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by Frank Burghause

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"Das Y-Organ von Orconectes limosus (Malacostraca, Astacura),"
Z. Morph. Tiere 80, 41 - 57, 1975

The Y organ of Orconectes limosus (Malacostraca, Astacura)

by

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Summary - The crayfish Orconectes limosus has a paired Y organ and a paired mandibular organ. The Y organ is located in the epidermis near the attachment of the posterior dorsoventral muscle. It is an oval disk of epidermis that appears hypertrophied; it consists of closely packed cone-like projections into the connective tissue. The Y organ is a ductless endocrine gland without any innervation. The gland is separated from the connective tissue by a basement membrane. During molting, cyclic alterations in the Y organ were observed. During the pre-molt period, the organ became thicker and the nuclei were enlarged. During the post-molt period, the nuclei again decreased in size, but were elongated. No mitotic events were observed in the organ throughout the investigation. Upon expirtation of the paired Y organ, two of 17 individual succeeded in molting compared to 14 of 22 control animals. It is suggested that the Y organ may be considered to represent the organ responsible for the molting process.

[1] I am indebted to Professor Dr. R. Keller for friendly support.

A. Introduction

For a long time, workers have tried to find molting glands in astacurans corresponding to the prothoracic glands of insects. In about one hundred different different malacostracans, Gabe (1953; 1954; 1956) described an endocrine gland, which he called the Y organ; however, his descriptions of the position and of the shape of his organ were so general in character that identification of the Y organ has been confirmed by other workers only in a few species. In the case of the European shore crab (Carcinus maenas), Echalier (1959) was able in an unequivocal manner to identify the Y organ with the aid of extirpation and re-implantation experiments. On the basis of his work, research on this organ has been concentrated on the Brachyura. Matsumoto (1962) investigated this gland (ventral gland) with regard to its alterations in the course of molting. Knowles (1956) and Bressac (1973) have published photographs of the ultrastructure of this organ. Spazani and Kater (1973) have established the cholesterol metabolism of the Y organ of Hemigrapsus and, thus, provided the first direct evidence that this organ actually plays an important role in the metabolism of ecdysterone.

Definite demonstration of the existence of the Y organ in Astacura (Macrura) has hitherto not been made. In fact, there exist several reports on an endocrine gland of that type, but the respective authors—carrying out physiological experimental work—have not described the position and the structure of this organ in a precise manner, or have not supplemented their histological findings with corresponding experiments. A good review of these rather obscure conditions has been provided by Sochasky et al. (1972). The morphology has been described by Le Roux (1974) and by Aoto (1974). It must furthermore be mentioned that Maissiat and Legrand (1970) as well as Blanchet (1974) have demonstrated the existence of a Y organ in the isopods.

B. Material and Methods

Freshwater crayfish (Orconectes limosus RAFINESQUE) were captured in the Havel River near Berlin and then kept in a subdivided Eternite® basin in running water. We have employed male animals only, in order to eliminate the effects of oogenesis on the processes of molting. During the winter, the water temperature amounted to 18°C. During the summer, the animals were kept outside, and the water temperature varied then between 18 and 23°C depending on the weather conditions prevailing. The individual crayfish weighed between 15.5 and 33.0 grams. The animals were fed with cat food (manufactured by the firm Friskis, Hamburg). Assessment of the different molting stages was carried out on the basis of Drach's (1939) table taking into consideration the investigations reported by Skinner (1962), Travis (1965), Keller and Adelung (1969), Stevenson (1972), and Willig and Keller (1972).

The Y organ was prepared in the following manner: The animals were sacrificed, and the tail and the abdominal appendages were removed; the carapace was opened along the median line, and the mouthparts, the branchiae and the bases of the cursorial limbs (pedes cursorii) were removed. In the branchial chamber there lies a window-like zone on the apical side close to the condyle of the mandible; this zone is surrounded by a cuticular bracelet. The Y organ is located directly under this thin, oval structure bearing delicate hairs.

In the course of surgical extirpation of the organ, the external cuticle (integument) was opened—right in front of the neck furrow—with the aid of a cylindrical dentist's drill, and the organ, close to the lateral projections, was separated as completely as possible. This technique is elaborate in character, and it is difficult to remove the glandular tissue completely. The wound was closed with the aid of Nobekutan® (manufactured by the firm Nobel-Bofors)

and protected with a small disk of warmed wax. The same procedure was carried out on the control animals, with the exception that the Y organ was left in place. The crayfish were then observed over an entire summer.

For histological examination, the Y organs were exposed in ice-cold Harrevelt mixture, fixed in Bouin's mixture, and dehydrated with ethanol and dioxane. The azan method of staining after Heidenhain turned out to be best suited in the case of our sections measuring six to seven µm in thickness.

The nuclei were measured at 800-fold magnification with the aid of an eyepiece micrometer. The average value obtained in about 50 measurements per animal are reported (Figure 4, and Table 1). Measurements of absorption were carried out at a wavelength of 578 nm (yellowish-green) with the aid of a Leitz cytophotometer. The measuring area was circular and had a radius of 47.06 µm.

C. Results

I. Structure and position

Careful scanning of our serial sections from the rostrum into the branchial region revealed the presence of two paired ductless glands in the maxillary segments.

The one gland, which is called the mandibular organ (cf. also Table 3), is located posteriolateral to the esophagus and dorsolateral to the nerve trunk of the pharyngeal ring, in the corner between the apodeme of the posterio adductors of the mandible and the major adductor of the mandible, close to the cephalic apodeme (Figure 1). The mandibular organ consists of several, loosely connected cellular filaments. A connection to the ventral epidermis was not found to exist. The cells have no specific form and show identical development. In particular, inclusions or secretory granules were not found.

The other one of the two glands found in the maxillary segments is located caudal to the plane of attachment of the posterior dorsoventral muscle. A layer of connective tissue is found at that site, and a branched blood sinus passes through this tissue. A disk-shaped piece of epidermis—giving the impression of being hypertrophied—is located on that layer. This gland must be regarded as the Y organ of the crayfish. The elongated oval organ measures about 1.5 mm in length and 0.7 mm in width (Figure 1). With regard to both structure and position, this gland corresponds best to the description given by Gabe (1956). In the region of the Y organ, the epidermis forms numerous, closely arranged, cone-like projections, which attain a depth of 260 µm (Figures 2 and 3). Between the individual projections, one occasionally finds formation of intercellular spaces, which are then lined by a basement membrane or lamina. At the margin,

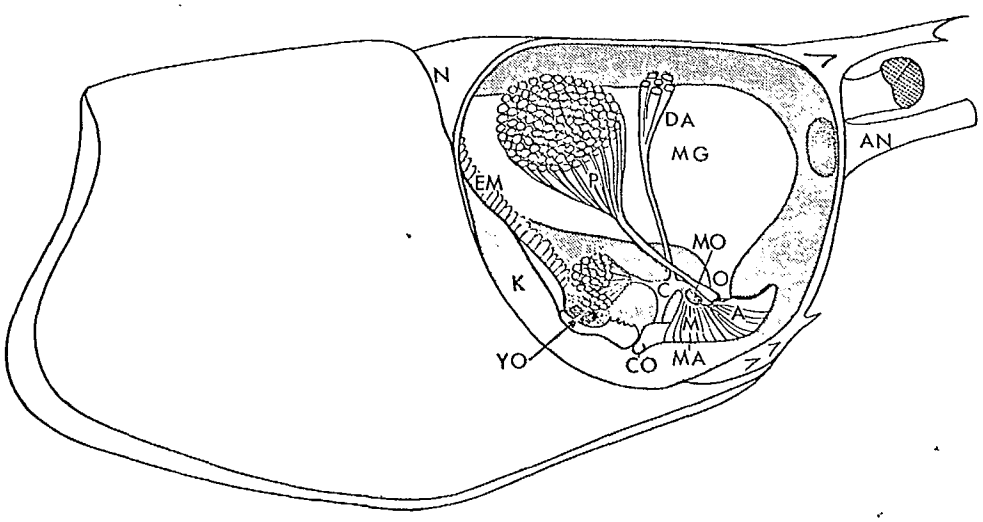


Figure 1 - Sketch of the carapace opened from the side illustrating the locations of the Y organ and of the mandibular organ.[1]

[1]Translator's note: The key to the abbreviations appears at the end of this Manuscript (in front of the Bibliography). To avoid confusion, I have not changed the German abbreviations into English ones, but have given the English definitions.

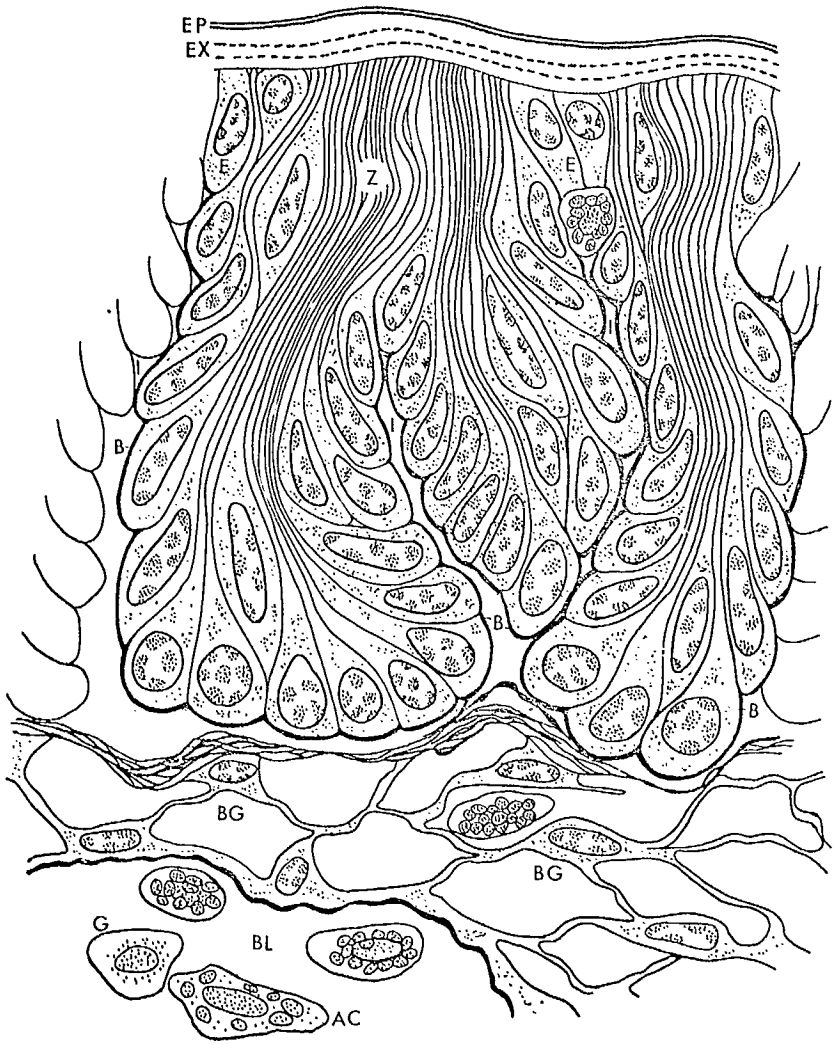
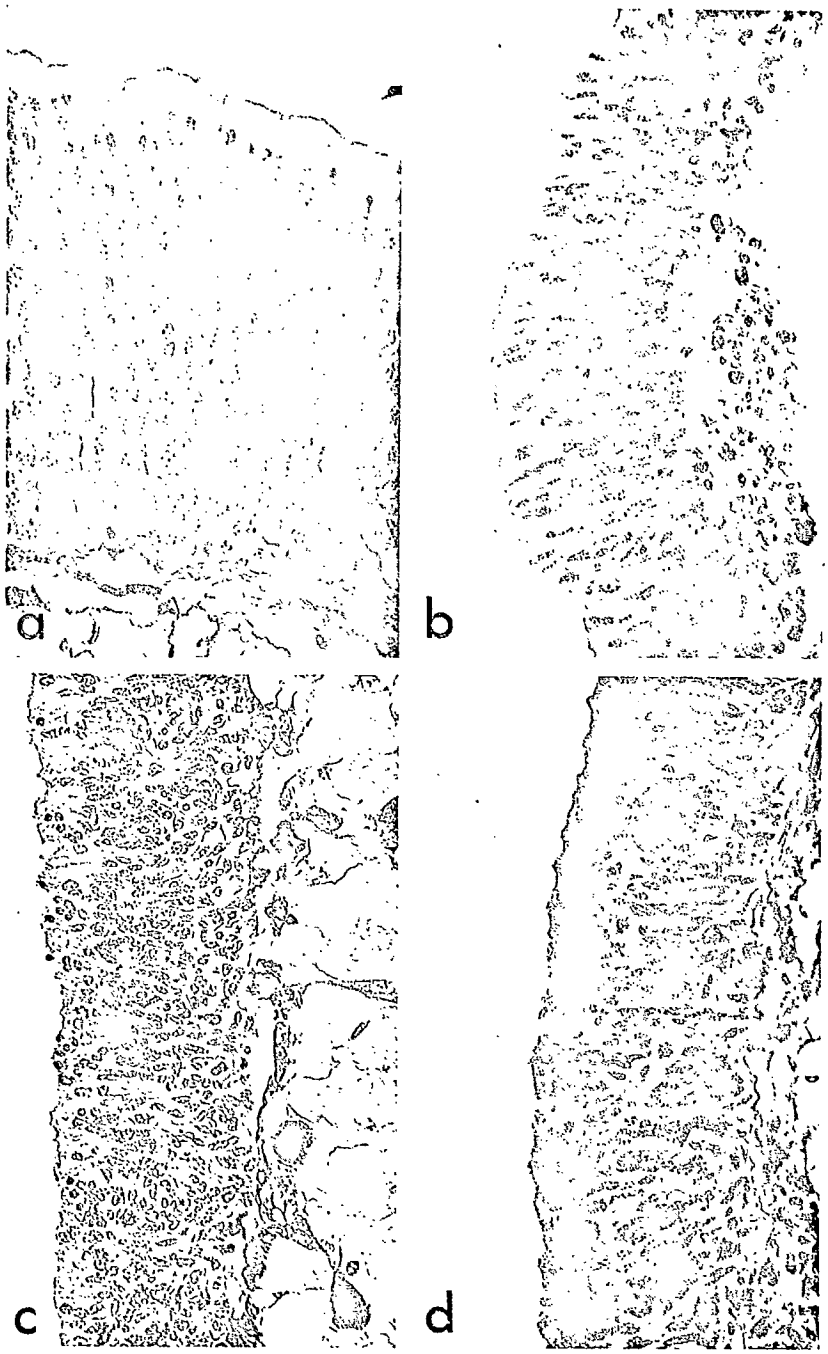


Figure 2 - Diagrammatic cross-section through the Y organ in the inter-molt stage.

the organ rapidly becomes thinner and passes into the normal epidermis. The entire organ consists of one type of cells, if we disregard the blood cells, which actually do not belong to the organ proper. These cells are spindle-shaped to droplet-shaped, and they exhibit a long apical process, which, as a rule, reaches up to the cuticle. The cytoplasm is granulated. The chromatin of the—mostly elongated oval—nuclei is divided over six to eight well defined areas.



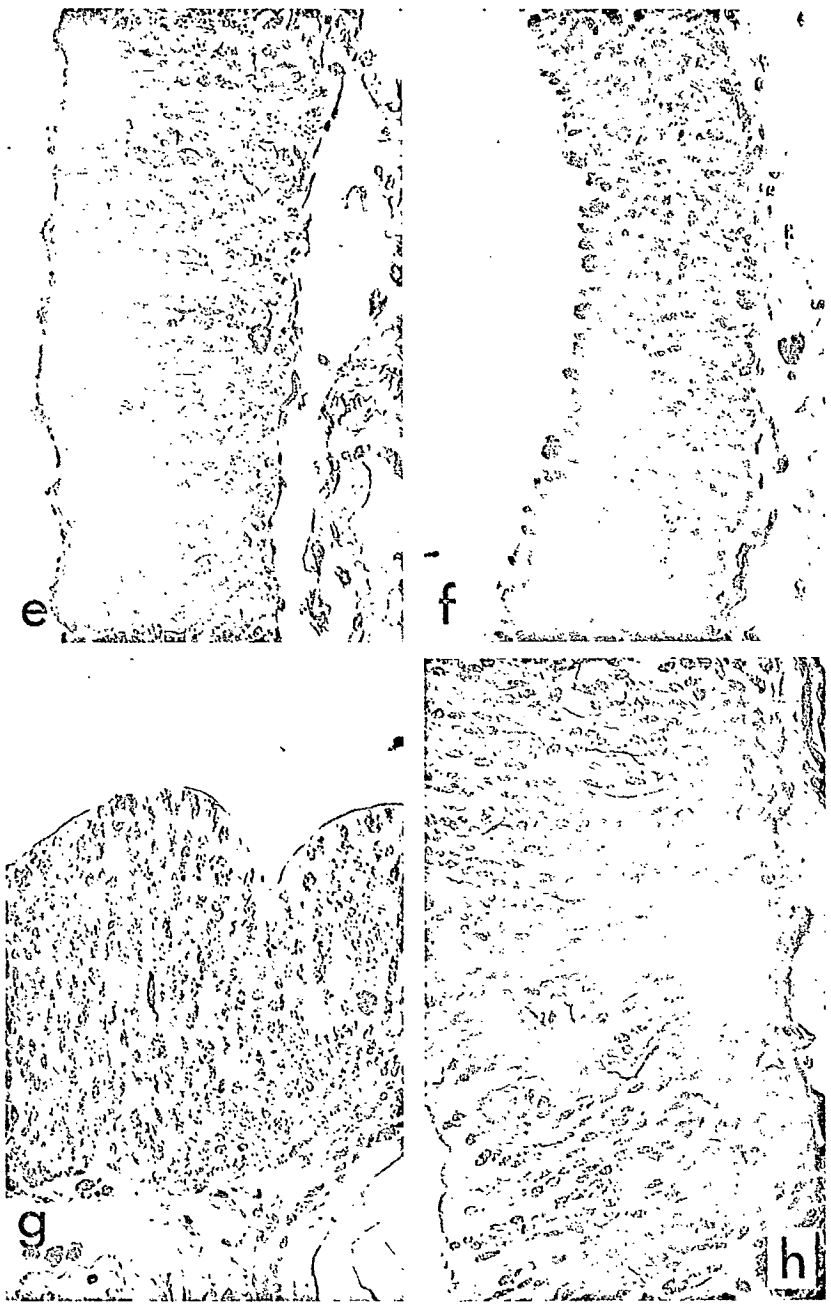
Figures 3a to 3d - Cross-sections through the Y organ during different molting stages. x 250.

Figure 3a - A, with elongated nuclei and nucleus-free edge.

Figure 3b - B, the organ has flattened.

Figure 3c - C, with nucleus-free edge following molting or during the winter.

Figure 3d - C, in preparation for molting, the nuclei have migrated toward the apical edge.

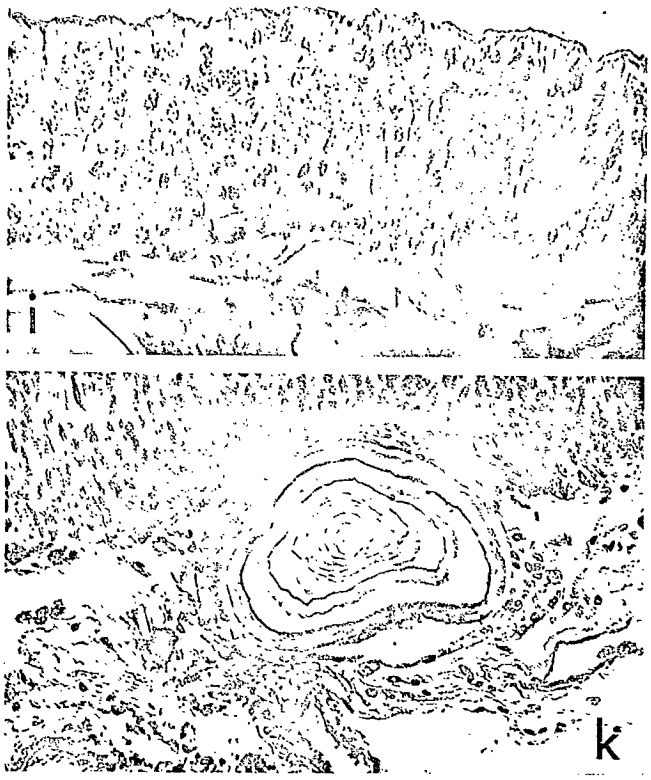


Figures 3e to 3h - Cross-section through the Y organ during different molting stages. x 250.

Figure 3e - D_0, with numerous red globules above the edge. Figure 3f - D_1.

Figure 3g - D_3, the epicuticle has formed.

Figure 3h - D_3, the nuclei are retreating from the apical edge.



Figures 3i and 3k - Cross-sections through the Y organ during different molting stages. x 250.

Figure 3i - D_4, the epicuticle and the exocuticle can be distinguished.

Figure 3k - A 'crayfish pearl'

One or rarely two nucleoli have been observed. Between the projecting cones, there lie a few cells, which resemble normal epidermal cells. The cuticle is loosely attached to the organ and can be pulled off during the inter-molt phase without doing injury to the organ as such. Against the connective tissue, the organ is separated by a thick basement lamina, which, in part, is fibrillated. The ramifications of a blood sinus border directly on that lamina. Blood cells frequently penetrate into the spaces between the cones and may also be found between the cells of the Y organ. Silver staining after Palmgren (1955) did not reveal the presence of nerves in this organ.

In several animals, we found "crayfish pearls" (Blass, 1941) directly under the Y organ (Figure 3k). These concentric, spherical structures gave the impression that they had been formed in the course of several moltings from an initially rather small cuticular grain (cf. also Danini, 1928). An unequivocal explanation for these structures could not be given.

II. Changes occurring in the course of the molting cycle

The appearance of the Y organ changes in connection with the molting cycle. Effects of seasonal or diurnal rhythms could not be determined. The changes taking place at the apical edge or margin are the most striking ones. During phases D_3 to C (for the division of the molting cycle into stages, cf. in "Material and Methods"), that apical portion is almost free from nuclei (Figures 3a, 3b, 3c, 3h and 3i). However, during the other phases, nuclei were present directly along the margin, and this frequently in large numbers. A part of the Y organs exhibits numerous nuclei directly along the apical margin also during phase C during the summer (Figure 3d).

In order to demonstrate also other changes occurring in the Y organ, we have carried out measurements of both nuclear sizes and absorption in preparations, in which the tissue had been cross-sectioned. The results of these measurements—which are summarized in Table 1 with regard to values important for the division into phases—represent average values for the individual animals. The overall thickness of the organ also undergoes alterations. The thickness increases during the pre-molting period up to phase A.

The shape of the nuclei undergoes alterations during the molting cycle. The relations existing between nucleus length and nucleus width are illustrated in Figure 4. The nuclei acquire a more spherical shape during the pre-molting phase. However, during actual molting and shortly after that event, the nuclei

Table 1 - Comp lation of data obtained in individual experimental animals. Key: 1, No.; 2, Stage; 3, Weight (in g); 4, Carapace length; 5, Gastrolith; 6, Organ thickness (in µm); 7, Ratio of organ thickness to carapace length; 8, Length of nucleus; 9, Width of nucleus.

1 Nr.	2 Stadium	3 Gewicht (g)	4 Carapaxlänge (mm)	5 Gastrolith	6 Organdicke (µm)	7 Organdicke / Carapaxlänge	8 Kernlänge (µm)	9 Kernbreite (µm)	Absorption (578 nm)
46	A	15,0	35,0	109,4	260	7,69	8,5	4,0	50,6
47		17,8	36,6	53,6	128	3,50	6,9	3,3	65,4
30	B	21,5	38,4	13,54	131	3,42	7,9	2,6	67,0
26		18,0	36,4	8,26	109	3,00	8,5	3,1	85,2
41		23,8	39,4		128	3,25	8,7	2,9	85,2
33		20,5	37,0	30,27	147	3,98			68,5
49		20,1	34,7	30,83	141	4,06			
35		21,5	35,2	17,90	96	2,73			
19	C	24,1	37,3		128	3,44	7,6	3,3	72,2
31		23,0	37,0		115	3,12	8,9	3,2	
40		33,1	42,4		176	4,16	6,5	3,6	
57		21,7	36,3		115	3,18	6,7	3,2	22,25
48	D_0	25,5	39,6	1,01	128	3,24	6,7	3,0	50,0
54		18,6	35,0	1,14	147	4,21	7,26	3,72	66,9
58		18,5	36,4	1,92	128	3,52	7,6	3,2	53,4
21		27,2	38,3	4,81	135	3,51	5,8	4,0	65,0
43		31,3	38,9	4,52	141	3,63	6,9	2,9	
15		32,1	42,5	7,76	112	3,01			
16		28,3	39,3	9,92	147	3,74	8,1	3,3	
13		31,3	40,5	16,36	153	3,80	7,6	3,6	
32		20,8	36,2	16,57	135	3,72			71,0
37		22,8	36,4	10,60	122	3,35			76,2
38		19,2	36,1	24,38	154	4,26			
14	D_1	27,8	40,1	25,49	173	4,31	7,3	3,7	65,0
20		27,2	38,6	35,49	179	4,65	8,1	3,5	67,4
42	D_2	30,2	40,7	26,44	160	3,94	7,4	3,4	47,4
28		26,7	40,1	95,26	153	3,84	7,7	3,7	61,9
12		25,7	38,8	119,85	192	4,96	7,2	3,8	65,5
9		23,9	36,2	108,01	151	4,16	8,1	3,5	67,9
52	D_3	16,2	33,1	64,05	154	4,65	7,2	3,1	61,0
53		20,5	37,2	90,86	192	5,17	7,4	3,5	61,3
56		18,3	35,4	131,36	244	6,88	7,4	3,7	59,9
36	D_4	15,8	33,4	133,77	144	4,31	7,5	3,6	68,5
44		23,8	37,2	101,61	147	3,96	7,5	4,1	
17		28,9	40,6	172,70	192	4,77	8,6	4,3	55,0

undergo pronounced stretching. In the latter Figure, we have also plotted the product of nucleus length and nucleus width. That product represents a measure for the sectioned area. Since the nuclei usually exhibit shapes that resemble rotational bodies, we must-at equal sectioned areas—assign the smaller volume to the nuclei exhibiting elongated shapes. The nuclear volume increased greatly during phases D_1 to A.

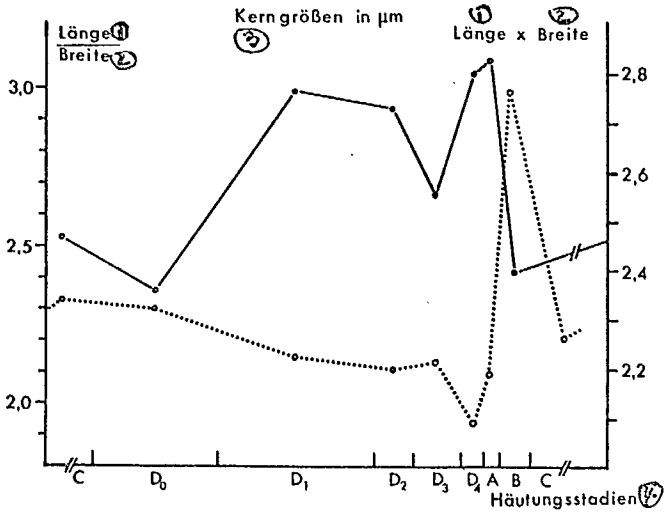


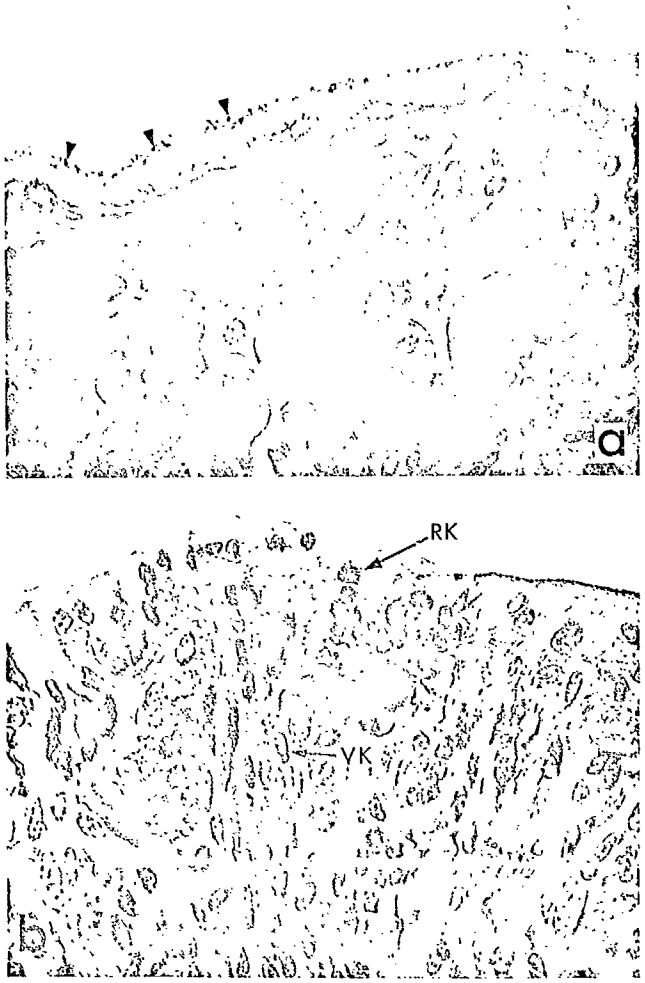
Figure 4 - Product of length of nucleus and width of nucleus (——) and ratio of length of nucleus to width of nucleus (. . .) during different stages of molting. Key: 1, Length; 2, Width; 3, Nuclear sizes, in µm; 4, Molting stage.

Using a cytophotometer we have measured the absorption on cross-sections; at a wavelength of 578 nm, absorption is caused almost exclusively by the stained nuclei. That absorption, then, represents a measure for the relation of total area to cross-sectioned area of the nuclei. At size of the measuring area, we obtain an indication for the number of nuclei present per volume cytoplasm. Figure 5 reveals that the nuclear quantity increased greatly following molting and then, in relation to the cytoplasm, decreased again up to the next molting. If we take into consideration the alterations of the thickness of this organ, it appears that the number of nuclei in the entire organ must be approximately constant.

The cuticle above the Y organ is also involved in the molting process. The epicuticle is formed during phase D_2, and the exocuticle then during phase D_3. The latter cuticle, however, remains very thin, and only during phase A is about ten times as thick as the epicuticle. During phase C—shortly before

Figure 5 - Absorption of a certain area of a cross-section at 578 nm during different molting stages. The respective values provide an indication for the relation between nuclear quantity and cytoplasmic quantity. Key: 1, Molting stage; 2, Absorption in per cent at 578 nm.

other animals under the same conditions start with their molting preparations— a layer measuring seven to ten µm in thickness is found, which layer appears bluish on staining. This layer is connected with the cells by means of small, narrow bridges (Figure 6a). Small, red-stained bodies are embedded in the surface of the layer (indicated by arrows). Both the size and the number of the spherical structures increase during the following phase D_0 (Figure 3e). In the subsequent course of the cycle, we observed only a few red globules, which then, however, exhibited almost the size of nuclei. Bodies of that nature were no longer observed following appearance of the epicuticle during phase D_2. Structures of that type were not found in the normal epidermis. Shortly before molting, there appeared other red-stained structures, which, with regard to both shape and size, corresponded to the nuclei. These structures were stained a homogenous red. They gave the impression of degenerated nuclei (Figure 6b,



Figures 6a and 6b - Formations on the apical edge of the Y organ. x 620.

Figure 6a - Toward the end of stage C, a bluish layer containing numerous red bodies (indicated by arrows) is formed between the organ and the cuticle.

Figure 6b - In addition to normal nuclei, there appear, shortly after molting, also nuclei with indistinct chromatin plaques as well as homogenous red bodies.

RK [red bodies]), because in their vicinity there were nuclei, whose normally distinct plaque patterns were blurred (Figure 6b, VK [nucleus with obliterated plaque pattern]). It is surprising that no mitotic stages have been found in the Y organs, despite a thorough search.

The limit of detection of ecdysone lies around 10 ng. We had available in each instance only about 25 mg of organ tissue for processing for the Musca assay. In order to be demonstrated in that assay, the ecdysone content would have to be about ten times greater than the quantity Willig and Keller (1973) found using a maximum of 50 ng/g fresh weight. We have been unable to demonstrate the presence of ecdysone in any phase.

III. Extirpation experiments.

The Y organs of 28 crayfish were removed by surgical means from both sides. Twenty-three control animals were subjected to sham operations. Eight of the animals without Y organs dies, without demonstration by us of gastrliths, which represent a positive sign for molting preparations. Table 2 summarizes our results. This Table illustrates the times at which the animals underwent moulting or died, respectively. Three of the animals subjected to surgical extirpation underwent moulting, and two died exhibiting signs of molting preparations. Four of these five animals were subjected to histological examination. Three of these crayfish exhibited residues of the Y organ (Figure 7), i.e. extirpation had not been complete in these instances.

Among the control animals, only one crayfish died without showing signs indicating molting preparations. Three animals died during the pre-molting period. Eleven crayfish underwent molt successfully. One crayfish, in fact, underwent molt twice.

The causes of death of our crayfish are not known. The midgut gland usually was very small and had acquired a grey color. The animals, which succumbed without molting preparations, therefore, will not be taken into further consideration. Among the twenty operated animals remaining, we found that three still exhibited residues of the Y organ, i.e. only two of the 17 [properly]

Table 2 - Key: 1, Crayfish subjected to surgical extirpation of the Y organ; 2, Number of animals; 3, Days after extirpation; 4, exhibiting residues of the Y organ; 5, Dead showing no gastrolith; 6, Dead showing gastrolith; 7, Molted; 8, Control animals; 9, Molted twice; 10, Remaining.

(1) Operierte Krebse	(2) Tieranzahl	(4)	(3) Tage nach dem Eingriff
Tot ohne Gastrolith 5	8		39, 43, 43, 62, 68, 84, 133, 171
Tot mit Gastrolith 6	2	1) mit Resten	147, 151
Gehäutet 7	3	2) des Y-Organs	140, 149, 162
Rest 10	15		188
Kontrolltiere 8			
Tot ohne Gastrolith 5	1		50
Tot mit Gastrolith 6	3		131, 144, 147
Gehäutet 7	11		118, 118, 120, 120, 123, 128, 128, 130, 140, 143, 145
Zweites Mal gehäutet 9	1		179
Rest 10	9		188

Figure 7 - Part of an Y organ left behind during surgical extirpation.

operated animals underwent molt. Fourteen of the remaining 22 control animals underwent molt or exhibited molting preparations.

In addition, it must be mentioned that animals without Y organs, in contrast to the control animals, did not form extremity regenerates.

D. Discussion

The results of our investigations demonstrate that the crayfish possesses both an Y organ and a mandibular organ, and that the Y organ is required for molting.

According to Gabe (1953), the Y organ is an organ analogous to the prothoracic gland. However, since the Y organ does not show nerves, it is very difficult to compare its position with that of the prothoracic gland. We then use the concept of Y organ for the endocrine gland eliciting molting. The superior concept of molting gland or ecdysial gland also is frequently used. In literature, the Y organ has frequently been mistaken for other structures. A review of the names used by the different authors is presented in Table 3. In addition, we must mention the investigations carried out by Miyawaki et al. (1971), which perhaps dealt with the mandibular organ. Carlisle and Connick (1973) probably have taken the antennal glands for the Y organ, which, no doubt, may contain molting-active products of degradation of ecdysone. Y organs have hitherto been found in Metapenaeus (Dall, 1954), Pamdalus (Hoffmann, 1967), Homarus (Le Roux, 1974) and Palaemon (Aoto et al., 1974), but so far it had not been possible to demonstrate their function in molting.

The changes in the glandular cells during the molting cycle described by Aoto et al. (1974) represented for these authors a sign for the activity of the Y organ as molting gland. Their data on the relative cytoplasm quantities coincide with the relations of nuclei to cytoplasm (Figure 5) determined in the present work. Similar conditions have also been described by Matsumoto (1962) in the case of Hemigrapsus (Brachyura).

The finding showing that several of the ablated crayfish underwent molting can be explained by the incomplete extirpation of the Y organ. In most of

Table 3 - Key: 1, Authors; 2, Gland in the antennal segment; 3, Lymphogenis tissue; 4, Hypertrophied strip of hypodermis.

Autor (1)	(2) Drüse im Antennen-segment	Mandibular-organ	Y-Organ
Chaudonneret (1956)		Y-Organ	
Durand (1969)		Y-Organ	
Dall (1965)			Y-Organ
Hoffman (1967)	(3) lymphogenes Gewebe	Mandibular-organ	
Sochasky *et al.* (1972)		Mandibular-organ	(4) hypertrophierter Hypodermisstreifen
Carlisle u. Connick (1973)	Y-Organ	Mandibular-organ	
Le Roux (1972)		Mandibular-organ	Y-Organ
Aoto *et al.* (1974)		Mandibular-organ	Y-Organ

these cases, we have been able to demonstrate the presence of organ residues. It is very easily possible that a portion of the organ remained in the wound during surgical extirpation and was then washed into the body cavity by way of the blood sinus. The rate of blood flow is high at that site. As endocrine glands, these parts can well be active at other sites within the body, as long as no "moult inhibiting hormone" is released. In this way it is possible to explain the moulting of these animals, in which no remaining organ residues were find postmortem at the site of the Y organ.

Re-implantation experiments could not be carried out, since captured animals undergo molt only rarely more than once a year, and the operated animals usually die during the following winter. For that reason, we have been unable to determine the effects of subsequent re-implantation of the glands.

The alterations of the integumental tissue of Orconectes limosus during the moly cycle have been described by Keller and Adelung (1970). Comparison

of their results with the alterations of the Y organ under the same conditions reveals certain parallels. For instance, the thickness of the tissues changed in both cases. However, these alterations took place in the integument much later in the molt cycle, and then were also much more pronounced. Since several changes occur in the Y organ already at a time where otherwise no molting preparations are in evidence, we must consider whether the onset of phase D_0 should not be redefined. The differences between epidermis and Y organ are particularly distinctly in evidence during the phases C to D_1; during these phases, the apical margin of the organ is distinguished by numerous bodies stained intensively red by azocarmine, which bodies are not found in the integument. It is worthy of note that there existed signs for the presence of degenerated nuclei during phases D_3 and D_4, but that no mitotic events were observed during the entire investigation. Despite obscurities of that nature concerning this organ, there can be no doubt on the basis of these new results regarding the existence of the Y organ in the macrurans, as has been doubted still by Sochasky et al. (1972).

Abbreviations

A anterior mandibular adductor
AC amoebocyte
AN antenna
B basement lamina
BL blood sinus
C cephalic apodeme
DA anterior dorsoventral muscle
DP posterior dorsoventral muscle
E epithelia cells between the cones
EM epidermal attractor muscle
EP epicuticle
EX exocuticle
G coagulation cell
I intercellular space
K branchial chamber
M major mandibular adductor
MA mandible
MG stomach
MO mandibular organ
N neck furrow
O esophagus
P posterior mandibular adductor
RK red body
VK nucleus with obliterated plaque pattern
YO Y organ
Z cellular processes

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