The Renal Organs of Certain Decapod
Crustacea.

By

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With Plates XXI & XXII.

In a paper published during the summer of 1889, I gave an account of the excretory apparatus of Palæmon serratus, in which I drew attention to the enormous development of the bladder, which extends dorsally from the level of the green glands to the anterior boundary of the pericardium.

The existence of a well-developed nephro-peritoneal sac, having many of the relations of the "coelomic" body-cavity of other types, had not, at the time of publication of my paper, been recognised in any Crustacean. I have since observed the occurrence of a similar sac in a large number of Decapoda; and M. P. Marchal, who has evidently worked without any knowledge of my observations, has described similar structures in a considerable number of genera.

The object of the present communication is to give an account of the renal organs of certain Carididæ (Pandalus, Virbius, and Crangon) in which the structure of the green gland itself is modified in a very remarkable manner.

Before proceeding to a description of the genera which it is proposed more particularly to consider, it may be well to give

1 'Journal of the Marine Biological Association,' N.S., vol. i, p. 162.
2 'Comptes Rendus,' exi, 12, and exi, 16.

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a short summary of the results already arrived at concerning the structure of the excretory apparatus in the Prawn.

The nephro-peritoneal sac of Palæmon is a median, unpaired structure, lying in the cephalothorax, dorsal to the alimentary canal, and ventral to the ophthalmic artery and to the median dorsal blood-sinus. Its walls are composed of a single layer of flattened excretory epithelium, which has the power of absorbing indigo carmine and similar substances when these are injected into the blood of the living animal. Posteriorly the nephro-peritoneal sac is in close contact with the anterior extremity of the generative gland; anteriorly it gives off on each side a narrow tube, which passes vertically downwards beside the òesophagus, and, after passing under the òesophageal nerve-commissure, bends outwards to open into the urinary bladder of its own side. The ducts of opposite sides communicate with one another, not only dorsally, through the cavity of the nephro-peritoneal sac, but also vertically, by means of a transverse commissure which passes in front of the òesophagus, and bears a conspicuous dilatation in the cavity of the upper lip.

A diagram of the whole arrangement is given in Pl. XXII, fig. 9; the relations to the other systems of organs, as seen in transverse section, may be gathered from figs. 1 and 2.

The bladder, besides receiving the openings of the nephro-peritoneal ducts, gives off on the one hand the ureter, and on the other the system of excretory tubules of the green gland. These last form a complex mass of branching tubules, which are in close contact one with another, and which form the glandular substance of the green gland. In my former paper I pointed out the existence, in this glandular plexus, of several excretory tubules, an observation confirmed by M. Marchal. I was unable last year, and have still been unable, to convince myself that the various tubules anastomose freely with one another in the way described by this observer. Be this as it may, however, the tubules, after a tortuous passage through the substance of the green gland, unite to open by a common aperture into the "end-sac," whose structure has been re-
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peatedly described, especially by Grobben, Marchal, and myself.

In my former paper I described only the arrangement found in P. serratus, and the observations of M. Marchal, which are in complete agreement with my own, relate also to this species. I have since satisfied myself that the excretory system of P. squilla, and that of Palæmonetes varians, are practically identical with that of the species described.

In the genera Virbius, Pandalus, and Crangon, a series of modifications may be observed, resulting in the disappearance of the whole tubular portion of the green gland, and the hypertrophy and specialisation of the end-sac. The nephro-peritoneal sacs are also arranged in a manner strikingly different from that which obtains in the Prawns.

The nephro-peritoneal sacs are nearly identical in arrangement in the three genera in question. Their relations will be readily understood from the diagram, fig. 10, and the transverse section of Pandalus brevirostris, fig. 3. The bladder gives off from its internal aspect a duct, which is both wider and shorter than the corresponding duct of Palæmon, the duct from each bladder passing inwards under the oesophageal commissure of its own side, and opening into a large sac, which does not communicate with its fellow of the opposite side, and which does not extend to the middle dorsal line above the alimentary canal. The median wall of each sac is closely applied partly to the lateral and ventral wall of the stomach, and partly to the median face of the sac of the opposite side, so that the stomach appears in section to be supported by a well-marked ventral mesentery, which exists beneath the part of that organ which projects in front of the oesophagus, as well as beneath its post-oral region. Both bladder and sac give off numerous processes, which ramify in the base of the antennæ and among the organs of the thorax. The epithelium forming the walls of these organs is in all cases striated and excretory, being very closely similar to the corresponding epithelium of the Prawns. In none of
the three genera is there any connection between the wall of the nephro-peritoneal sacs and the generative glands.

The structure of the "green gland" differs in each of the three genera.

In *Virbius* (varians) a horizontal section through the bladder and "green gland" has the appearance represented in fig. 4. The bladder itself is bounded by a single layer of epithelial cells, whose inner margins frequently project irregularly into the cavity of the organ. These cells exhibit, especially in their peripheral portions, the well-marked longitudinal striation which is so constantly noticed in excretory tissues; their internal portions are, however, frequently vacuolated, and their free internal borders are ragged and indefinite. When this condition prevails the cavity of the bladder is seen (in stained sections) to contain an irregular, granular coagulum, which absorbs haematoxylin with readiness. The nuclei of the bladder-cells are oval, and of moderate size; they stain deeply, and do not, in preparations preserved in corrosive sublimate, exhibit any very evident reticulum. The cells composing that portion of the wall of the bladder which invests the end-sac are flatter and more regular than the others; they stain more deeply with haematoxylin, and the longitudinal striation is perhaps more evident in these than in the other bladder-cells.

The renal tubule is single, and has a much wider lumen than any of the corresponding tubules of *Palæmon*. It leaves the bladder at the postero-external margin of that organ, and is at first directed nearly horizontally outwards. After passing outwards for a very short distance, however, the tubule turns backwards and then inwards, so that it becomes U-shaped, and opens into the end-sac. The general direction of the single renal tube is that just described, but it does not lie in one plane with such accuracy as to enable it to be included in a single section. In the section figured (Pl. XXI, fig. 4) the two ends of the tube only are seen, the one leaving the bladder, the other entering the end-sac. By examination of the following sections, the course of the tube was determined
as that shown by the dotted lines in the figure. [The determination of such a point is so easy that it has not seemed worth while to publish the figures of the sections upon which it rests.]

It is evident that the single, wide, U-shaped tube, running from the bladder to the end-sac, is the only representative in _Virbius_ of the complicated plexus which goes to make up the mass of the green gland in the Prawn. In structure, its walls somewhat resemble those of the bladder already described. They are, however, higher and more regular, their internal extremities of the component cells being less given to the exhibition of vacuoles and irregular processes. The longitudinal striation is more evident, and the nuclei are larger and stain more deeply with hæmatoxylin. Before opening into the end-sac, the lumen of the renal tubule contracts considerably, so that the orifice, by which the cavities of the two structures communicate, is very small. Owing to its size and position, it is exceedingly difficult to demonstrate this opening in transverse sections, but in carefully adjusted horizontal longitudinal sections it is, as will be evident from the figure, easily to be seen.

The end-sac itself is completely enveloped by a layer of bladder epithelium, the wall of the bladder being invaginated by it. The epithelium of the bladder is, however, not in absolute contact with that of the end-sac, the two being separated by a blood-space (left white in the figure). I have not been able to detect any epithelium bounding this blood-space; and I am inclined to believe, after careful examination, that no such epithelium exists. The account given by Grobben of the end-sac of _Palæmon treillianus_ leads to the belief that the renal vessels of this species end in lacunæ which are devoid of epithelial lining; and I have been unable to demonstrate an epithelium in the smaller blood-spaces of the kidney of _Pandalus_ (annulicornis and brevirostris). Professors Claus1 and Lankester9 have, as is well known, arrived inde-

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2 This Journal, vol. xxv, p. 518.
pendently at the conclusion that the blood system of the Decapod Crustacea is everywhere closed; but I am not aware that either of these observers has paid special attention to the blood-supply of the renal organs. Nevertheless, the positive testimony of two such accomplished anatomists makes me hesitate to lay undue stress upon my own failure to demonstrate an epithelial lining to the particular spaces under consideration.

The epithelium of the end-sac, like that of the rest of the excretory system, is everywhere one cell thick. The individual cells stain more deeply than do those of the bladder and renal tubule; their protoplasm is crowded with granules, which are, however, not arranged in regular rows, so that the cells do not exhibit a longitudinal striation. The nuclei stain very deeply, and exhibit, in specimens preserved in corrosive sublimate, one or two large nucleoli, with no recognisable trace of a chromatin reticulum. The inner extremities of these cells are much vacuolated, and are very irregular; the vacuoles frequently containing spherical concretions of a homogeneous material, which stains slightly with haematoxylin, less readily with borax carmine. The cavity of the end-sac is generally found to contain a greater or less quantity of granular clotted material, which appears in sections as a deeply staining, finely granular reticulum.

In Pandalus (annulicornis and brevirostris) a further deviation from the tubular type of nephridium occurs, the renal tubule being in the adult condition entirely absent, while the whole body of the "green gland" is built up of the curiously modified end-sac and the associated portion of the wall of the bladder.

I have not followed the early phenomena of the development of the kidney; but in the late "Mysis" stage the relations of kidney and bladder present a striking resemblance to those which are permanent throughout life in Virbius. The appearance presented at this stage in horizontal longitudinal section is shown in Pl. XXI, fig. 5.

The bladder is large compared with the size of the renal
tubule and end-sac; its cells are, for the most part, pale and uniformly granular, having no trace of longitudinal striation; their nuclei are rounded, and do not stain deeply. At this stage there is little difference in appearance between that portion of the bladder-wall which is immediately adjacent to the end-sac and the remainder. The cells adjoining the end-sac are slightly smaller than the rest, and their margins slightly more regular, but in other ways the characters of the bladder-cells are everywhere the same; and the sac, though closely applied to the wall of the bladder, causes hardly any invagination of that structure.

The renal tubule (Pl. XXI, fig. 5) is very short, being simply represented by the curved neck which connects the end-sac with the bladder. Its walls are very similar in structure to those of the bladder itself, and its lumen is very narrow.

The end-sac (Pl. XXI, fig. 5) is small, and bounded by finely granular or nearly homogeneous cells, the nuclei of which are clear and vesicular in appearance. Between the end-sac and the wall of the bladder is a lacunar blood-space; and both here and on the outer side of the end-sac are groups of connective-tissue cells.

In a very young Pandalus annulicornis, which had apparently only just acquired the adult characters, the appearance presented by a transverse section through the excretory organs is shown in fig. 6. [I have only obtained a single individual of this age, and before the present investigation was commenced I had prepared transverse sections of the specimen. I have therefore been unable to figure a section in the same plane as those above described.]

The wall of the bladder exhibits already a distinct specialisation into two regions, one lying beside the end-sac, the other having no relation with that organ. In the latter portion, which of course includes the greater part of the bladder, the cells exhibit distinct indications of longitudinal striation in their peripheral parts, and their inner extremities are often vacuolated. The portion which adjoins the end-sac consists of cells which are more columnar than those of the general
surface of the bladder, which stain more deeply, and are more crowded with granules. The nuclei of these cells exhibit frequent indications of division.

The end-sac is by this time more closely applied to the bladder, the wall of which it invaginates to such an extent that about half its surface is invested by a layer of bladder-cells. The epithelium of the end-sac is made up on the side next the bladder of small cubical cells, and on the opposite side of cells which are somewhat flattened. The protoplasm of all these cells is pale and coarsely granular, as it remains throughout life. The connective tissue, which was noticed in the last stage, has slightly increased in amount, and the blood-spaces between end-sac and bladder are much better developed than during the "Mysis" stage. The renal tubule has ceased to be distinguishable as a separate region, and the end-sac now opens by its posterior extremity directly into the bladder.

The stages in the further development of the bladder I have been unable to observe, my remaining material consisting entirely of adult individuals. It is evident, however, that the end-sac becomes completely surrounded by the wall of the bladder, so that it finally projects freely into the cavity of that organ, being attached to the bladder-wall by a narrow stalk, on which is situated the communication between the cavities of the two structures.

While the process of enclosure of the end-sac by the bladder is going on, the wall of the first-named organ becomes produced into a number of complicated branched papillæ, which project into the cavity of the bladder, each being, of course, covered by a layer of bladder epithelium. At the same time the whole organ increases in size till it becomes about as large as the whole "green gland" of Palæmon.

A section through the adult end-sac is drawn in fig. 7, where the extent of the papilliform prolongations into which it is produced is rather below the average. The epithelium is flattened and irregular, composed of a pale, granular protoplasm. The cells do not exhibit vacuoles, and I have not observed the presence of concretions in any of my specimens.
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The nuclei are small, rounded, and pale, with scattered, deeply staining chromatin granules. The communication between the cavity of the organ and that of the bladder is seen to lie at one side of the stalk, and to be quite direct, without the intervention of anything which can be held to represent the system of tubules of Palæmon, or even the simple U-shaped tubule of Virbius.

Between the wall of the end-sac and the investing portion of the bladder there is a certain quantity of connective tissue, which in places forms fairly conspicuous masses, the characters of which tissue will be gathered from the figure. Besides the connective tissue a system of blood-vessels ramifies between end-sac and bladder, consisting in part of larger vessels, in which it is easy to recognise an epithelial lining, and in part of smaller, apparently lacunar spaces. These vessels are supplied by one or two main trunks which pass along the neck of the end-sac. Two of these vessels, cut transversely before their entrance into the space referred to, are seen in fig. 7 lying outside the wall of the bladder.

The epithelium of the bladder itself is everywhere the same. The cells are columnar, and very regular in outline, showing no trace of vacuolation or of production into irregular processes. They exhibit an exceedingly well-marked longitudinal striation, and stain deeply both with hæmatoxylin and with borax carmine. The internal border of the bladder-cells seems always to be darker and more homogeneous than the rest, but there is no indication of the existence of a definite cuticle. The nuclei are rounded and granular, and stain fairly deeply.

The youngest individuals of Crangon vulgaris which were examined had already attained the external characters of the adult, although they were scarcely larger than the oldest "Mysis" larvae.

These specimens correspond in age to the second stage in the development of Pandalus, as above described, and the condition of the excretory system is practically identical in the two species.

The bladder-wall in the young C. vulgaris (see Pl. XXI,
fig. 8) exhibits already the characteristic longitudinal striation, and as in the young Pandalus it surrounds half the end-sac. The communication between its cavity and that of the end-sac is direct, there being no trace of the renal tubule.

The end-sac is bounded by a layer of pale, finely granular cells, the protoplasm of which exhibits the well-known “ground-glass” appearance. The epithelium of that half of the sac which is enclosed by the bladder is more columnar, that of the unenclosed portion being flatter. The cells of both regions exhibit numerous vacuoles at their inner margins, but no concretions were observed.

Between the end-sac and the bladder is a well-developed, apparently lacunar blood-space, and outside the end-sac is a layer of connective tissue.

The excretory system of an adult shrimp resembles that of Pandalus in the direct communication between end-sac and bladder, and in the formation of papillae upon that surface of the end-sac which projects into the bladder. The whole sac is not, however, enveloped by the bladder so completely as it is in Pandalus.

It is evident from what has been said that the excretory system of the Decapoda is much more varied in its structure than has hitherto been supposed. The observations here recorded, together with those of M. Marchal already referred to, enable us to divide the modifications into groups as follows:

In the Schizopods (Mysis) the whole excretory system appears, according to Grobben,¹ to consist of a single coiled tubule, opening by one extremity to the exterior, and by the other to an irregular end-sac, whose walls are composed of an irregular epithelium, and are not apparently very highly specialised. The single renal tubule may dilate into a small bladder near its external opening, but there is no indication of the extension into the thorax of a nephro-peritoneal sac.

In all the Decapods proper the end-sac has become more highly specialised, possessing a lining epithelium of definite characters, a well-defined system of blood-vessels, and so on;

but the characters of the remaining portions of the excretory system vary greatly.

In the Thalassinidæ (Axius and Gebia) the number of the tubules, and the complexity of their arrangement, have increased, so that several tubules lead from the ureter to the end-sac; but there is no vesicular dilatation of any part of the system.

In the Astacidæ (Astacus, Homarus, and Nephrops) several tubules run from the ureter to the end-sac; but by the dilatation of one of these, which receives the openings of the others, a bladder is constituted; and this bladder intervenes between the plexus of tubules, forming the mass of the "green gland," and the ureter. In this group the bladder has no considerable extension into the thorax.

In the Loricata (Palinurus) the bladder has the same relations as those described in the Astacidæ; but the number and complexity of the tubules forming the green gland is very largely increased.

In the Carididæ the structure of the excretory system varies greatly, the four modifications described in the previous section of this paper all occurring within the limits of the group.

In the "Anomura" there is a well-marked nephro-peritoneal system, which in Pagurus forms a median dorsal sac, situated far back in the abdomen. The end-sac is frequently produced into papillæ, which are surrounded, not by a modified portion of the bladder, as in Pandalus and Crangon, but by a layer of renal tubules.

In the Brachyura the nephro-peritoneal sac sends well-developed prolongations into the thorax; there are, at least frequently, two such prolongations on each side, one dorsal and one ventral. The end-sac is frequently produced into papillæ, which are covered by the epithelium of the short, wide renal tubule, the cavity of this tubule being frequently broken up by a system of trabeculae.¹

¹ In this sketch of the various Decapods, the account of the Thalassiniidae and of the Brachyura is taken directly from Marchal's paper.
It appears, from the foregoing statements, that the nephroperitoneal sacs of the Decapoda should be regarded rather as enlarged portions of a tubular system, such as that found in *Mysis* and in the *Thalassinidæ*, than as persistent remnants of a "celomic" body-cavity, into which tubular nephridia open.

The presence of coxal glands in *Nebalia*,¹ and of tubular nephridia in the *zoæa* of *Eriphya*,² gives much interest to the search for an embryonic cælom in these animals, which may be expected to behave like the cælom of *Peripatus*.

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EXPLANATION OF PLATES XXI & XXII,

Illustrating Professor W. F. R. Weldon's paper on "The Renal Organs of Certain Decapod Crustacea."

List of Reference Letters.


**Fig. 1.**—Transverse section through the head of a *Palæmon serratus*, showing the connection between the dorsal nephro-peritoneal sac and the bladder.

**Fig. 2.**—Transverse section through the same specimen, rather behind Fig. 1, showing the dilated median ventral portion of the nephro-peritoneal system lying in the upper lip, and the dorsal portion lying above the stomach.

**Fig. 3.**—Transverse section through the head of *Pandalus brevirostris*, just in front of the oesophagus, showing the ventral mesentery formed by the two nephro-peritoneal sacs.

**Fig. 4.**—Horizontal section through the bladder and end-sac of an adult *Virbius*. The dotted lines indicate the course of the single renal tubule.

Fig. 5.—Horizontal section through the bladder and "green gland" of *Pandalus annulicornis* in the *Mysis* stage.

Fig. 6.—Transverse section through the kidney of *Pandalus annulicornis*, just after the final metamorphosis.

Fig. 7.—Section through the end-sac and associated wall of the bladder in an adult *Pandalus*. The letters *Bl.* lie in the cavity of the bladder.

Fig. 8.—Horizontal section through the kidney of a young *Crangon vulgaris*, just after the final metamorphosis.

Fig. 9.—Diagram of the excretory system of *Palæmon*.

Fig. 10.—Diagram of the excretory system of *Pandalus*. 