—The skin covering the notum is thick and leathery, richly pigmented, and free from adherent mucus. It is granular in texture, with a large number of small tubercle-like processes dotted about irregularly. In some species these are coloured differently to the general body-surface. Thus in *maximus* the colour is gray as a whole, the tubercles are sooty black. In section these tubercles stand out well from the surface. The sections are too thick to allow of detailed study of their structure.

The deeper part of the skin is much vacuolated, and under the dorsal keel the vacuoles are enlarged and form a definite areolar tube, co-extensive with the keel itself.

Below this vacuolated layer lies the muscle layer of the body-wall. The innermost fibres of this are mainly circular, the outer fibres are radial and longitudinal.

Ventrally this muscle layer coalesces with the musculature of the foot, forming a long tube narrowing at each end, and entirely enclosing the internal organs of the body, except in front where it gives place to the structures forming the head.

This tube is pierced by the rectum, the pneumopore and nephropore, all on the right side of the body, at about the end of the first fifth of the body-length. These all open close together into the top of the groove separating the notal flap from the foot; and at a slightly lower level, and separated from them by a ridge the female gonopore also opens.

The penile opening is on the right side of the head, whilst the right and left Simroth glands (when the latter is present) open into the pyramidal space just at the base of the lower pair of tentacles.

In addition the pedal gland opens in the middle line on the very front of the sole. (In the specimen from the Cameron Highlands the front end of this gland is actually everted; whether this can occur in a living specimen I do not know).

A number of bilaterally symmetrical, vascular sinuses run in the musculature of the foot and body-wall.

On the floor of the body cavity several strands of muscle diverge backwards from a muscular 'knot' which lies below the level of the retracted radula-sac. These strands unite with the musculature of the foot. Ghosh (1913) suggests that they are the homologue of the columellar muscle of other molluscs.

Alimentary canal.—The mouth is without jaws. The pharynx is continued back into an eversible radula-sac, and the whole of this part of the canal has when retracted the appearance of a narrow amphora with one handle, represented by the gullet. The base of the amphora is attached to a slender cord, perhaps a protractor muscle. This runs forward below the sac and is attached to the ventral body wall in front of the circum-œsophageal nerve ring. Along this cord pass the connectives of the buccal ganglion.

Many spirit specimens show the radula-sac or proboscis at least partly protruded. It is a small cylindrical tube, projecting from the mouth, about 5–7 mm. in length.

The pharynx is very muscular; bundles of longitudinal fibres can be seen almost completely surrounding it. These no doubt assist in the sucking process described by Rathouis. The radula-sac is separated from it by a narrow neck, on it I have not found any longitudinal muscles.

(Note by Col. Peile)

"The radula figured, from one of the Kedah specimens of "'*sarasini*' measures 6.5 × 1 mm. when flattened out. It has "about 50 V-shaped rows of formed teeth with formula 21-1-21. "The outer lines in the front rows are missing owing to use, "the radula is therefore rounded in front. The central and "outermost marginal are vestigial and absent in some rows. The "rest of the teeth are aculeate, subequal in lines 1 to 10 and the "area of attachment to the basal membrane is about the length "of the tooth. In the outer lines the teeth diminish in size while "the area of attachment gets smaller in proportion to the length "of the tooth. The outline of the junction with the base, as seen "through the transparency of the tooth is evidently what is "referred to by Ghosh (1913), as 'cuplike process' or 'crescentic "notch.' "

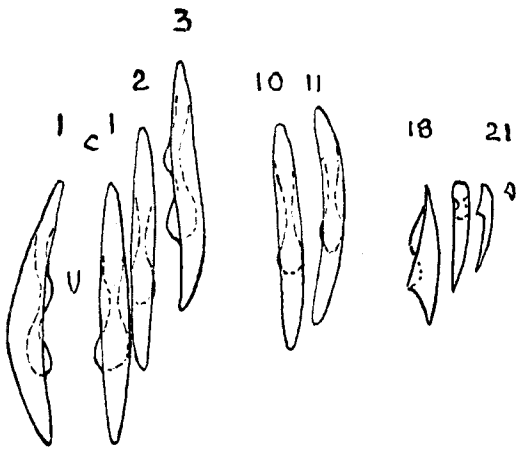

Fig. 1. *Atopos sarasini.* Drawing of individual teeth from radula figured on pl. xxxiii, 1.

The gullet starts from the dorsal side of the pharynx at the point where this passes back into the radula-sac. Because of the presence of this sac the gullet cannot run directly down to the nerve ring, but passes (when the sac is fully retracted) first to one side, then forward, and then turning down it hooks back through the nerve ring, and is continued back towards the hind end of the body, lying a little to the right of the middle line. It is very slender and has thin walls, its free part in front of the nerve ring no doubt allows it freedom of movement for the protrusion of the radula-sac. As it passes back it lies below the salivary glands and the pedal gland. When it reaches the

liver it passes for some distance under that organ, then turning up it finally opens into an irregular chamber in the substance of the liver itself.

The large liver generally fills up the hinder half of the body cavity, and conforms in shape to it. Its outer wall is smooth, and the whole organ has a characteristic yellow colour. It has a large central cavity into which opens a large number of crypts. These openings give the central cavity a certain resemblance to the '*reticulum*' of a ruminant. The central cavity and the crypts are lined with columnar epithelium which has a granular protoplasm the nuclei being indistinct, and the protoplasm rather vacuolated at the base. The epithelium rests on a basal membrane.

The liver cavity is continuous with that into which the gullet opens. This latter space, the mid-gut, can be distinguished in section by the character of the epithelium lining it. This is columnar, with hyaline protoplasm and very well-stained nuclei.

At about the level at which the gullet passes into the mid-gut the rectum opens from the latter. It lies first on the left side of the liver, then after running back a short distance turns upwards and crosses over the dorsal surface of the liver, embedded in it to some extent, and finally on the right side of it becomes a narrow, free tube which runs to the body-wall on the right side, ending by opening into the cloaca.

During its course in the substance of the liver the rectum has a wide lumen, and it is in this part of the alimentary canal alone that I have seen any trace of food material. The nature of this cannot be determined from the sections.

The lining epithelium of the rectum is similar to that of the mid-gut except for the last part of its course where its walls become muscular and the lining epithelium flattened.

Pallial complex.—This lies dorsally, close under the body-wall at about the end of the first quarter of the body length. As a whole it is circular in outline, and conforms to the curvature of the body-wall lying over it so that in transverse section it shows as an arch, lying above the anterior end of the liver, between that organ and the liver itself. (pl. xxxii).

The kidney is the largest single organ in the complex. Seen from above it is almost semilunar in shape, the two horns projecting forward, so as to enfold the pericardium in the middle line, whilst the right horn is encroached on by the lung. Its structure is that of a spongy reticulum, the cells bounding the numerous spaces of the network contain numbers of minute, refringent granules, which give the organ a characteristic appearance in sections. These cells are rather flattened, and lie on a basal membrane. The ureter rises at the hinder part of

the right side of the kidney and runs forward and downward, against the inner surface of the lung, to open close to the end of the rectum in common with the latter, by the cloaca.

The lung lies on the right side of the complex, and does not extend so far back as the kidney. Its walls are folded to some extent but there is no dense reticulum such as occurs in the kidney and the flattened cells lining the walls are entirely devoid of refringent granules. A little way back from the lung opening there is a marked thickening of the lower part of the wall of the lung on its outer side. This thickened part is folded so as to make a sort of pocket which extends back to the hind end of the lung. No nerve has been traced to it, and its function is unknown. The lung opening (pneumopore) lies just behind that of the cloaca, and immediately above that of the vagina (pl. xxx).

The pericardium lies immediately below the dorsal sinus, in front of the concave anterior margin of the kidney and is partly enfolded by it. The reno-pericardial canal opens into the pericardium from behind almost in the middle line. The auricle lies to the left of the space, the ventricle to the right. This latter is directed to the right and forward. From its anterior, outer end the short aorta continues in the same line for a short distance, and then divides into anterior and posterior branches. The former runs towards the front end of the body, close along the œsophagus, as far as the nerve ring; the latter passes back into the liver running for some distance below it and giving off branches to the hermaphrodite gland.

The appearance of the cavity of the ventricle has been figured by Ghosh (1913). Our sections show a very similar condition. (pl. xxxi).

Reproductive organs.—The account below is of the large specimen of *maximus* from Bukit Besar, Jalor. This individual was fully mature sexually. The example figured by Collinge was not so mature, but on the whole his account agrees with what we found in the riper specimen. The hermaphrodite gland has been pushed to the extreme hind end of the body-cavity. It consists of a number of closely packed follicles which are very friable. The hermaphrodite duct runs from it as a convoluted tube into a mass of tissue which consists of a mucilaginous core, surrounded by a cortex of orange coloured material. The whole swelled up so much when the specimen was put in water for dissection that it is quite impossible to distinguish any structure in it. The cortex has the consistency of a Dutch cheese and a similar colour. Presumably the genital duct runs as a convoluted tube through this structure which is called by Collinge the albumen gland. In our specimen the gland has a length of about 40 mm. At its front end, and pressed closely against it is a smaller body, measuring about 10 mm. of a pale yellow colour and of a firmer

character which is probably a prostatic gland. The oviduct and vas deferens leave the mucilaginous gland, which passes forward a short distance below the 'prostate' at the anterior end of the former.

The oviduct is a short stout tube, which runs forward and outward to the right to pass into the body-wall, through this of course it opens immediately by the female gonopore. Just as it passes into the wall it receives the opening of the receptaculum seminis, a short, stout tube which is rather club-shaped, and nearly as long as the free oviduct.

The vas runs into the body-wall close in front of the oviduct, and runs forward in the wall, along the right side of the foot, just beneath the epidermis. Simroth (1891), has figured a section of the foot showing its position. It travels forward as far as the pyramidal space and then re-enters the body cavity.

Its position is indicated in the photograph of the section figured (pl. xxx) though it does not actually lie in that section. On passing again into the body it runs as a fine convoluted duct along the penis, passing into its upper end. It is a muscular organ, about 12 mm. long in our specimen of *maximus*, enclosed in a sheath, to which it is attached at its upper end. The inner wall of the sheath, which permits the protrusion of the penis, is slightly folded into a number of longitudinal plicae, the upper end is fastened to a retractor muscle, which passes back into the musculature of the body-wall.

Rathouis did not interpret his dissection of the genital apparatus correctly. He took the R. Simroth gland to be the testis and seminal vesicle, and the vas where it is attached to the penis he labelled the flagellum. Later writers too found the interpretation of these structures difficult, though they were clearly described and figured by Simroth (1891).

(*Note.*—In this individual the hinder part of the liver was flattened and displaced by the great development of the hermaphrodite duct and associated structures. In fact the hinder half of the liver was reduced to a thin sheet of pigmented tissue, lying above the duct. Nothing like this was found in other specimens, nor anything comparable in figures given by other authors. In contrast the whole of these structures, the hermaphrodite gland its duct and prostate, in the specimen from which sections were cut have a total length of about 6 mm. The specimen is of course sexually immature).

Simroth glands.—These are either present as a fully developed pair, or the left is entirely absent.

The glands are paired in *maximus*, in the specimen of *sarasini* from which the sections were prepared, and in *australis*. Collinge found them unpaired (*i.e.* Right gland present only) in his specimen of *sarasini*, Ghosh notes that they are

unpaired in *gravelyi, kempi,* and *aborensis.* I found the gland unpaired in the specimen from the Cameron Highlands.

The gland consists of a coiled secretory part, a narrow rather convoluted tube with a layer of cubical epithelium; this is followed by a long, convoluted conducting part, slender and thread-like; lastly there is the ejaculatory part, a small spindle-shaped structure, with muscular walls.

The right Simroth gland must be homologized with the dart-sac of other land-molluscs. The fact that these glands are paired, in some species at least, suggests that primitively this organ was not connected with the reproductive apparatus, this latter being essentially unpaired in the Pulmonata.

Central nervous system.—The ganglia are concentrated and connected by stout short commissures leaving only a very narrow ring for the passage of the gullet and salivary ducts.

The plane of the circumœsophageal ring is oblique, so that the cerebral ganglia lie in front of the subœsophageal ganglia but almost on the same horizontal level. The buccal commisures on the other hand are long and slender, and run along the lower surface of the radular sac to the small buccal ganglia. From the cerebral ganglia also run large nerve trunks to the labial palps, tentacles, and muscles. The other ganglia are so closely connected that it is difficult to distinguish them externally. Odhner's account (1917) may be quoted. "The posterior half of the nervous ring is occupied by the parietal ganglia, which send nerves to the penis, and the musculature of the body sides. A very inconspicuous pleural ganglion exists between (each of) them and the cerebral centre. At the hindermost side of the ring, between the parietal ganglia, a very indistinct visceral centre is recognized by the visceral nerve that emanates here near the right parietal ganglion, and follows the intestine backwards, till it ramifies in the hermaphrodite gland and the liver.

The whole underside of the posterior portion of the nerve centre is occupied by the elongated pedal ganglia. From their anterior end they send nerves to the pedal gland, and from the posterior end of each a very strong nerve cord stretches back innervating the foot and hyponotum.

Sense organs.—The eyes are well developed as might be expected in a predatory form (pl. xxxiii, 2). The lower pair of tentacles, or palps, are richly supplied with nerves, and the appearance in section suggests that they are sensory. The central part of either palp is traversed by nerve tissue, which as it approaches the margin of the palp radiates fan-wise, each branch running into a paired column of small, darkly-staining cells, the columns lie at right angles to the margin of the palp, and in every case are in pairs, each pair uniting at its base, where it is

entered by the nerve, and each pair having a slight enlargement near the base. The whole series may be likened to a series of tuning forks, lying side by side.

Rathouis (1884) figures otocysts from the species *leonina*. Odhner (1917) did not observe any such structures in *australis* Heyneman. Owing to the thickness of my sections, and to the curvature of the head end of the animal I cannot be sure of their presence.

Some of the more important references to the genus *Atopos*.

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1892: Simroth: Nachr.-bl. d. Deutsch. Malak. Ges., (following last).
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1915: Watson: Ann: Natal Mus., III, p. 252.
1917: Odhner: K. Svensk-Vet. Ak. Handl. LII, pp. i-ii5, Pl.
1918: Bellinger: Rev. Suisse Zool. XXVI, pp. 309–340.
1920: Simroth: Abh. Senckb. Ges. XXXVII, p. 278.
1925: Hoffmann: Vidensk. Medd. fra Dansk Naturh. Foren., LXXIX.

(Dr. Th. Mortensen's Pacific Expedition 1914–16).

Explanation of lettering in plates XXX, XXXI and XXXII.

Ar.	Artery.
Cl.	Cloaca.
D.S.	Dorsal sinus.
G.	Genital glands.
H.	Liver.
L.	Lung.
Musc.	Muscles.
Nep.	Kidney.
N.F.	Notal flap.

Oe.	Oesophagus.
Ov.	Oviduct.
P.	Pericardium.
Ped.	Pedal gland.
Pn.	Lung opening.
P.C.	Reno-pericardial canal.
R.	Rectum.
Sal.	Salivary gland.
V.	Vagina.
Vasc.	Vascular sinus.
Ven.	Ventricle.
X.	Thickened wall of lung.
Z.	Position of vas deferens in its course in the body-wall.

Explanation of Plates

Atopos sarasini Collinge

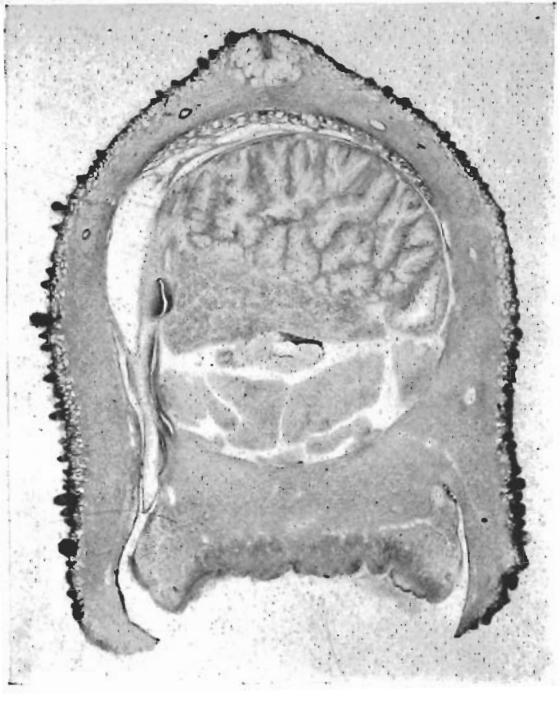
Plate XXX. Microphotograph of section through the body at level of the opening of the pneumopore and vagina.

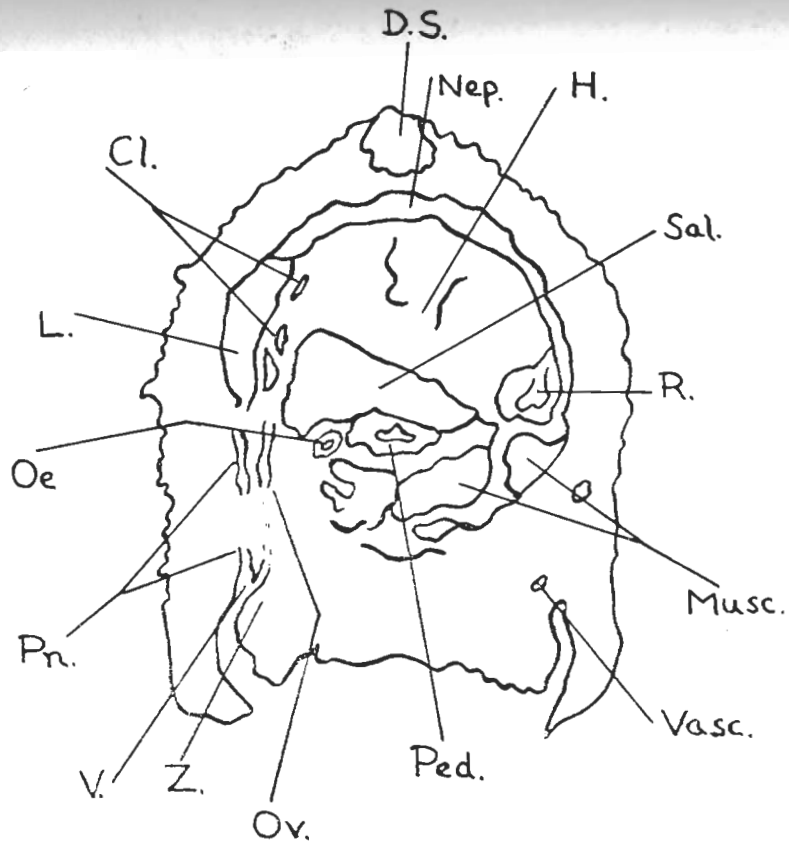
Plate XXXI. Microphotograph of section through the heart and pericardium.

Plate XXXII. Microphotograph of section shortly behind the pericardium.

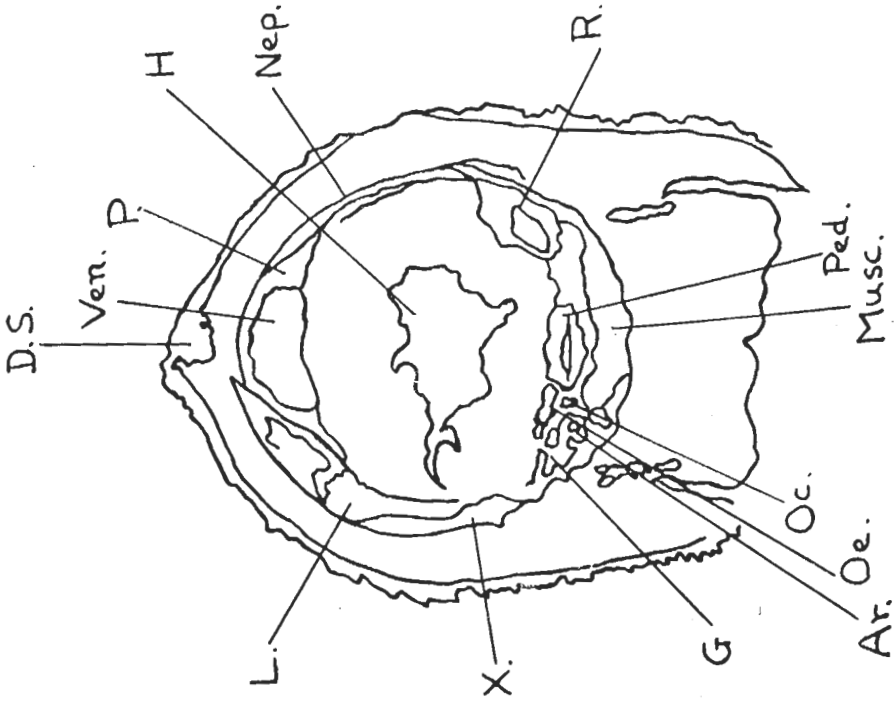
Plate XXXIII. 1. Microphotograph of radula, from preparation by Col. Peile. (Specimen from Kedah).

2. Microphotograph through the anterior tentacle, shewing the structure of the eye.





Atopos sarasini Collinge.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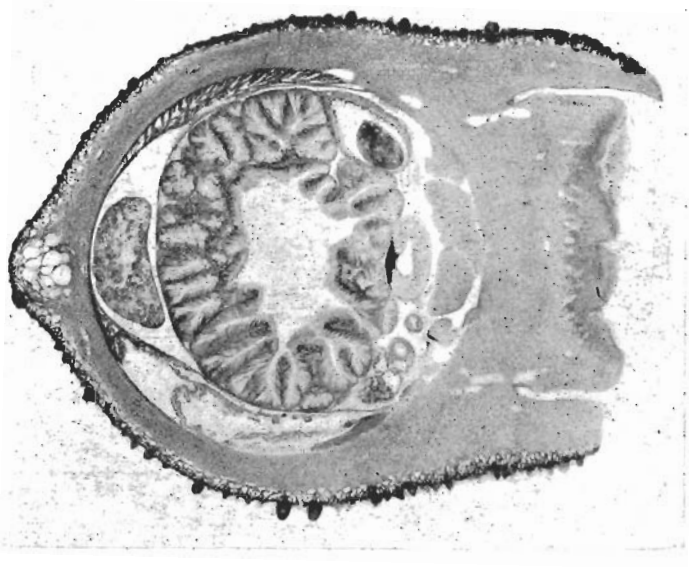
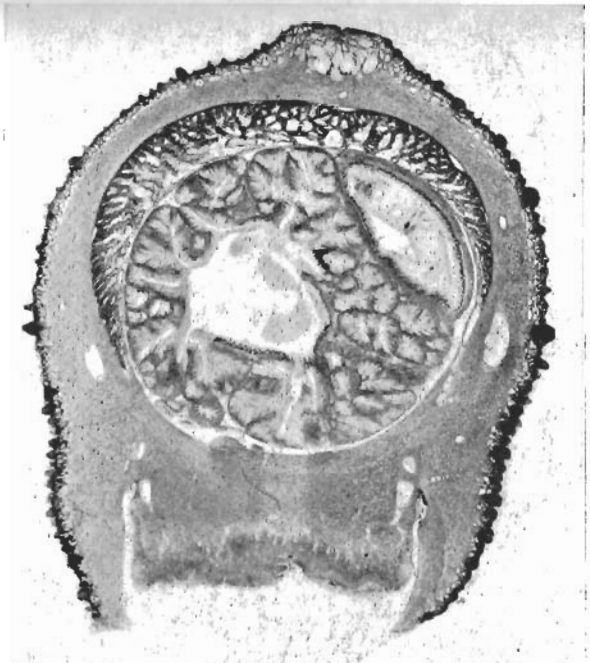
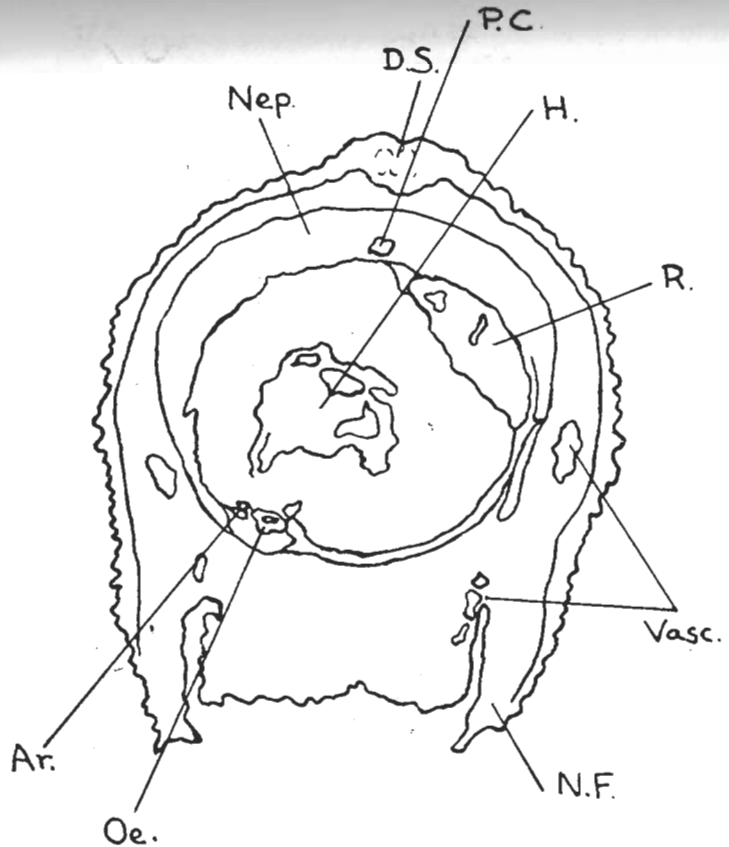
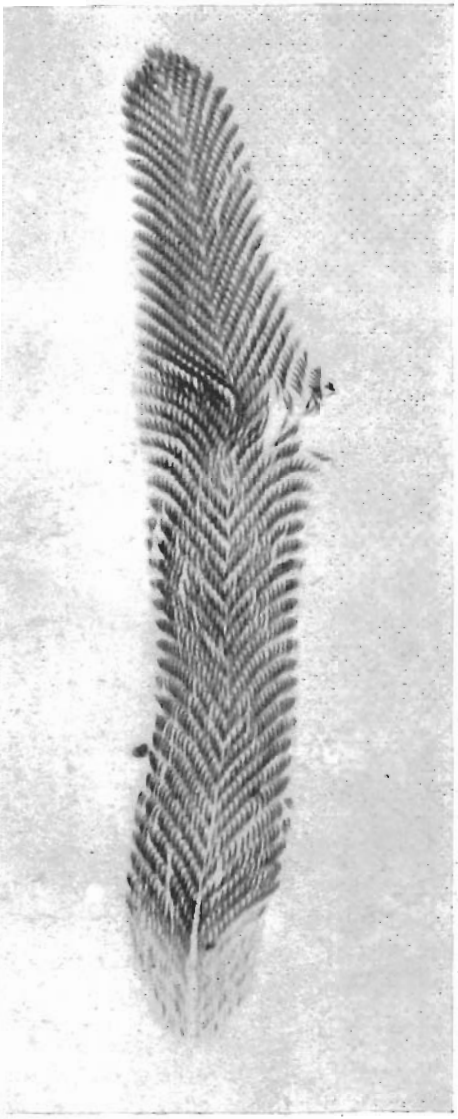






Atopos sarasini Collinge.



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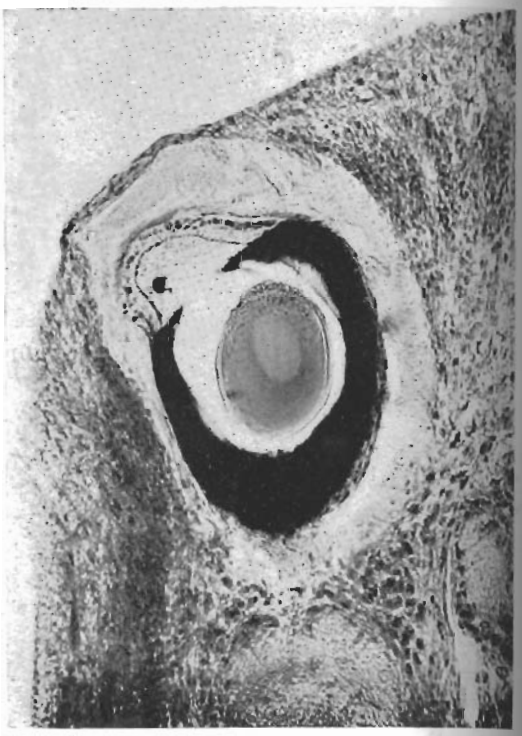

2

Atopos sarasini Collinge.