ON THE SEXUAL BIOLOGY OF *PANDALUS BOREALIS* (CRUSTACEA DECAPODA)

I. HISTOLOGY OF INCRETORY ELEMENTS

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(Text-figs. 1–16)

Anatomical and histological details are here given of two organ systems, which, my experiments lead me to believe, may secrete hormones concerned in the sex reversal that overtakes all male *Pandalus borealis* Krøyer. The descriptions eschew any attempt at detailed cytology, and refer exclusively to prawns taken from the population of Gullmarfjord in south-west Sweden. There is reason to believe that, as with *Palaemon* (= *Leander*) *serratus* (cf. Carlisle, 1955), different populations may vary widely in the detailed topography of the endocrine organs, as well as in appearance, life history and growth rate (cf. Horsted & Smidt, 1956).

The organ systems to be described are the X organ-sinus gland complex of the eye-stalk and the vas deferens gland system or *glande androgène*.

A note is necessary on the orientation of organs within the eye-stalk. When a prawn is at rest the eye-stalks are held outwards. In this position the eyes themselves are lateral. When a prawn is lifted out of the water, or when it is looking forward, the eye-stalks are turned forward and (in the former situation) are held in close against the head, so that the eyes hold an anterior position. This mobility of the eye-stalk, one of the characteristic features of the stalk-eyed Crustacea, makes the use of the terms anterior and posterior confusing. Following a suggestion made by Dr F. S. Russell, therefore, I propose using the terms abaxial and adaxial, with the same sense as their usage in descriptions of medusae. Under this terminology the eye will be referred to as distal (never as anterior); the side of the eye-stalk which is towards the axis of the body, i.e. the side which is medial when the eye-stalks are held in close or which lie anteriorly when the eye-stalks are turned outwards, will be called the adaxial side; the opposite side, i.e. the lateral side when the eye-stalks are held close, or the posterior side when they are turned outwards, will be called the abaxial side.

THE X ORGAN-SINUS GLAND COMPLEX

In decapods the sensory papilla has been reduced to a sensory pore, or, in many species, lost. The pore is retained in *P. borealis* and this is the only point where the X organ-sinus gland complex approaches the superficies of the eye-stalk. The gross internal anatomy of the eye-stalk differs little from that which has been reported as normal in decapods. The eyes are large as befits a deep-water animal, and the eye-stalks are relatively short and stubby, though highly mobile.

The main nervous nuclei present in the eye-stalk are the medulla terminalis (perhaps more correctly, though less usually, called the lobus terminalis) of the protocerebrum, and the medullae interna et externa. The last is succeeded by the lamina ganglionaris, the most proximal layer of the retina. The neuro-secretory cells are concentrated into three major groups, one in each of the
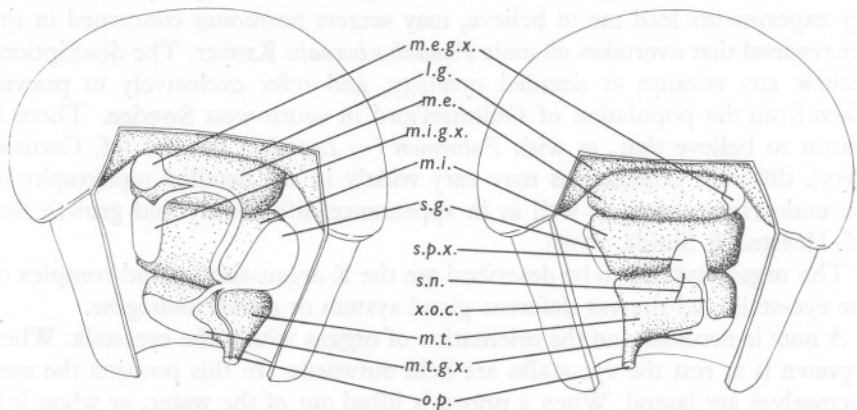

Fig. 1. Dorsal (left) and ventral (right) dissections of a left eye-stalk of *Pandalus borealis*, with all the non-nervous tissue omitted.

Lettering guide to Figs. 1–8. *d.p.s.*, dorsal pigment spot; *l.g.*, lamina ganglionaris; *m.e.*, medulla externa; *m.e.g.x.*, medulla externa ganglionic X organ; *m.i.*, medulla interna; *m.i.g.x.*, medulla interna ganglionic X organ; *m.t.*, medulla terminalis; *m.t.g.x.*, medulla terminalis ganglionic X organ; *o.p.*, optic lobe peduncle; *s.g.*, sinus gland; *s.n.*, sensory nerve of sensory pore; *s.p.*, sensory pore; *s.p.x.*, sensory papilla X organ; *x.o.c.*, X organ connective.

medullae. They may, following the terminology of Knowles & Carlisle (1956), be called the medulla terminalis ganglionic X organ (*m.t.g.x.*), the medulla interna ganglionic X organ (*m.i.g.x.*) and the medulla externa ganglionic X organ (*m.e.g.x.*), respectively (see Figs. 1–8). From these organs neurosecretory fibres run more or less directly to the sinus gland, which lies dorso-adaxially against the medulla interna. The tracts of fibres unite before entering the sinus gland and are joined by a relatively minor group of fibres coming from the brain; the four tracts thus enter together and the gland is not divided into separate lobes as in *Palaemon* (see Carlisle & Knowles, 1959). A further tract

of neurosecretory fibres, the X organ connective, runs from the $m.t.g.x.$ to the sensory papilla X organ ($s.p.x.$), which is attached ventrally to the medulla terminalis and projects like a finger into the ventral blood sinus of the eye-stalk, bathed on all sides by blood (see Figs. 2, 6–7), until at its distal end it attaches to the sensory pore. This, a thinning of the cuticle, ventrally on the eye-stalk near the limit of the eye, is lined by a continuous layer of sensory nerve cells, whose axons form a nerve, distinct from the X organ connective, running to the medulla terminalis (see Figs. 1, 2).

The ganglionic X organs

Each of these groups of neurosecretory cells consists of about 30 cells compactly arranged into a discrete organ with no intermixture of normal neurones; nor are there any isolated neurosecretory cells scattered among the association areas, such as are to be found in *Lysmata* (see Carlisle, 1953c). The cells are about $75 \times 45\mu$, densely granulated with granules about at the limit of resolution of a $\times 45$ objective ($0\cdot4$–$0\cdot5\,\mu$). The granules have the same staining properties as in other decapods (see Carlisle & Knowles, 1959). In my preparations the cells are roughly rhomboidal in shape, with the axon forming the continuation of one end of the long diagonal (see Fig. 9). The nucleus is about 20–$22\,\mu$ in diameter and in most cells contains three well-defined nucleoli.

In the $m.t.g.x.$ the more adaxial cells send fibres to the sinus gland while the more abaxial ones direct their fibres to the $s.p.x.$ About two thirds of the cells fall into the former and one third into the latter category. The axons of the adaxial cells leave the $m.t.g.x.$ on the surface of the medulla terminalis at the adaxial corner of the X organ, and run along the surface of the medulla distally to the sinus gland, following the shortest route along the surface of the ganglionic chain. The fibres from the abaxial cells also leave on the surface of the medulla, forming the X organ connective, and run directly along the ventral surface distally to the $s.p.x.$, again following the shortest route (see Figs. 1, 2).

The axons of the $m.i.g.x.$ all leave together at the distal corner of the X organ on the surface of the medulla interna. The tract runs distally on to the dorsal surface of the medulla externa, where it is joined by that from the $m.e.g.x.$, turns in a broad bend back on to the medulla interna and, first making another bend, joins with the tract from the $m.t.g.x.$ which runs to the sinus gland. This tract, then, makes a broad S-bend on the dorsal surface of the medullae interna et externa.

All the tracts are on the surface of the ganglionic chain and are readily visible in the fresh dissection as opaque bluish white lines. In some few dissections there appears to be a nerve linking the $s.p.x.$ with the sinus gland via the dorsal pigment spot. I am uncertain of this.

The cytology of the neurosecretory cells is in no way remarkable. Using Potter's methods, however (Potter, 1954, 1958), it was possible to distinguish

of neurosecretory fibres, the X organ connects with the s.*p.x.* to the
sensory papilla X organ (*s.p.x.*), which is placed ventrally to the medulla
terminalis and projects like a finger into the ventral blood sinus of the eye-
stalk, bathed on all sides by glossy blood (see Figs. 4, 5, 6), until at its distal end it
attaches to the cuticular eye. This, a thin layer of cuticle, ventrally on the
[...] of the eye, is lined by [...] a basic layer of sensory
[...] into a nerve [...] the organ terminals,
running to the [...] terminalis (see [...]

The ganglionic X organ [...]

Both of these groups of neurons [...] groups of nerve cells
compose [...] into a discrete organ [...] a mixture of normal
neurones; nor are there any isolated neurones or cells scattered among the
association areas, such as are to be found in the [...] (see Carlisle, 1953*c*).
The cells are about 75 × 45μ, densely granular, with granules about at the
limit of resolution of a × 45 objective [...]
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In the [...] the more abaxial cells send their [...] to the sinus gland, the
more abaxial ones direct their fibres to the *s.p.x.* About two thirds of the cells
[...] into the [...] and one third into the latter, on [...] The axons of
the [...] run over the *s.p.x.* on the surface of the medulla terminalis and
[...] corner of the X organ, and run along the surface of the medulla
down [...] to the sinus gland, following the shortest route along the surface of the
ganglionic strata. The fibres from the abaxial cells also leave on the surface of
the [...] Ganglionic X organ connective, and run through the strata of normal
[...] to the sinus gland, again following the shortest route (see Figs. 1, 2).
Thus these two sets of cells will leave together at the corner of the X organ and
on the [...] terminalis. The [...]
[...] where it is joined by [...]
in a [...] medulla interna and [...] the other hand,
joins the [...] *s.p.x.*, which runs to the [...] sinus. The other,
[...] placed on the dorsal surface of the medulla terminalis or ex-
ternal [...]

[...] the surface of the ganglionic X organ are readily
visible [...] dissection as opaque bluish-white lines. [...] few
sections three [...] to be a nerve linking the *s.p.x.* with the sinus gland via
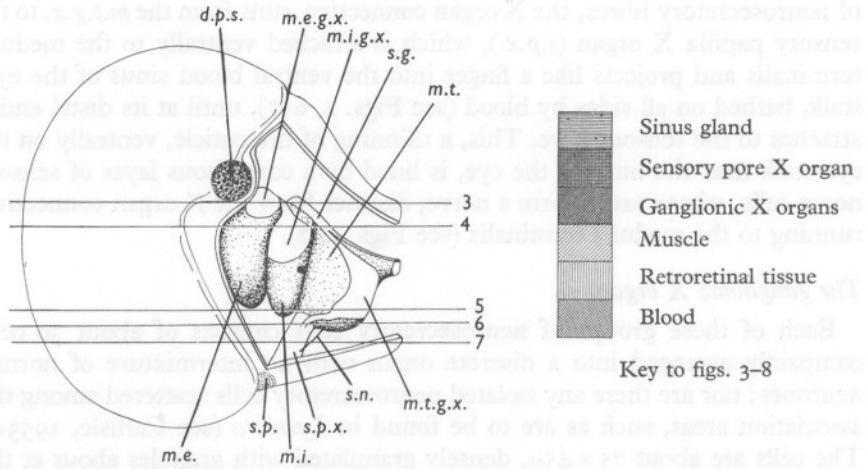[...]

Fig. 2. Abaxial dissection of a left eye-stalk, with all the
non-nervous tissue omitted. The numbered lines indicate
the approximate planes of the sections illustrated in the
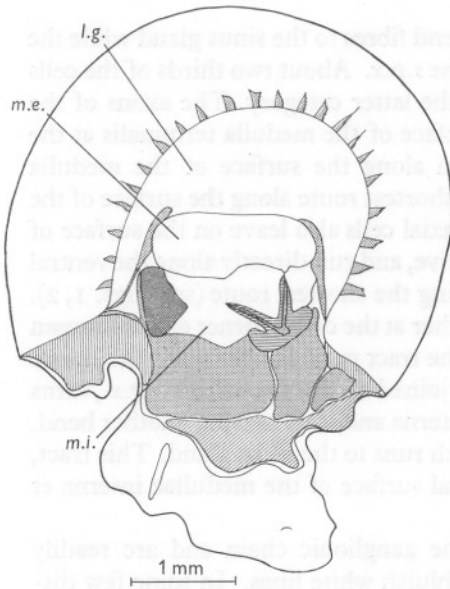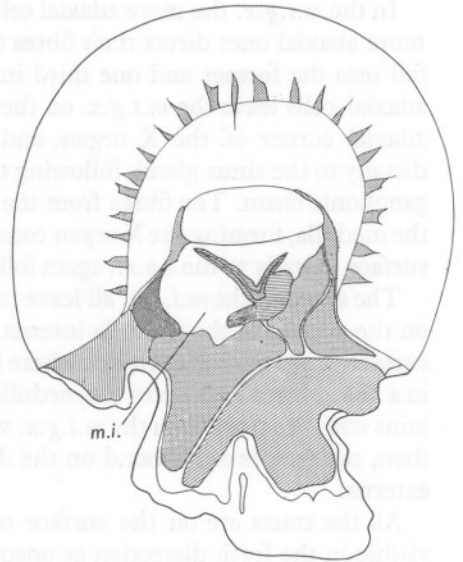like-numbered figures. For lettering guide see Fig. 1.

Key to figs. 3–8

- Sinus gland
- Sensory pore X organ
- Ganglionic X organs
- Muscle
- Retroretinal tissue
- Blood

Fig. 3.

Fig. 4.

Figs. 3–7. Horizontal sections through a single left eye-stalk taken in June at the levels in-
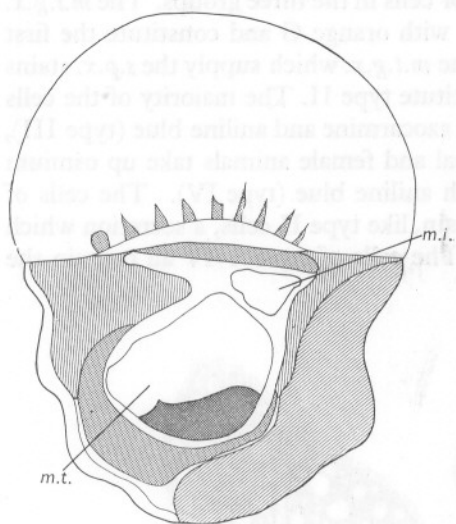dicated in Fig. 2. The abaxial side is to the left. The lettering guide is given below Fig. 1.
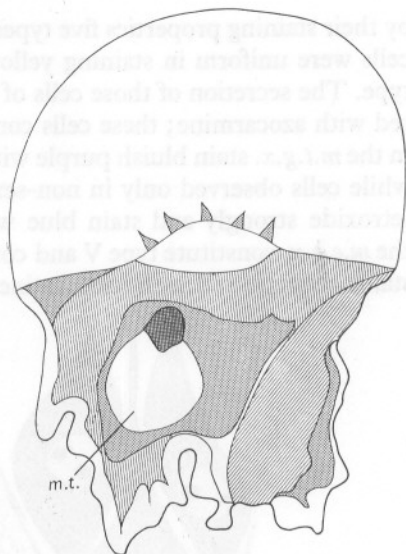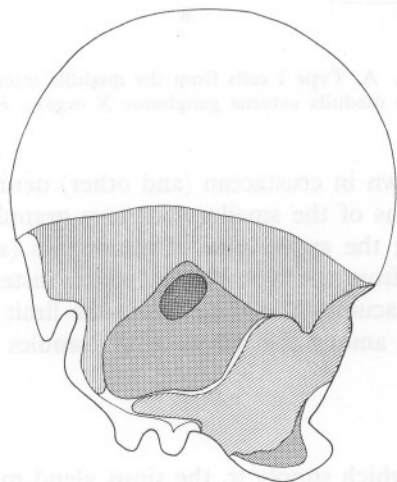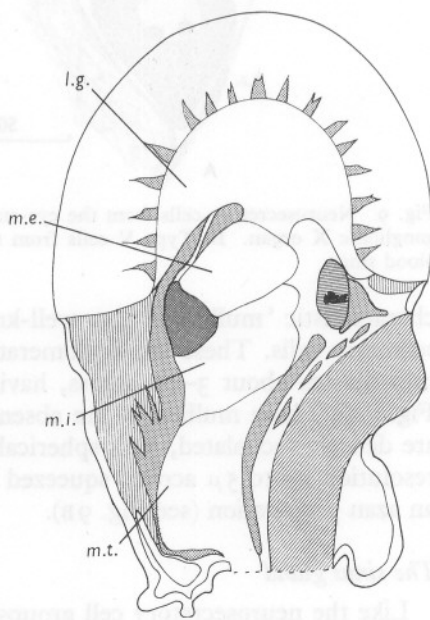
Fig. 5

Fig. 6

Fig. 7

Fig. 8

Figs. 5–7. See legend to Fig. 3 opposite.

Fig. 8. An approximately horizontal, somewhat oblique section of a left eye-stalk. The adaxial side is to the left of the figure. Note particularly the position of the type IV nerve endings indicated in black in the sinus gland. The patch of retroretinal tissue to the right of the eye-stalk retains the acinar structure, although this animal was killed in June. The lettering guide is given below Fig. 1.

by their staining properties five types of cells in the three groups. The $m.i.g.x.$ cells were uniform in staining yellow with orange G and constitute the first type. The secretion of those cells of the $m.t.g.x.$ which supply the $s.p.x.$ stains red with azocarmine; these cells constitute type II. The majority of the cells in the $m.t.g.x.$ stain bluish purple with azocarmine and aniline blue (type III), while cells observed only in non-sexual and female animals take up osmium tetroxide strongly and stain blue with aniline blue (type IV). The cells of the $m.e.g.x.$ constitute type V and contain, like type II cells, a secretion which stains strongly red with azocarmine. The cells of types I–IV all contain the
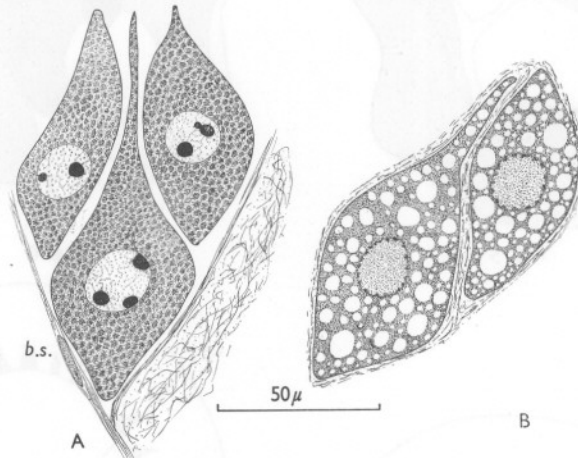
Fig. 9. Neurosecretory cells from the eye-stalk. A. Type I cells from the medulla interna ganglionic X organ. B. Type V cells from the medulla externa ganglionic X organ. $b.s.$, blood sinus.

characteristic 'mulberries', so well-known in crustacean (and other) neurosecretory cells. These are agglomerations of the smaller secretory granules into masses about $3–4\,\mu$ across, having the appearance of mulberries (see Fig. 9A). These mulberries are absent from the type V cells, which instead are densely vacuolated, with spherical vacuoles of all sizes from the limit of resolution up to $5\,\mu$ across, squeezed in among the red staining granules in an azan preparation (see Fig. 9B).

The sinus gland

Like the neurosecretory cell groups which supply it, the sinus gland may be shown to consist of at least four kinds of elements of differing tinctorial affinities. The staining properties, however, do not correspond exactly to those of the cells and it seems likely that, as in *Palaemon* (Carlisle, 1958), the secretory material undergoes a physico-chemical change as it passes down the axons. Those nerve endings which are strongly osmophilic are stained red by

azocarmine. Tracing of individual fibres shows that these endings derive from cells which are likewise osmophilic, but which stain blue with aniline blue (type IV cells). These endings are rather closely circumscribed in position (see Fig. 8). The centre of the gland is occupied by two inter-mingled types of endings, one staining blue with aniline blue and the other reddish mauve with azocarmine and aniline blue. The blue endings derive from type III cells, while the reddish mauve ones appear to correspond to type V cells. These latter endings are also found scattered throughout the rest of the gland among the fourth type of endings, which stain red with azocarmine and come from the type I cells of the *m.i.g.x.* The sinus gland consists almost entirely of these nerve endings of varying tinctorial affinities.

The body of the gland in a large female forms a perforated disc about $500\,\mu$ in diameter and $250\,\mu$ thick. Not more than about 25 nuclei of the con-nective tissue supporting cells may be seen in it and this tissue forms a minor fraction of the total tissue of the gland. As always, the gland surrounds the point where the blood vessels from the interior of the eye-stalk emerge into the outer blood sinus of the eye-stalk. It is usually stated that these blood vessels run from the inner blood sinus of the ganglionic chain, but in *Pandalus*, as in other Natantia that I have examined, there is no such inner blood sinus. The blood supply of the ganglionic chain consists of a number of small vessels which unite into two main vessels, running from the medulla interna and the medulla externa respectively to unite within the sinus gland before debouching into the outer blood sinus. As may be seen from Figs. 3 and 4, sinus gland tissue surrounds the outer part of these two blood vessels and the body of the gland is arranged around the opening into the blood sinus.

The tract of fibres from the various neurosecretory centres enters the sinus gland by the proximo-abaxial corner (see Fig. 4). The fibres im-mediately split up and the numerous club-shaped endings of each fibre run perpendicularly to the surface of the gland to abut on to the blood sinus or on to one of the blood vessels.

The sensory papilla X organ

Since the sensory papilla has been reduced to a sensory pore lying close against the border of the eye, this organ has come to lie internally. In *P. borealis* the cuticle is almost as thick over the sensory pore as elsewhere on the eye-stalk so that the term becomes something of a misnomer (see Fig. 12). The bulk of the organ is made up of neurosecretory axons and nerve endings, together with a rather large amount of supporting connective tissue and a groundwork of epithelium-like cells. The cytoplasm of these cells will not take up any of the common stains. About 8–10 neurosecretory fibres run into the *s.p.x.* and divide several times before terminating in the characteristic 'onion bodies' of the *s.p.x.* Each branch terminates in one of these bodies, which in section looks much like a section of an onion; the onion bodies

corresponding to all the branches of any one axon lie together and are bound into a group by a fibrous membrane. They stain with aniline blue in Heidenhain's azan technique. The whole organ is bounded on all sides, except where attached to the medulla terminalis or to the sensory pore, by a connective tissue sheath. It is cylindrical and abuts into a blood sinus (see Figs 2, 6 and 7). A few small blood vessels penetrate into its tissue. The sensory nerve cells which line the sensory pore are in no way remarkable, having scant cytoplasm and fine axons. The staining of the nuclei suggests that there may be two types, one about three times as abundant as the other (see Fig. 12).

There is a very noticeable seasonal variation in females in the histology of the *s.p.x.* (cf. that in *P. kessleri*, Aoto & Nishida, 1956). In April–June, a period between breeding seasons, when the eggs have recently hatched and the ovary has not yet begun to grow for the next breeding season, the epithelioid cells of the *s.p.x.* appear to lose the cell boundaries and to become syncytial; there is little trace of secretory material in the onion bodies (Fig. 10). In September, when the ovaries have begun vitellogenesis for the forthcoming oviposition in December, the epithelioid cells are discrete, and there is much secretory material in the onion bodies and around them. The space between the onion bodies and the surrounding fibrous sheath may be grossly distended with colloid (hyaline or loaded with secretory granules) so that the sheath surrounds a space ten times the volume of the contained group of onion bodies (Fig. 11). The younger males show a condition approximating to that of the April females; the males approaching sex reversal a condition similar to that of the September females. This is true of the males at all times of the year; there is no obvious seasonal variation in the male *s.p.x.*

THE RETRORETINAL ORGAN

The retroretinal organ of the eye-stalk lies behind the lamina ganglionaris of the retina. Like the *s.p.x.* it shows strong seasonal variation. The structure is the same in both males and females and the seasonal cycles are in step in the two sexes. It does not, therefore, vary with the state of the *s.p.x.*, which has no seasonal variation in the male. At certain seasons of the year, notably September, it has the appearance of a secretory organ, but at other times it has the appearance more of adipose tissue. It does not seem to vary with the stage of the moult cycle.

In a specimen taken in September the retroretinal organ has the appearance roughly of a portion of the exocrine tissue of a mammalian pancreas, with circular nests of cells (acini) surrounding a central lumen (Fig. 13). The cells, which are columnar, are loaded with granules. Little material is visible in the lumen of the acini. These acini fill any available space behind the retina; their distribution varies widely in different individuals and seems
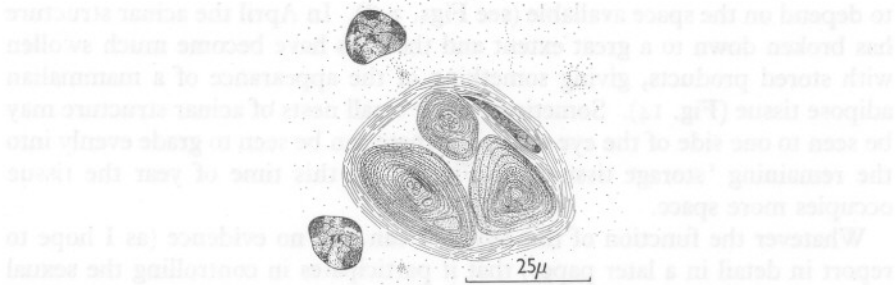
Fig. 10. A single group of onion bodies embedded in a syncytium of epithelioid tissue from the sensory papilla X organ of the eye-stalk drawn in Figs. 2–6, a specimen taken in June.
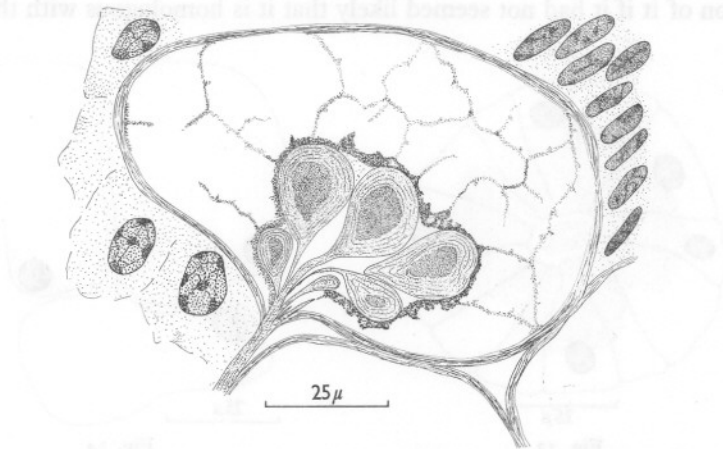

Fig. 11. A single group of onion bodies from a sensory papilla X organ of a specimen taken in September. In this section the branching of the axon into the various branches, each terminating in an onion body, is clearly seen. The onion bodies are full of secretion and the sheath is grossly distended into a cyst. Portions of other cysts are seen by the lower right corner, the discrete epithelioid cells to the left, and the nuclei of the sensory neurones of the sensory pore by the top right corner.
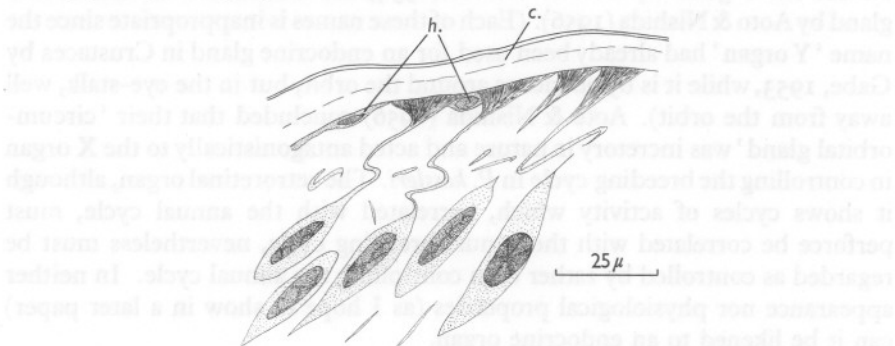
Fig. 12. Sensory cells of the sensory pore, from the same specimen as Fig. 9. Note the relative thickness of the chitinous cuticle over the pore and to one side. *c.*, chitinous cuticle; *h.*, hypodermal cells.

to depend on the space available (see Figs. 3–8). In April the acinar structure
has broken down to a great extent and the cells have become much swollen
with stored products, giving something of the appearance of a mammalian
adipose tissue (Fig. 14). Sometimes a few small nests of acinar structure may
be seen to one side of the eye-stalk, but these can be seen to grade evenly into
the remaining 'storage tissue' (cf. Fig. 8). At this time of year the tissue
occupies more space.

Whatever the function of this tissue, I can find no evidence (as I hope to
report in detail in a later paper) that it participates in controlling the sexual
cycles of *Pandalus*. Nor do I believe it to be an endocrine organ at all. Indeed,
so unlike an endocrine organ is it in appearance that I should have made no
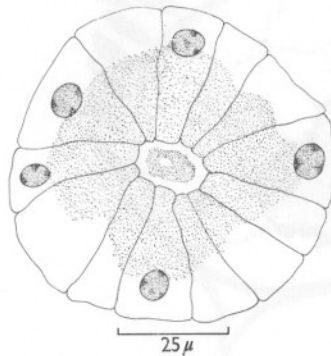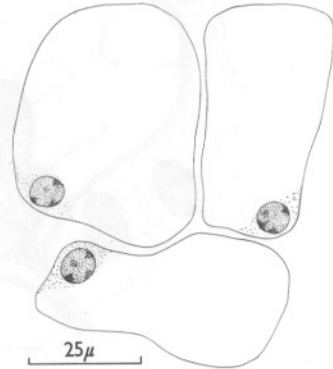mention of it if it had not seemed likely that it is homologous with the organ

Fig. 13. An acinus of the retroretinal organ from a specimen taken in September.

Fig. 14. Retroretinal tissue from the eye-stalk of a specimen taken in June.

termed the Y gland by Aoto & Nishida (1954) and termed the circum-orbital
gland by Aoto & Nishida (1956). (Each of these names is inappropriate since the
name 'Y organ' had already been used for an endocrine gland in Crustacea by
Gabe, 1953, while it is by no means around the orbit, but in the eye-stalk, well
away from the orbit). Aoto & Nishida (1956) concluded that their 'circum-
orbital gland' was incretory in nature and acted antagonistically to the X organ
in controlling the breeding cycle in *P. kessleri*. The retroretinal organ, although
it shows cycles of activity which, correlated with the annual cycle, must
perforce be correlated with the annual breeding cycle, nevertheless must be
regarded as controlled by rather than controlling the annual cycle. In neither
appearance nor physiological properties (as I hope to show in a later paper)
can it be likened to an endocrine organ.

THE VAS DEFERENS GLAND

This gland lies in and on the wall of the vas deferens and was first described in *Orchestia* by Charniaux-Cotton (1954), who at first gave it no name. Knowles & Carlisle (1956) called it the vas deferens gland, while the original discoverer (1956) later named it *la glande androgène*. The former name seems preferable, for, by common anatomical convention, it is customary to
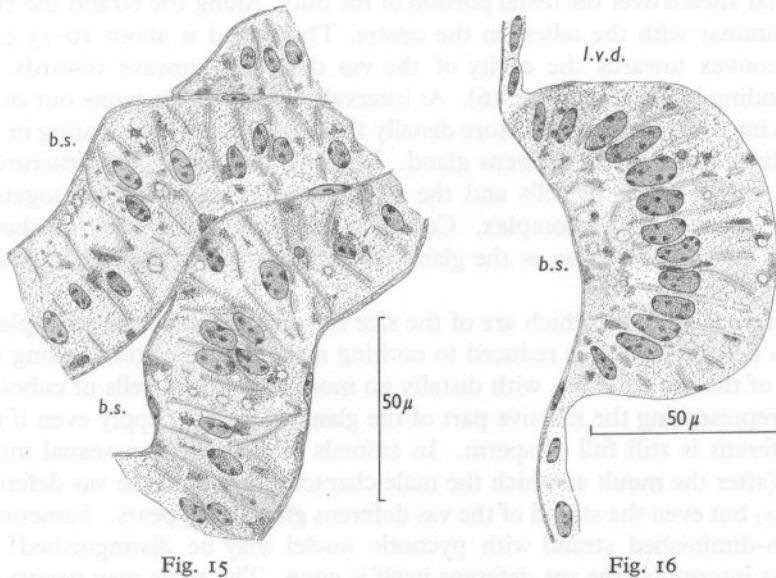

Fig. 15. Part of the massive portion of the vas deferens gland. Note the fibrous sheath. *b.s.*, blood sinus.

Fig. 16. A transverse section of the strand of the vas deferens, with a portion of the squamous epithelium of the duct. Note the continuous fibrous sheath over the outer side of both duct and strand. *b.s.*, blood sinus; *l.v.d.*, lumen of the vas deferens.

name an organ from its appearance or topography and not from its supposed function; for even if the function is correctly induced this may not be the only or the main function of the organ.

In a fully functional male *P. borealis*, some few moults before sex reversal, the gland is well developed. The bulk of the organ is attached to the distal end of the vas deferens, near where it swells as a vesicula seminalis. It consists of two or more cords of cells which entwine round one another making an irregular heap (Fig. 15). The cells are columnar, about $45 \times 10\,\mu$, with nuclei about $10 \times 7\,\mu$. The cytoplasm is granulated and frequently (though not always) vacuolated. The general structure is of entwining strips of columnar epithelium, covered by a tenuous, though definite, connective tissue sheath. Close inspection shows that this massive organ (about $250 \times 100\,\mu$) is attached

to a strip of specialized epithelium of the vas deferens. In serial section this strand of cells, of the same nature as those of the bulk of the vas deferens gland, is seen to run the whole length of the vas deferens along one side. Most of my series of sections are disorientated but I believe that this strand runs along the median edge of the vas deferens. The epithelium covering the vas deferens is a single-layered pavement epithelium with much flattened nuclei covered by a thin connective tissue sheath which burgeons into a muscular sheath over the distal portion of the duct. Along the strand the cells are columnar with the tallest in the centre. The strand is about 10–15 cells wide, convex towards the cavity of the vas deferens, concave towards the surrounding blood sinus (Fig. 16). At intervals along it there twine out cords of cells into the blood sinus. More distally these are bigger, culminating in the most distal massive vas deferens gland. I believe that the whole structure—strand, minor cords of cells and the major massive group—form together the vas deferens gland complex. Certainly the massive part may be shown to have the same function as the gland of *Orchestia*, while the rest is closely connected with it.

In male *P. borealis*, which are of the size at which sex reversal takes place, the vas deferens gland is reduced to nothing more than the strand along the length of the vas deferens, with distally no more than 10–20 cells of cuboidal shape representing the massive part of the gland. This may apply even if the vas deferens is still full of sperm. In animals of the first non-sexual inter-moult (after the moult at which the male characters are lost) the vas deferens remains, but even the strand of the vas deferens gland disappears. Sometimes a much-diminished strand with pycnotic nuclei may be distinguished. In the next intermoult the vas deferens itself is gone. The testis may persist for several moults after the animal has become fully functional as a female, but eventually it too degenerates leaving no trace.

DISCUSSION

The X organ-sinus gland complex of *P. borealis* is of the type which seems to be primitive in decapods and somewhat similar to that found in *Lysmata* (Carlisle, 1953c). It differs from that in *Palaemon* chiefly in that the latter has lost the sensory pore. One secondary feature of the system in *Pandalus* appears to be the shortening of the X organ-sinus gland tract, which seems primitively to run in an S-shaped curve (or more complicated convolutions) from the *m.t.g.x.* to the sinus gland (see Carlisle & Knowles, 1959). The complications of the course of this tract are presumably a consequence of the distortion of the topography of this region by the development and elongation of the eye-stalk. The straight route of this nerve tract in *Pandalus* is thus presumably secondary.

The vas deferens gland is not yet sufficiently well known in many species

to enable one to say whether the condition of this gland in *P. borealis* is exceptional. In Mme Charniaux-Cotton's description and figures of the gland in *Orchestia*, where it was first described (Charniaux-Cotton, 1956), the gland is seen to lie entirely outside the muscle and connective tissue sheath of the vas deferens. This I also find to be the condition in *Processa canaliculata* and *Palaemon serratus*, in both of which the sheath is continuous between the vas deferens and the gland. In four species of Pandalidae, however, the sheath runs outside the gland, which is nowhere delimited from the vas deferens, but forms indeed, in places, part of the wall of the duct (see Fig. 14). Only when sex reversal is imminent does the gland become detached from the vas deferens, and the muscular sheath pass between them. Which of these conditions is primitive and which is the more widely distributed we have as yet no means of knowing. One species which would most repay study in this connexion is *Lysmata seticaudata*, the only non-pandaloid natatian which is known to be a protandric hermaphrodite. It may be that the condition found in *Pandalus* is bound up with protandric hermaphroditism.

A cursory examination which I have made of two other species of *Pandalus* —*P. montagui* Leach and *P. bonnieri* Caullery—and of the related *Pandalina brevirostris* (Rathke), revealed but minor variations in the two incretory systems from the conditions described here for *P. borealis*. It seems likely, then, that it represents the norm for the genus. The two organ systems which I have described—the X organ-sinus gland complex and the vas deferens gland system—are known in other species of crustaceans to act as endocrine organs affecting or, in part, controlling the sexual biology. I hope to show in later papers that they have this function also in *P. borealis*. In this histological investigation it has become abundantly clear that the structure of these two systems gives one every ground for ascribing an incretory activity, and, indeed, in so far as secretion is a histological concept, these organs are, by definition, organs of internal secretion.

SUMMARY

The X organ-sinus gland complex of *Pandalus borealis* illustrates a condition which is relatively primitive in decapods. The complex is described and the histology and topography of the various parts figured. The only major departure from the primitive condition is the secondary shortening of the X organ-sinus gland neurosecretory tract. The annual cycle of activity in the sensory papilla X organ is briefly described and discussed. The vas deferens

gland (*glande androgène*) is described and its special features noted. The correlation between its condition and the sexual state of this protandric hermaphrodite is stressed.

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