

Notes on Common Species of Trochus.

By

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With Plate 28.

WHILE the present work was in progress a paper on Trochus was published by Randles (10), and stated several results to which our study had also led us. In view of these published results, the present paper has been shortened as far as possible, and includes only some supplementary observations on special points not particularly studied by Randles.

Our observations, in the main, confirm those he has described. We find, for example, the pericardial communications of the kidneys just as he has stated, and are thus led to the belief that the Rhipidoglossa possess, typically, a pericardial canal for each kidney, the gonad communicating with the pericardial canal of the right kidney.

Randles rightly refers to the unsatisfactoriness of Pilsbry's subdivision of the old genus Trochus or the family Trochidæ from the anatomical point of view, and we have found the two commonest species of Trochus of interest in this connection. In Pilsbry's work *Trochus lineatus*, Da Costa, often, and perhaps better, styled *T. crassus*, Montagu, becomes *Monodonta crassa*, Montagu, and belongs to the group of the Trochininæ. In discussion we shall use for it the name *T. crassus*, Montagu. Pilsbry makes *T. umbilicaris*,

Montagu, into *Gibbula obliquata*, Gmelin, belonging to the group of the *Gibbulinæ*. For the purposes of this paper we call it *T. obliquatus*, Gmelin. The fault of the Pilsbry system is that it is based too exclusively on conchological differences, too little being known about detailed structure to make an anatomical survey possible. In the definition of the group *Trochininæ*, however, we find that members of this group do not possess jaws, and, as those structures are present in *T. crassus*, Montagu, just as in *T. obliquatus*, Gmelin, the unsatisfactoriness of the system is further demonstrated. These jaws also show very interesting adaptations in their structure and relations.

They are paired chitinous plates formed in the same way as those of *Haliotis* (3). Here, as in *Haliotis*, the anterior and downward-pointing ends of the jaw-plates do not lie against the actual gut wall, but against mouthward-outgrowths of the latter, so that the anterior edges of the plates are to some extent free (fig. 1). The jaw-plates in these species are much smaller and thinner than those of *Haliotis* and the *Docoglossa*. In *T. crassus*, Mont., they are merely a pair of dorso-lateral plates on projections of the wall of the buccal cavity, continuous with one another across the median line. The tissue beneath them, instead of being primarily muscular, as in *Haliotis*, has a structure (fig. 2) rather like that of the superficial parts of the odontophore cartilages. It shows muscle-fibres running in small strands through what is practically a mass of "cartilage" of loose texture. The contrasts in structure point to functional differences between the jaws of *Trochus*, and those of *Haliotis* and other *Rhipidoglossa*. In *Haliotis* the jaws are distinctly lateral, and their strong brush-like free edges help actively in the work of bringing food fragments into the mouth. In *Patella* the two jaws are connected dorsally, and the edges form a strong arch which leaves space enough beneath for the protrusion of the unusually broad and solid odontophore cushion; the dorsal part of the jaws is fairly flexible, and the lateral edges are thus able to help in cutting food when the animal is browsing on a

seaweed. The jaws in the species of *Trochus* mentioned are not strong enough to be useful in these directions. They probably protect and give firmness to the upper lip, leaving the work of drawing in food particles to the odontophore and the lip papillæ.

Randles states that there is close agreement in anatomical characters between the various species of *Trochus* studied by him, and this agreement is very marked in the two species already named. Still, there remain differences between *T. crassus*, Mont., and *T. obliquatus*, Gmel., which it seems possible to correlate with the differences in their habits. This must not be taken to imply, however, any belief that the two species are specially related to one another, we have no evidence at present on this point.

T. obliquatus, Gmel., occurs in abundance where there is a reasonable amount of plant life and adherent growth on rocks washed by the tide, and it frequents both the upper and the under sides of boulders, often retiring beneath when it is exposed to strong tide wash, or to heat, strong light, or possibilities of drought when the tide is away. It crawls over and browses on a great variety of Algæ, but has hitherto been classed too exclusively as a vegetable feeder. It is almost omnivorous, and in early summer may often be found attacking the egg-fringes and chains of Nudibranchs and other forms. Remains of eggs and other animal matter are frequently seen in sections of the gut.

T. crassus, Mont., is found, to some extent, with the previous species, but it lives, for the most part, nearer high-tide level, so much so that specimens may remain for a considerable time in corners washed only by high spring-tides. It crawls over the rocks chiefly above half-tide level, but is more lethargic than *T. obliquatus*, and less inclined to browse on the larger Algæ. During stormy periods, especially in winter, numbers may be found huddled in sheltered nooks, often with a number of *Littorina littorea* as companions.

As is well known, the spire of *T. obliquatus* is typically much lower than that of *T. crassus*, and this is probably

correlated with the greater activity of the former in the shore-zone where a high spire would give too much purchase to a side blow from a wave.

BRANCHIAL CAVITY.

(a) Mucus Gland.—The mucus gland of *T. obliquatus* is developed on the right side of the rectum in ridges and furrows running towards the anus (fig. 5). This tissue is evidently the equivalent of the mucus gland of the right side in *Haliotis* and *Pleurotomaria*, and its disposition reveals its primary function of coating rough excreted fragments (expelled from the right kidney or the anus) with slime, so that they may be less likely to injure the gill-leaflets and other delicate organs before being washed away. There is also a special aggregation of this tissue around the aperture of the right kidney (fig. 5). The mucus gland of the left side is not nearly so well developed in *Trochus obliquatus* as in the more primitive *Rhipidoglossa*. It forms ridges which coat the transverse pallial vein just in front of the external aperture of the left kidney, and stretches forward along the rectum to some extent; it is developed also along the afferent axis of the ctenidium, where this axis unites with the roof of the branchial cavity, and especially at the front end of the uniting fold. This indicates that its special function is to protect the main blood channels of this region and the gill leaflets hanging in the branchial cavity from the damage due to grit or hard fragments which may have wandered into the cavity or may have been expelled from the kidneys or the anus.

In *T. crassus* the mucus gland epithelium is found in the corresponding places, but is also present on ridges in the roof of the branchial cavity between ctenidium and rectum to a far greater extent than in *T. obliquatus* (fig. 4). This comparatively greater development of the mucus gland in a

high tide form contrasts with the reduction of the gland observed by Pelseueer (6) in the high tide *Littorinas*. There can be no doubt, however, that the roof of the branchial cavity in the latter, with the prolongation of the ctenidial leaflets across it, is much more specialised for respiratory purposes. The mucus gland of *T. crassus* preserves the condition found in many other species of the genus, and, in spite of its approach to a high-tide habitat, there is greater need for damp protecting slime here than in *Littorina*. *T. crassus* keeps its foot in contact with the rock throughout a period of exposure, while a high-tide *Littorina* withdraws deep into its shell, the edge of which remains adherent to the rock by means of a dried film of mucus. In other words, the branchial cavity of *T. crassus* cannot be nearly so completely protected (by retraction) from drying during a period of exposure as can that of *Littorina*, and the greater development of mucus gland may be a compensation for this. *T. crassus* is found in shadier and less exposed corners than the high-tide *Littorinas* often manage to occupy, and not usually so far up the shore.

(b) Gill.—The gill is built on the same lines in the two species under discussion, but shows several specialisations on the condition found in more primitive *Rhipidoglossa*. The loss of the right gill and the migration of the anus and excretory openings towards that side has been discussed by Ainsworth Davis (1) as a device for more complete separation of incurrent and excurrent streams through the branchial cavity. The surviving left ctenidium in *Trochus* remains biseriolate, as in *Haliotis* and *Pleurotonaria*, but the details of its disposition are very different, as is well known. In those more primitive types a median axis between the two series of leaflets contains the longitudinal afferent and efferent blood channels of the ctenidium, and that axis is attached to the wall of the branchial cavity on the side of the efferent channels only. Right at the back of the cavity the afferent axis is also attached to the roof on either side (fig. 8), and the basi-branchial sinus, which feeds the afferent ctenidial

channels, runs across the roof of the cavity in the region of these attachments.

In *Trochus* this connection of the afferent side of the gill axis with the roof of the cavity has extended much farther forwards. This has raised the lower series of gill-leaflets so that they hang in the cavity instead of almost, if not quite, resting on its floor. In this new position they are more efficiently bathed by the incoming water, and are less likely to impede its course, and they are also more easily kept from "packing together." The dorsal series of leaflets is, however, necessarily enclosed in a pocket through this development, and, in the species considered, this series is reduced as compared with the more freely hanging ventral leaflets.

In detailed structure the ctenidial leaflets of *Trochus* resemble in the main those of *Haliotis* (fig. 6). They are epithelial folds with a foundation of elongated cells below the epithelium of each surface, and bridges of cells across the cavity, which is a blood space. Between the epithelium and the cells which more or less line the blood space, we find, as in *Haliotis*, a development of chitinous substance, the ends of the chitin plates towards the "efferent" border of ctenidial leaflet being thickened. Away from this thick part, the chitinous layer thins out, and is soon no longer observable; but, where the efferent border of the leaflet meets the efferent side of the gill axis, it can be seen that, as in *Haliotis*, the chitinous plate of one side of a leaflet is continuous with that of the opposite face of the next leaflet. A nerve runs along each border of the leaflet beneath the epithelium. The epithelium (fig. 6) along the efferent border is mostly ciliated, and it is composed of high and narrow cells, some of which have basal nuclei, and apparently nerve connections, so that they are very probably sensory cells. A little way in from this border the epithelium is a good deal higher, very regular, and close set, and the surfaces of these extra high cells have a thick covering of uncertain nature (fig. 6). In this way the height of the band is much increased, and, as the bands of successive leaflets are opposed

to one another, they must act as cushions to keep the leaflets from packing together, the thickened chitinous plates already mentioned contributing to stiffen the leaflet.

The surface of the leaflet is thrown into folds, which run fairly parallel with the line where the leaflet unites with the gill axis. The epithelium of this part of the gill varies very much in appearance according to the exact direction in which it happens to be cut, but it is not nearly so high as that along the efferent border.

The afferent border of the leaflet is the one which is most directly exposed in the branchial cavity. Along this edge the epithelium is fairly high and regular, and includes mucus-secreting cells; we do not think it is ciliated (fig. 6). There are no supporting chitinous plates and no cushions near this border; if the topographically lower efferent edges of the leaflets are stiffened and held apart that suffices to keep the leaflets from packing against one another. The mucus-secreting cells of the afferent border must help to keep the leaflet from injury due to rough fragments rubbing against this exposed part. In *Trochus*, but not in *Haliotis*, we find the afferent border somewhat expanded (fig. 6), and this may be a cushion arrangement, so the statement above made perhaps needs modification. The appearance of odd fragments in the mucus outside the expanded border suggests that the swelling may have the added value of hindering the entry of these fragments into the chinks between the leaflets.

NOTES ON THE KIDNEYS.

The kidneys of *Trochus* were described by Perrier (8) and Haller (4), and Thiele (12) added the observation of a "nephridial gland" along the left side of the left kidney. Randles (10) and Pelseneer (7) have both described the pericardial communications of the kidneys, and Randles has added correct sketches of the cells typical of the right kidney. We

give sketches illustrating the types of cell found in both kidneys (figs. 10—12), with the corresponding cells from *Haliotis* (figs. 14 and 15) to show the close agreement between these two types; our figures do not agree with those of Perrier and Haller.

The nephridial gland of *Trochus* (cf. Perrier's *Glande nephridienne* of *Monotocardia*) is composed of a set of branching tubules opening into the kidney cavity, and embedded in a tissue rich in blood vessels (Perrier's *Glande hématique* of *Monotocardia*). The cells lining the tubules of this gland (fig. 12) are much lower than those of the left kidney. The function of this tissue, as, indeed, the function of the whole left kidney, is quite unknown, but it is, perhaps, important to notice that it occurs along that side of the kidney from which blood channels go to join the efferent ctenidial vein, and to form with it the left auricle. If the nephridial gland of *Trochus* is really the homologue of the nephridial gland in the *Monotocardia*, this is an argument in favour of the view of Lankester (5), Pelseener (7), and the embryologists that the kidney of *Monotocardia* is equivalent to the left kidney of the *Diotocardia*. Perrier, Woodward (13), and one of ourselves have urged the opposite view on other grounds which cannot be altogether set aside, and the question must be further discussed after more comparative and embryological research, some of which is now being undertaken.

Circulation.—In its main features, the circulatory system of the species of *Trochus* considered agrees with that described by one of us for *Haliotis* (3). Blood leaves the ventricle by the aorta, the communication being guarded by a simple valvular flap. The aorta bifurcates soon after leaving the heart, and one branch goes to the visceral hump while the other runs forward and ensheathes the radular sac. This is as in *Haliotis*, but here the blood channel is practically embedded in the side of the shell muscle for some distance. Still surrounding the radular sac it reaches the head where a great deal of its blood seems to be directed into spaces

surrounding the pedal ganglia and pedal cords. Thence blood is distributed throughout the foot. It appears to gather again in a median sinus above the nerve-cords, which opens in front into the general cavity of the head. The blood in the head is thus in part returned from the foot, and in part supplied from the branch of the aorta which surrounds the radular sac. The muscles of the odontophore are probably mainly supplied from the latter channel, while the blood from the former source is very likely partly aerated in the head when the animal is extended and active.

The blood from the general cavity of the head is collected into a fairly definite channel which carries it back to the right kidney. These species of *Trochus*, however, differ from *Haliotis* in that the anterior lobe of this kidney is much reduced, so that the blood channel does not run nearly all the way in the kidney wall, as is the case in *Haliotis*. The right kidney also receives blood from the visceral hump further back. In fact the blood flow from the head is by no means so intimately connected with the right kidney as in *Haliotis*. That organ must, in *Trochus*, be mainly a purifier of blood from the visceral hump.

An afferent channel from the right kidney takes blood from these two sources into the roof of the branchial cavity at the back, and runs across beneath the rectum to the left kidney, but first gives off a channel into the branchial roof. We look upon this last channel as a probable homologue of the afferent channel of the right ctenidium of *Haliotis* which has been lost in *Trochus*. The efferent channel from the right kidney thus corresponds with a part of the basi-branchial sinus of that type.

The blood reaching the neighbourhood of the left kidney, as just described, goes in part to that organ, but the main flow runs forward in a subrectal sinus, and then turns to the left, crossing the roof of the branchial cavity, as the transverse pallial vein of most authors (figs. 4 and 5).

Before reaching the left kidney, however, it communicates with the right auricle, which also receives a channel from the

branchial roof. Following Thiele, we homologise the latter channel with the efferent vein of the right ctenidium (lost in *Trochus*) of *Haliotis*.

In *Haliotis* the right auricle is supplied from the right efferent ctenidial vein, and also connects with the basi-branchial sinus, so conditions are essentially similar in *Haliotis* and *Trochus*, allowance being made for the loss of the right ctenidium in the latter.

The channel from the right to the left kidney in *Trochus* together with the forwardly running subrectal sinus and the transverse pallial vein, may be homologised with the basi-branchial sinus of *Haliotis*. The changes in detail are connected with the large size of the left kidney and its position in the roof of the branchial cavity.

As already stated, the blood spaces beneath the epithelium of the left kidney are supplied from the channel arriving from the right kidney, and so some of the blood (particularly that from the visceral hump) may be purified from nitrogenous waste. That from the head is, however, by no means so completely purified as it has really only skirted the right kidney.

The transverse pallial vein shows interesting differences in the two species considered. It is equally obvious on dissection in both, mainly owing to the covering ridges of the mucous gland, but the blood space is relatively larger in *T. obliquatus*, Gmel., than in *T. crassus*, Mont. In the former, also, its anterior and posterior branches are essentially afferent ctenidial channels sending blood through the gill axis into the leaflets. In *T. crassus* the gill does get some blood in this way, but a great part of the contents of the transverse pallial vein goes out into the roof of the branchial cavity which also receives blood from the sub-rectal sinus. There seems, therefore, ground for the opinion that the roof of the branchial cavity in this mid- to high-tide form is of considerable importance in respiration, while the ctenidium cannot have quite so much importance as in the other species.

The blood from the ctenidium together with that brought

by various channels from the roof of the branchial cavity goes back along the efferent ctenidial channel to the left auricle, which also receives important supplies from the left kidney. The left kidney thus gets its blood from the efferent channel of the right kidney, and passes it on to the left auricle, but its blood spaces are intimately associated with those of the neighbouring part of the roof of the branchial cavity, so perhaps a good deal of what it contributes to the left auricle has been aërated.

As the efferent channel from the right kidney communicates with the right auricle before reaching the left kidney, past which blood flows to the left auricle, it follows that right and left auricles are not so very indirectly connected with one another. This is another point of resemblance between *Trochus* and *Haliotis*.

Reference has been made to the possible respiratory activity of the roof of the branchial cavity, especially in *T. crassus*, Mont., and it is interesting to notice that the corresponding tissue seems to have acquired respiratory functions in *Patella*, which is also often a mid- to high-tide form.

In a recent paper Spillman (11) incidentally mentions the course of the circulation, but the vagueness of the statements made renders a discussion of his views unnecessary. He has evidently not given any special attention to this particular subject.

Bionomical Notes.—*T. crassus*, Mont., is often found in fairly large numbers huddled together in protected gullies and corners during the winter, especially when the weather is stormy. In summer it is interesting to watch these animals, often following one another's tracks as if the fresh trail of mucus were a help in progression. They also have the habit of mounting on one another's shells, where they apparently browse the small Algæ, etc., on the surface. As *Trochus* has no mating habits (in common species, at any rate), these peculiarities in behaviour may be thought of as the indistinct beginnings of that mutual recognition, perhaps

mainly through chemical sense impressions, which must be a first step in the evolution of the mating tendency.

Probably some of the ancestors of the Montocardia, which have mating habits, went through somewhat similar stages in the course of their evolution. Prof. Ainsworth Davis has suggested to us that the egg-eating habit of certain species of *Trochus* should also be considered in connection with the development of mating habits.

Our material was obtained from the shores of Cardigan Bay, south of Aberystwyth, which show for many miles as a plane of marine denudation formed by fairly evenly worn ridges of Silurian grits and slaty shale. The old valleys in the Silurian rocks, of which most of the coast cliffs are built, are filled in some cases by the boulder clay of the glacial epoch. The small streamlets which run down from the cliffs thus drain sometimes off the boulder clay, and sometimes off the shales and grits. We find that in several cases *T. crassus* occurs in abundance where the shore is washed by streams from the boulder clay, but disappears sometimes almost abruptly when the boulder clay makes way for the Silurian rock. The same thing is true, though in a lesser degree, for *Trochus obliquatus*, and the fact seems to be of sufficient interest to be chronicled, though we have not yet been able to approach an explanation. The boulder clay is found on analysis to be rich in salts of potash and magnesium. *Trochus* is not found much within three miles of Aberystwyth at present; the boulder clay in this immediate neighbourhood has probably been carried by a different set of glaciers from that flowing seawards further south. The pollution of the Ystwyth and Rheidol rivers by lead works may also be a determining factor.

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EXPLANATION OF PLATE 28,

Illustrating the paper by Dr. H. J. Fleure and Miss Muriel M. Gettings on “Notes on Common Species of Trochus.”

REFERENCE LETTERS.

Aff. Afferent side or axis of the ctenidium. *Ch.* Chitinous plate. *Ct.* Ctenidium. *Ct.Aff.* Afferent blood channel of the ctenidium. *Ct.Eff.* Efferent blood channel of the ctenidium. *Eff.* Efferent side or axis of the ctenidium. *L.Au.* Left auricle. *L.K.Eff.* Efferent channel from the left kidney. *L.K.* Left kidney. *Muc.gl.* Mucus gland. *N.G.* Nephridial gland. *Osph.* Osphradium. *R.* Rectum. *R.K.* Excretory channel of the right kidney. *R.Au.* Right auricle. *S.R.S.* Subrectal sinus. *St.* Strengthening tissue beneath the jaw-plates.

- FIG. 1.—The jaw-plates of *Trochus crassus*, Mont.
- FIG. 2.—A section of the jaw-plates.
- FIG. 3.—Cells from the strengthening tissue beneath the jaw-plates.
- FIG. 4.—The roof of the branchial cavity in *Trochus crassus*, Mont.
- FIG. 5.—The roof of the branchial cavity in *Trochus obliquatus*, Gmelin.
- FIG. 6.—An oblique transverse section of a gill leaflet of *Trochus*.
- FIG. 7.—Section of the roof of the branchial cavity and gill of *Trochus*.
- FIG. 8.—Section of the roof of the branchial cavity and gills of *Haliotis*.
- FIG. 9.—Section of the left kidney of *Trochus* in the region of the nephridial gland.
- FIG. 10.—Epithelium of left kidney of *Trochus*.
- FIG. 11.—Epithelium of right kidney of *Trochus*.
- FIG. 12.—Epithelium of nephridial gland of *Trochus*.
- FIG. 13.—Section of pericardium of *Trochus* showing the blood channels which feed the left auricle.
- FIG. 14.—Epithelium of the right kidney of *Haliotis*.
- FIG. 15.—Epithelium of the left kidney of *Haliotis*.

