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Micro-cauterization of the Y-organs in *Orchestia gammarella* permanently ends molting. Exogenous ecdysone, by re-establishing molting, substitutes for Y-organ secretions. Thus Y-organs are really the source of ecdysone or of a precursor of this hormone. The "molt" hormone, applied at a relatively low hemolymphatic rate, enables the functioning of the claw-building processes (period C); applied at a higher rate, it triggers period D and induces byssus formation. The "exuviation factor", released as $D'$, would also be secreted by the Y-organs; it enables exuviation to take place.

Because of their close resemblance to the molt gland of insects, the newly discovered Y-organs were thought to be glands regulating molting in shellfish (1). This hypothesis was confirmed by experiments involving removal and grafting of Y-organs in the crabs *Carcinus maenas* ([2], [3]) and *Sesarma reticulatum* ([4]) and the isopod *Ligia oceanica* ([5]). The Y-organs were then given the name "molt glands".

*Crenzon vulgaris* ([6]) and *Carcinus maenas* ([7]) extracts prove to be active in the Calliphora test. Conversely, extracts taken from the locust *Schistocerca* cause "pro-ecdysis" in *Carcinus* ([8]). Thenceforth the fact was known that the molt hormone of shellfish is a compound closely resembling ecdysone, the molt hormone of insects.

Crustecdysone (20-hydroxyecdysone, ecdysone) was isolated
and ecdysone are both present in extracts taken from the crayfish Orconectes propinquus, but the biological action of ecdysone is never one-tenth as effective as crustecdysone's. The latter appears particularly active in several species of crustaceans, and rapidly triggers the phenomena that initiate molting \((11)\) to \((14)\). Crustecdysone may be considered as the molt hormone of crustaceans.

It is generally agreed that, in insects, ecdysone is secreted by the prothoracic glands. However, this hypothesis is much debated at present, and new arguments are found by those who believe ecdysone is not produced by the thoracic glands but in another region of the insect's body \((15)\). The problem also arises in the case of crustaceans: do the Y-organs, which are considered to be molt glands, secrete crustecdysone?

Structural changes are observed in Y-organ cells after an injection of ecdysterone \((16),(17)\), but these cytologic findings do not present a decisive argument as to the site of molt hormone synthesis. It therefore seemed to us interesting to inject ecdysterone into Orchestia gammarella experimentally deprived of their Y-organs.

MATERIAL AND METHODS.— The Y-organs of O. gammarella were first located by Gabe \((1)\) "in the 2nd maxillary metamere". We found them in the same location. They are, in effect, two cellular bodies located lateroventrally and subjacent to a local cuticular thickening. The two glands extend longitudinally and their average dimensions are \(300 \times 100 \times 30 \mu\). The cuticular thickening, visible from the outside, enables us to detect the site of the Y-organs during the operation.

The Y-organs are destroyed by galvanocautery under a
three-dimensional microscope. The two operations are carried out with a 1- or 2-day interval. The intermolt stage is then noted. At the conclusion of the experiment, seriated histologic sections enable us to see whether the destruction of the Y-organs has been complete and elective.

More than 250 animals were microcauterized. Considering the high post-operative mortality rate and especially the low proportion of successful operations, our findings cover only 40 individuals; they survived about 2 months. About 15 received ecdysone 2 weeks after the operation.

The method of injecting ecdysone, the dosages used, and the diagnosis for the intermolt stages in *O. gammarella* were reported previously (12).

FINDINGS.—1. Y-organ microcauterization. — When the Y-organs are destroyed in period B, i.e., during the hardening of new cuticle—there is no immediate disturbance; the new skeleton continues to thicken; the matrix of the future claw works loose and starts retracting (stage Cq). The intermolt cycle then blocks at this stage, apparently for good. In fact, animals remained blocked in this state for up to 56 days before dying.

Period C in *O. gammarella*, as in all land Talitridae, is characterized by the early formation of the future claw on the pereiopode dactyl (18). It starts when the matrix of the future claw works loose and retracts (stage Cq); a circular split form in this matrix (stage Cq); secretion from the cuticular sheath completes the claw’s formation (stage Cq). If the operation occurs at any of these stages, the development of the claw is immediately halted. Nevertheless, a few animals operated on
in stage $\Theta$ start to work the epithelium loose in the antero-
distal angle of the propodite, then are permanently blocked
in stage $D_0$.

If molt-initiating processes are under way (the working loose
of the epithelium from the old cuticle = stage $D_0$, the beginning
of byssus formation = stages $D'$, $D''$), destruction of the Y-organs
immediately brings these processes to a halt.

A few days later, while the formation of byssi is coming to
completion (stage $D'$) or the pre-exuvial layer of cuticle is
secreted (stage $D''$), the operation for the time being shows no
action. The molt-initiating processes finish and exuviation takes
place. The new skeleton is normally formed, but the animal
remains blocked at stage $C_\infty$ of the new intermolt cycle.

2. Injection of ecdysone in animals deprived of Y-organs. -
Ecdysone was injected into individuals that had been blocked
for about 15 days at intermolt-cycle stages $C_\infty$ or $D_0$.

The animals injected at stage $C_\infty$ are found 3 days later
at stage $D'_\infty$. The circular split in the claw and byssi matrices
has appeared, but it is not deep (the future claw and byssi will
be shorter than the old ones). The next day, the pre-exuvial
layer of new cuticle is laid down, forming a border on the claw,
the byssi and the circumference of the future pereiopode (= stage $D''$).

In animals injected at stage $D_0$, stage $D'_\infty$ also begins 3 days
after the operation. The claw has a cuticular sheath of normal
thickness (it was already secreted, it will be recalled, when
the Y-organs were destroyed), and the circular split in the tricho-
genic matrices is of normal depth. Twenty-four hours later
stage $D''$ begins.

No exuviation was observed in the batch of animals given the
double operation (microcauterization of Y-organs, ecdysone injection)
although the molt-initiating processes are incomplete.

DISCUSSION.—The destruction of Y-organs in *O. quadrata* permanently halts the molting processes. Exogenous ecdysone immediately starts these processes again, thus taking the place of the hormone secreted by the Y-organs. The latter are thus the source of the ecdysone, or a precursor of this hormone.

The findings obtained with animals deprived of their Y-organs in Period C show that these glands are necessary for claw formation. Ecdysone not only reactivates the new claw-formation processes but also, and simultaneously, "proecdysis". The earliness of future claw formation (Period C) in the normal animal seems due, therefore, to the presence of a relatively low amount of molt hormone in the hemolymph since it does not enable period D to be triggered. In other words, the claw matrix would have an exceptionally low threshold of sensitivity to the molt hormone compared to the trichogenic matrices and the pereiopode epithelium.

Our experiments also show that the presence of Y-organs is necessary for stage D₀ as well as for stages D₁₋₁, D₂₋₁. Ecdysone reactivates the body-building activities that normally occur at these stages. In the normal animal the amount of molt hormone in the hemolymph is higher than during period C, since it enables the triggering of period D (stage D₀) and the succeeding stages (stages D₁₋₁, D₂₋₁).

At stage D₁₋₁ the destruction of Y-organs no longer prevents completion of "proecdysis" or exuviation. Comparable findings obtained with *C. maenas* suggest to the author the existence of a "critical period", lying between stages D₁₋₁ and D₂₋₁, beyond which organ-Y removal can no longer prevent the exuviation that was being prepared. This "critical period" would be at stage D₁₋₁.
Contrary to observations on *Ligia oceanica* (5) made under identical conditions, *O. gammarella* did not exuviate; they, lacking Y-organs, are however at the end of the intermolt cycle thanks to the exogenous ecdysone. This prompts us to corroborate a hypothesis formulated by Graf (13) - viz., that there exists an "exuviation factor". In *O. gammarella* Y-organs are necessary for this factor to manifest itself. The simplest hypothesis is to consider the Y-organs as the source of the "exuviation factor". This situation is to be reconciled with results obtained with the species *Sphaeroma serratum*; the halting of molt processes in pubescent males is connected with degeneration of the Y-organs (20), (21). Ecdysone injections in such animals reactivate the premolt processes, but do not permit exuviation (20), (22). The "exuviation factor" in *O. gammarella* would be present in the hemolymph from stage D, on, since the destruction of the Y-organs at stages D, and D, does not prevent exuviation. In the case of *Lysmata*, release of the "exuviation factor" would also occur at the end of stage D, (23). Finally, the "exuviation factor" cannot act in the presence of a high degree of ecdysone; injecting ecdysone in *O. gammarella* about to molt delays exuviation (13), (24); repeated injections of this same hormone in *Idotea balthica* completely block exuviation (14).

In conclusion, in *O. gammarella* the presence of Y-organs is necessary from the start of period C until the "critical period" (D,). During this time the Y-organs would be constantly secreting molt hormone. The relatively small amount of molt hormone in the hemolymph during period C would enable the claw-
building processes to take place. A relatively large amount of
hormone at the end of period C would trigger stage D₃ and
induce byssus formation. In the "critical period" (D'),
the effect is as though the Y-organ cells, which—until then—had
been secreting molt hormone, were directed towards new
syntheses. The Y-organs would then release the "exuviation factor".
As the amount of molt hormone in the hemolymph does not stop
decreasing throughout stage D₃, it would be minimal at the time
of exuviation. The "exuviation factor" would then trigger the
mechanisms leading to the shedding of the old cuticle.

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