ENTOMOPHAGA, 16 (2), 1971, 239-251

ANATOMICAL AND HISTOLOGICAL CHANGES DURING DORMANCY IN TWO *COCCINELLIDAE* (*)

BY

I. HODEK & V. LANDA
Institute of Entomology, Czechoslovak Academy of Sciences, Praha.

The gonads of both females and males of *Semiadalia undecimnotata* SCHNEID. were studied during the estivo-hibernation period (August - May). The ovaries remain unripe in diapausing females, the ovarioles being formed by mere germaria until late April (or early May) when the previtellogenesis begins. In some years, the stage of the first oocyte is attained in females staying still in the hibernation quarters. On the contrary, both the spermatogenesis and spermateliosis proceed in the testes of diapausing males so long as the ambiant temperature is sufficiently high (August - September, April - May). Only in the coldest period of dormancy (November - March) the tissue of testicular follicles ceases to be active. Since mid-April the spermatogenesis and spermateliosis are resumed completely and the males fertilize the females, as is shown by dissections of their spermathecae. Seminal vesicles are always full of sperms. The digestive tract is empty in inactive coccinellids and the size of the fat body gradually diminishes in the course of estivo-hibernation.

The dependence of the activity of the tissue of testicular follicles on the ambient temperature was proved experimentally in both *S. undecimnotata* and *Coccinella septempunctata* L. The temperature of + 12°C enables a natural regression, while an abrupt transfer to + 5°C renders gradual emptying of follicles impossible.

Entomophagous coccinellids are adapted to the alternation of favourable and adverse conditions of climate and particularly of food, by year cycles appropriate to particular distribution areas. A period of development alternates with developmental arrest which is expressed as hibernation in the temperate zone and as estivation in the tropical and subtropical zone. Both types of arrest may combine into one long resting period, estivohibernation (or semi-estivohibernation) which lasts about nine months.

This is literally true for *Semiadalia undecimnotata* SCHNEID. which is dormant from late July or early August till early or middle May, being a " hypsotactic " aggregator : the aggregations of hundreds to thousands beetles are formed every year in the same dormancy sites (usually on top of prominent hills) which they reach by optically oriented directional flight (HODEK, 1960, 1967). As this behaviour is convenient for continual sampling, this species has been used for the research on changes during dormancy — of body composition (HODEK & CHERKASOV, 1961, 1963), of diapause intensity (HODEK,

---

(*) Dedicated to Prof. Dr. HANS JOACHIM MÜLLER, Jena, on the occasion of his 60th birthday.

1970), of metabolic rate (HODEK & SLAMA, unpubl.) and of frost resistance (HODEK, unpubl.).

The study of anatomical and histological changes in gonads is essential because the arrest of their development, especially in females, is the most conspicuous criterion for imaginal diapause. Thus far only preliminary results of the dissections of *S. undecimnotata* (HODEK & CHERKASOV, 1958) have been published.

The hibernation behaviour of *C. septempunctata* L. is highly variable as to the choice of dormancy sites, to the size of aggregations, and to the onset and end of dormancy (HODEK, 1960, 1967). This species also prefers elevated localities; it, however, may hibernate also in the lowland near the forest edges or near groups of shrubs. The aggregations are much smaller than with *S. undecimnotata* and they are formed near or in the upper layer of soil. Thus the hibernating coccinellids are covered by snow and cannot be sampled continually. The dissections of autumnal and spring samples have already been published (HODEK & CHERKASOV, 1961). Here we studied only the effect of temperature on the testes of beetles collected in autumn.

Materials and methods

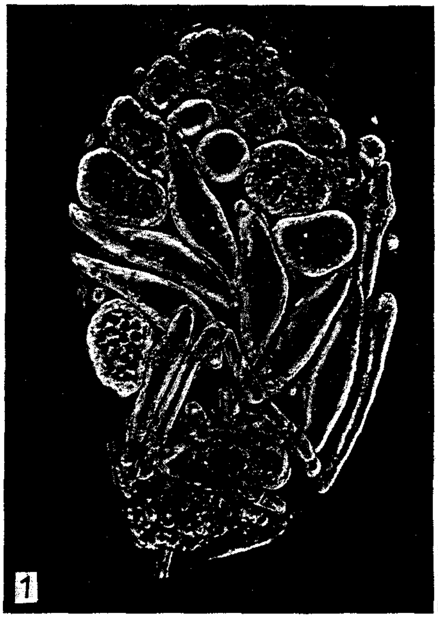
The coccinellids were sampled in the hibernation quarters in Louny-hills (northern Bohemia, near the town Louny), Pavlov-hills (southern Moravia, near the town Mikulov), Tribeč-hills (western Slovakia, near the town Nitra). For dissection of spermathecae the males and females were transported separately (except for the 1957 season). They were dissected under the Ringer's solution with the aid of a stereomicroscope where the fat body and the alimentary canal were evaluated. The prepared ovarioles, testicular follicles and smears from the spermatheca and from seminal vesicles were then examined by the phase contrast.

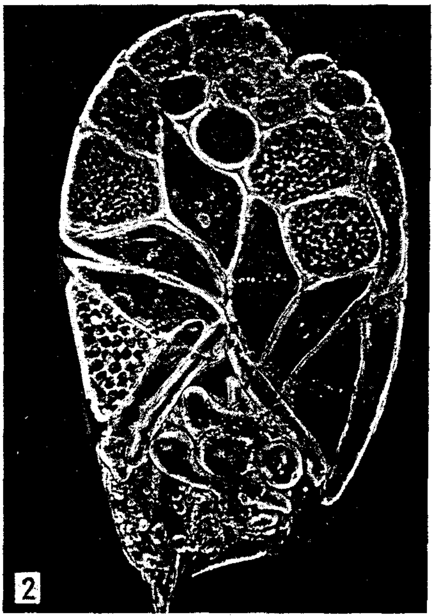
When preparing testicular follicles for taking photographs, we removed the membrane of the testes. Bundles of follicles were cut with a scalpel, till rosettes containing 2-4 follicles were left. Whole mounts were prepared in the physiological solution, single follicles were photographed by a phase or interference phase contrast. A different compression enables different details to stand out. The differences arise most conspicuously by comparison of figures 1 and 2.

Results

OVARIA

The ovaries remain unripe during the dormancy in outdoor conditions (Tab. 1). The ovarioles are formed by mere germaria having thin pedicels. The ovary is densely interwoven by tracheae and immersed in a massive fat body.





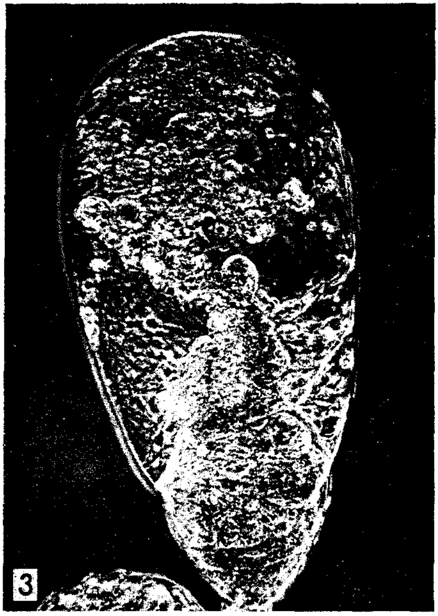


FIG. 1, 2, *Semiadalia undecimnotata*. A testicular follicle still active in the first period of dormancy (17 Sept. 1958). Fig. 1 less compressed, Fig. 2 more compressed.

FIG. 3, *S. undecimnotata*. Testicular follicle after the arrest of spermatogenesis (4 Nov. 1958).

FIG. 4, *S. undecimnotata*. Inactive testicular follicle (19 Dec. 1958).

TABLE 1

Dissections of dormant Semiadalia undecimnotata *females*

Date of sampling (1)	Ovaria		Spermatheca		Fat body			
	without egg chambers	with one oocyte	without sperm	with sperm	−	+	++	+++
6.12.56	15	—						
9.12.56	15	—						
6.2.57	15	—	15	—				
6.3.57	30	—			1	1	9	19
27.3.57	30	—			—	—	3	27
10.4.57	30	—	6	24	—	1	5	24
23.4.57	30	—			—	3	4	23
30.4.57	30	—			—	6	8	16
23.10.57	20	—	(17)	(3)	—	2	5	13
16.12.57	20	—	20	—	—	1	7	12
11.2.58	20	—	20	—	—	—	5	15
8.4.58	30	—	30	—	—	2	11	17
23.4.58	20	—	18	2	—	—	10	10
29.4.58	20	—	12	8	—	5	9	6
5.5.58	20	—	4	16	—	8	11	1
13.5.58	10	10	—	20	—	5	9	6
19.5.58	7	13	—	20	1	11	6	2
29.8.58	10	—			—	—	—	10
11.9.58	10	—			—	—	2	8
25.9.58	10	—			—	—	2	8
22.10.58	10	—			—		3	7
15.12.58	10	—			—	1	4	5
2.4.59	10	—			—	—	6	4
5.-10.4.59	10	—			—	3	4	3
16.4.59	10	—			—	2	4	4
28.4.59	10	—			—	1	4	5
9.5.59	7	3			—	2	4	4
26.5.59	7	3			—	—	5	5
8.8.61	10	—			—	—	2	8
18.9.61	10	—			—	—	1	9
9.10.61	20	—			—	—	5	15
18.4.62	10	—			—	4	3	3
22.5.62	10	3			1	3	8	1
22.5.62 (2)	13	7			2	8	10	—
7.6.62	11	8			—	1	10	8

(1) Place of sampling: Louny hills (5.-10.4.59 - Pavlov-hills)
(2) Kept until the next sample outdoors, without food.

The development of ovaries begins at the end of hibernation. In late April and early May the germaria begin to enlarge and at their proximal end the vitellarium is being formed. Since mid-May the first oocyte is visible. In coccinellids, this period of oogenesis — previtellogenesis — can proceed without food intake. When coccinellids emerge from hibernation earlier (1957), the females leave the winter shelters still before reaching this stage. When they emerge later (13 and 19 May 1958 and 9 and 26 May 1959), this period of maturation is found still at the hibernation quarters. For the further period of oogenesis — vitellogenesis — essential food is necessary (HODEK, 1967).

According to our data, the spring maturation of ovaries in *S. undecimnotata* and *C. septempunctata* occurs at about the same time, while it is earlier in *Adalia bipunctata* L. Ovaries of this species had one (in 50 % of females) or more oocytes (50 %) in the vitellarium on 21 April 1962, when the ovaries of *S. undecimnotata* and *C. septempunctata* possessed mere germaria.

The descent of the first oocyte (previtellogenesis) can be achieved in course of the whole dormancy by rearing the females from the open on alternative food at temperature fluctuating between 12-22°C. When essential food (i.e. certain species of aphids) and long-day photoperiod is employed (18 hr photophase in a 24 hr photoperiod), full maturation of the ovaries is attained (HODEK, 1970).

SPERMATHECA

The examination of the content of spermatheca revealed the time of fertilization (Tab. 1). From the beginning of dormancy till early April no spermathecae contained any spermatozoids. The percentage of spermathecae containing active spermatozoids kept then increasing until early May, when all females had a reserve of sperms in their spermathecae.

The populations from southern Moravia and even more those from southern Slovakia seem to differ in this respect. In 1970, IPERTI (unpubl.) found spermathecae full of active spermatozoids in 9 % of females collected on 1 Sept. in Pavlov-hills (74 dissected), in 26 % of males collected on 2 October in Tribeč-hills (31 dissected), and in 28 % of males collected 30 Sept. on Nagy-hegy (near Král'ovský Chlmec, 86 dissected).

TESTES

Spermatogenesis proceeds already in testicular follicles of male pupae. Under favourable environmental conditions the tissue of testicular follicles remains active even in dormant males (Tab. 2). During the first two months of estivo-hibernation (August, September) testicular follicles are filled with cellular elements of all stages of spermatogenesis and spermateliosis.

With the gradual decrease in ambient temperature in late or mid-September the number of cellular elements begins to reduce. In the coldest period of dormancy (November - March) the activity of the tissue practically ceases. The middle part of testicular follicles

TABLE 2

Dissections of dormant Semiadalia undecimnotata *males*

Date of sampling 1)	Testes 2) Spermatocytes in testicular follicles				Fat body			
	none	rare	present	plenty	—	+	++	+++
23.10.57	20		—		—	—	4	16
16.12.57	20		—		—	—	2	18
11.2.58	20		—		—	—	8	12
8.4.58	20		—		—	8	9	3
23.4.58	11		9		1	5	9	5
29.4.58	7		13		—	11	8	1
5.5.58	—		20		6	9	5	—
13.5.58	—		20		6	12	2	—
19.5.58	—		20		5	12	3	—
29.8.58	—	—		10	—	1	3	6
11.9.58	—	8		2	—	1	4	5
25.9.58	—	10		—	—	—	5	5
22.10.58	8	2		—	—	1	4	5
15.12.58	9	1		—	—	—	5	5
2.4.59	10	8		2	—	5	14	1
5.-10.4.59	—	—		10	1	7	2	—
16.4.59	—	—		10	—	7	3	—
28.4.59	—	—		10	—	3	2	5
14.9.62	—	—		10	not observed			
9.+12.10.62	2	6		—				
21.11.63	5	3		—				
6.3.63	6	4		—				
9.4.63	5	5		—				

1) Place of sampling: Louny-hills (5.-10.4.59, 9.+12.10.62 — Pavlov-hills).

2) Vesiculae seminales always full of sperm.

is empty in the majority of males; there is a small group of spermatogonies on the distal top, and the proximal part (usually about one-third) is filled with sperm bundles. Spermatogenesis ceases at the stage of the division of spermatogonies or of young spermatocytes.

Activity of the tissue is resumed in early or mid-April. In early April 1959 only 1/5 of dissected males were in an inactive state, whereas about 1/10 were fully active, with follicles filled with cellular elements. In about two-thirds of males the activity of the tissue of testicular follicles was incomplete. Spermatogenesis begins with the division of spermatogonies ; groups of growing spermatocytes are formed, enveloped by cyst-cells which fill the whole follicle in a short time (figs 5-8). Since mid-April the full activity of the tissue of testicular follicles with a completed spermateliosis was found in all males. At

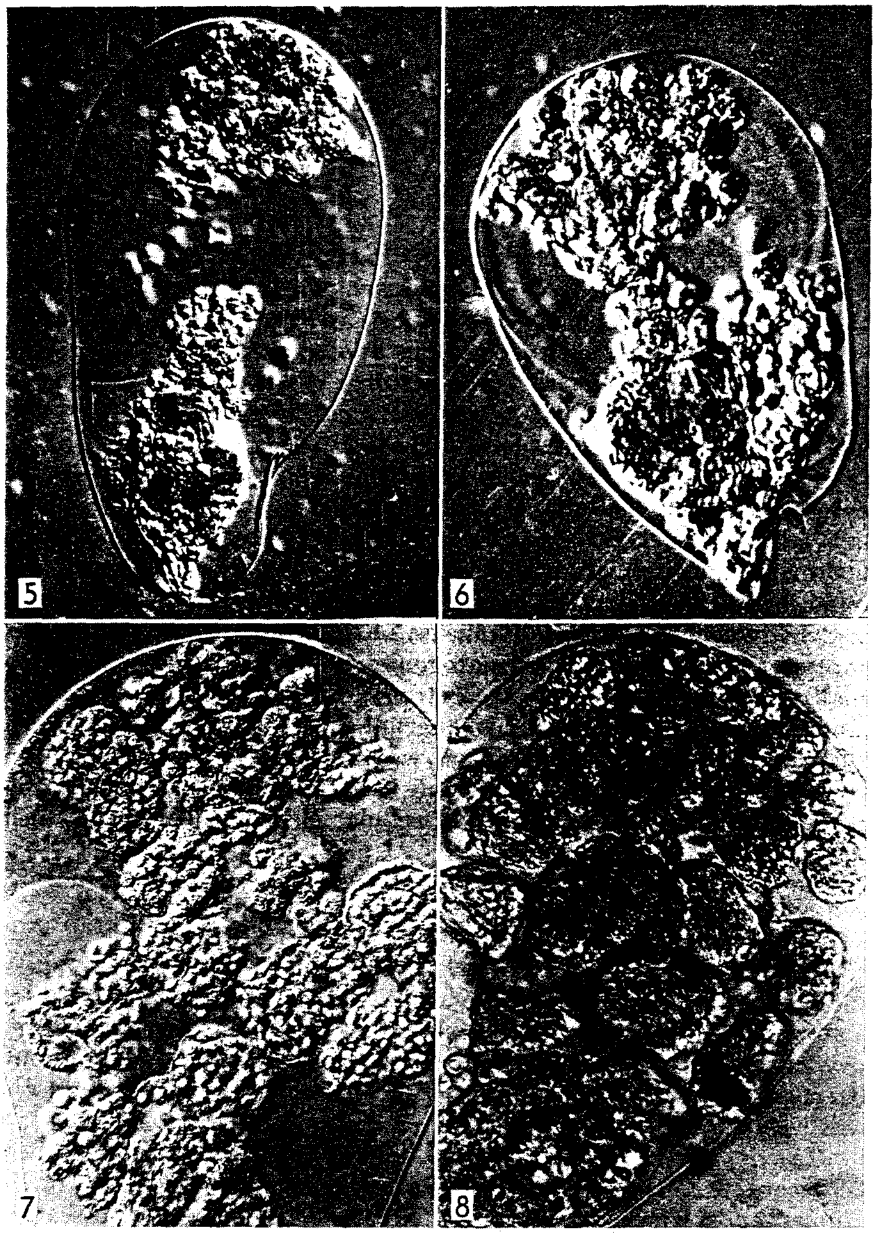


FIG. 5 - 8 - *S. undecimnotata*. Testicular follicle. A gradual resumption of spermatogenesis. (Whole mount. Interference phase contrast.)

that time the males fertilized the females, as it is evident from dissections of the spermathecae (see table 1). Seminal vesicles were always full of sperms.

We find a striking coincidence of inactivity of testicular follicles with low temperature. The causal relation was aimed to be proved experimentally in the season 1962-63.

TEMPERATURE TREATMENT OF *S. undecimnotata* MALES

Experiment 1 (sample from Louny-hills, 14 September)

Before the experiment (19 September) all males had fully active tissue of testicular follicles. The follicles were filled with cellular elements of all stages of spermatogenesis and spermateliosis. The males were kept either under low temperatures of + 5°C or + 12°C, or reared on honey solution at activation conditions (temperature 25°C, long-day regimen of L 18, D 6).

Dissections after 10 and 24 days did not show yet any changes under any conditions. An advanced inactivation was recorded after 33 days in 8 males kept under + 5°C : follicles were filled sparsely, in 3 males the spermatocytes were missing. Nearly no changes were found in males held under 25°C for 7 weeks, whereas all males stored at 12°C had inactive testicular follicles, i.e. follicles with the middle part empty, with a group of spermatogonies and sometimes with several small spermatocytes at the distal top of the follicle and with sperm bundles in the proximal third of the follicle. In males stored at 5°C (10 males dissected), the situation was heterogeneous (in 5 of them spermatocytes were found, in 3 only spermateliosis stages, in 2 just sperm bundles), and the density of cellular elements fluctuated considerably.

By a transfer of males from 25°C to 12°C regression of the activity of follicles was obtained.

Experiment 2 (sample from Pavlov-hills, 9 September)

Storage of the males in an outdoor cage for 6 weeks resulted in an advanced regression of the activity of testicular follicles : spermatocytes as well as stages of spermateliosis were sparse or absent. After 4 weeks in laboratory (daily fluctuation between 12-20°C) the follicles were full of spermatocytes or stages of spermateliosis.

The dependence of testes on the ambient temperature was proved. Favourable temperatures enable the dormant males to maintain or resume the activity of testicular follicles — if energetic losses are compensated at least by alternative food. The lower temperature (+ 12°C const.) enables the gradual emptying of follicles from spermatocytes and spermateliosis stages. An abrupt transfer of males early in dormancy to the temperature of + 5°C inhibits the gradual regression and produces irregular changes.

TEMPERATURE TREATMENT OF *C. septempunctata* MALES

Experiment 3 (sample from Tribeč-hills, 9 October)

A week after sampling, the regression of testicular follicles was very uneven. After a month of exposure to outdoor conditions the inactivation had progressed considerably. Only a minor part of males had single spermatocytes, the majority had merely sperm bundles and sometimes the advanced stages of spermateliosis. In some males the middle of the follicle was empty.

Three weeks after sampling the males were exposed, without food, to constant temperatures of 20° or 12°C, or to temperature fluctuating between 12° and 20°C. Under fluctuating temperature, one sample was reared on honey solution. In all cases, the long-day regimen (L 18, D 6) was maintained. After 16 days no significant differences were recorded. After 6 weeks the tissue of testicular follicles became inactive (for description see exp. 1) in males at 12°C constant in starving males at fluctuating temperatures single spermatocytes were found in some males. 80 % of males, fed at fluctuating temperatures, possessed sporadical spermatocytes in testicular follicles.

In the seventh week of experiment (from 21 Dec.), the males from 20°C const. were transferred to temperatures fluctuating between 17° and 22°C and fed on the water solution of honey. After 5 weeks of this new regimen (i.e. 12 weeks of experiment), all males reared on honey for the whole time, had the testicular follicles densely filled with spermatocytes. In the males fed only for the last 5 weeks, the cellular elements in the follicles were much more sparse : less than 10 cysts with spermatocytes in one follicle.

This experiment proved the significance of alternative food for the activity of testicular follicles. While the temperatures of 20°C const. or 12°/20°C were found to be suboptimal, that of 17°/22°C proved to be very suitable.

Experiment 4 (sample from Louny-hills, 21 November)

In spite of the late date 5 males of 10 had spermatocytes present in the follicles.

Since 23 November starving males were kept at 17-20°C, at constant dark or at long-day regimen (L 18, D 6). The dissection after 5 weeks showed that the males under " long day " had an active tissue with a variable density of spermatocytes, whereas those kept in dark exhibited only an enlarged group of spermatogonies. It seems that also light conditions affect the activity of the testicular tissue.

FAT BODY

In the course of inactive life the fat body gradually diminishes in both sexes (Tab. 1, 2). The subjective evaluation of its size is less precise than the biochemical analyses of fat and glycogen content that we carried out in collaboration with a biochemist (HODEK & CHERKASOV, 1961, 1963).

DIGESTIVE TRACT

In inactive coccinellids at hibernation quarters the digestive tract of both males and females does not contain aphids. Only exceptionally it does toward the end of hibernation (14 May 1958). Sometimes the digestive tract is not quite empty, containing clumps of yellow material.

Discussion

DISCUSSION OF RESULTS

There is a discrepancy between the fact that in the experiments 1-3 the starving males failed to resume the activity of their testicular follicles, and between the findings in late spring (especially in 1958 and 1959 - tab. 2), when we used to find males with an active tissue in hibernation quarters. Probably it was caused by different environmental conditions. Although fluctuating temperatures were used in experiments, they apparently increased the metabolism unnaturally and considerably accelerated the consumption of reserves. This is indicated also by the high mortality in the experimental starving males.

DISCUSSION OF LITERATURE

The arrest of ovarial maturation (previtellogenesis or early or advanced vitellogenesis) in diapausing females of insects has been commonly known (LEES, 1959; BECK, 1968). This fact is also most often used as a sign of adult diapause. It is impossible to sum up here all data of this kind. A survey of older data has been published (HODEK, 1962).

The regular connection of imaginal diapause in females with the arrest of ovarial maturation has even led to a rather frequent use of the expression " ovarial (ovarian) diapause " or " Gonadendiapause " (HODEK, 1962; BONESS, 1963; STRÜBING, 1963; SICKER, 1964; THIELE, 1966) which is not exact from the physiological point of view and may be even misleading. The ovaries, as a target organ of neuroendocrine mechanisms connected with diapause, are morphologically most conspicuous and easiest to study. Physiological changes connected with diapause, however, are not limited to this organ. And the maturation of ovaries may be arrested also by other reasons. Diapause in insects hibernating in temperate regions ceases usually during December or early January [*Coccinella septempunctata* L. (HODEK,

1962) [contains references to older works describing this phenomenon in 7 species : *Sitona cylindricollis* FAHR. (HANS, 1961); *Ischnodemus sabuleti* FALL. (Tischler, 1963; PRECHT, 1963); *Leptinotarsa decemlineata* SAY (LE BERRE, 1965); *Lema melanopa* L. (HILTERHAUS, 1965); *Lygus hesperus* KNIGHT (BEARDS & STRONG, 1966); *Chilocorus rubidus* HOPE (PANTIUKHOV, 1968); *Pyrrhocoris apterus* L. (HODEK, 1968)]. Under natural conditions, the maturation of ovaries is inhibited during the post-diapause by a low temperature, and even after the ambient temperature has attained the efficient range, the oviposition may be delayed by lack of essential food. Only if favourable temperature and food are furnished in the laboratory, the end of diapause may be revealed.

There has been much less attention given to the testes than to the ovaries, probably because their conditions is not apparent by mere dissection. At the beginning of our observations the knowledge was only sporadic. Thus in *Sitona cylindricollis*, DAVEY (1956) ascertained that the dormant testis contains no division figures and the almost differentiated spermatozoa remain encysted. In the subsequent 13 years some results were obtained in other species. A similar situation as in *S. undecimnotata* was found in *Anthonomus grandis* BOH. by a detailed study (BRAZZEL & NEWSOM, 1959). Spermatogenesis in this weevil also begins in the pupa, active spermatogenesis ceases in fall and is completely resumed without feeding during April and May still in the hibernation quarters. In *A. grandis*, the activity of testicular tissue ceases (spermatocytes are missing and only few or no sperm bundles are present) while the beetles are still in the field, whereas in *S. undecimnotata* both spermatogenesis and spermateliosis proceeds during the first two months (August, September) at the hibernation quarters.

The regression of testes in fall and the resumption of their activity in spring was recorded also in other hibernating adults, as for instance in *Exolygus rugulipennis* POPP. (BONESS, 1963; STEWART, 1968). KIRITANI (1963) found active sperms in the testes of about a half of hibernating *Nezara viridula* L. males. SICKER (1964) and ZASLAVSKI & BOGDANOVA (1965) proved that the day-length has no influence on the development of testes in *Tetrix undulata* (SOW.) and in *Chilocorus geminus* ZASL. and *bipustulatus* L., resp. BROWN (1962), who used the external form of the testes as a criterion of the progress of development, reports that their development continues even in fall and winter, in contrast to the ovaries in *Eurygaster integriceps* PUT. THIELE (1969) achieved .maturation in males (indicated by seminal vesicles containing spermatozoa and by accessory glands filled with secretion) also in conditions preventing the maturation of ovaries in 2 Carabids (*Nebria brevicollis* F., *Patrobus atrorufus* STROEM.).

RÉSUMÉ

Modifications anatomiques et histologiques au cours de la dormance chez deux *Coccinellidae*

Les femelles et mâles de *Semiadalia undecimnotata* SCHNEID., récoltés dans les quartiers d'estivo-hivernation dans les collines de Louny (Bohême du Nord) furent disséqués pendant la période de repos de cette espèce (du mois d'août au mois de mai).

Les femelles présentent en permanence des ovaires immatures dont toutes les ovarioles se réduisent aux seuls germaria. Les premiers ovocytes apparaissent au milieu de mai. Selon les années, cette période de prévitellogenèse peut être observée même sur les lieux d'hibernation. On observe des spermathèques vides pendant presque tout le repos, sauf au printemps. Depuis le commencement d'avril jusqu'au moment de la migration de retour, le pourcentage de femelles avec une spermathèque qui contient des spermatozoïdes actifs augmente graduellement jusqu'à atteindre 100 %.

Par contre, comme chez les mâles la spermatogenèse débute au stade nymphal, l'activité des tissus des follicules testiculaires se poursuit au cours des deux premiers mois de leur estivo-hibernation (août et septembre). A la fin de septembre et pendant le mois d'octobre la quantité des éléments cellulaires diminue en fonction de la diminution de la température. Pendant la période au climat le plus froid (de novembre à mars), la spermatogenèse s'arrête et les follicules testiculaires deviennent presque vides, à l'exception de leur partie distale qui contient quelques ovogonies et de leur portion proximale qui renferme les faisceaux de spermatozoïdes. En avril, la spermatogenèse reprend; pour cette raison, à partir de la mi-avril tous les mâles présentent une activité normale des follicules testiculaires qui leur permet de fertiliser les femelles.

Parce que nous avons décelé une coïncidence entre la régression de l'activité des follicules testiculaires et la diminution de la température, nous nous sommes attachés à préciser expérimentalement cette relation chez *S. undecimnotata* et *Coccinella septempunctata* L. Aux températures élevées, obtenues au laboratoire (25°C), mais également aux températures alternées (entre 17 et 22°C ou entre 12 et 20°C), l'activité des follicules testiculaires peut se maintenir ou reprendre, si on assure une nourriture miellée. Par contre, une température constante de 12°C détermine une régression normale de l'activité. Le brusque transfert des mâles aux températures qui avoisinent le zéro (+ 5°C const.) ne rend pas possible une régression de ce type et l'on observe des situations anormales.

REFERENCES

BEARDS, G. W. & STRONG, F. E. — 1966. Photoperiod in relation to diapause in *Lygus hesperus* KNIGHT. — *Hilgardia*, **37**, 345-362.

BECK, S. D. — 1968. Insect photoperiodism. — *Academic Press*, New York & London, 288 pp.

BONESS, M. — 1963. Biologisch-ökologische Untersuchungen an *Exolygus* WAGNER [*Heteroptera, Miridae*]. — *Z. wiss. Zool.*, **168**, 376-420.

BRAZZEL, J. R. & NEWSOM, J. P. — 1959. Diapause in *Anthonomus grandis* BOH. — *J. econ. Entomol.*, **52**, 603-611.

BROWN, E. S. — 1962. Researches on the ecology of *Eurygaster integriceps* PUT. [*Hemiptera, Scutelleridae*] in Middle East countries, with special reference to the overwintering period. — *Bull. ent. Res.*, **53**, 445-514.

DAVEY, K. G. — 1956. The physiology of dormancy in the sweet clover weevil, *Sitona cylindricollis*. — *Canad. J. Zool.*, **34**, 86-98.

Hans, H. — 1961. Termination of diapause and continuous laboratory rearing of the weet clover weevil, *Sitona cylindricollis* Fahr. — *Ent. exp. et appl.*, **4**, 41-46.

Hilterhaus, V. — 1965. Biologisch-ökologische Untersuchungen an Blattkäfern der Gattung *Lema* und *Gastroidea* [*Chrysomelidae, Col.*]. (Ein Beitrag zur Agrarökologie.). — *Z. angew. Zool.*, **52**, 257-295.

Hodek, I. — 1960. Zimování slunéček. (Hibernation - bionomics in *Coccinellidae.*). — *Čas. Čs. spol. ent.*, **57**, 1-20.

— 1962. Experimental influencing of the imaginal diapause in *Coccinella septempunctata* L. [*Col., Coccinellidae*]. 2nd part. — *Čas. Čs. spol. ent.*, **59**, 297-313.

— 1967. Bionomics and ecology of predaceous *Coccinellidae.* — *Ann. Rev. Ent.*, **12**, 79-104.

— 1968. Diapause in females of *Pyrrhocoris apterus* L. [*Heteroptera*]. — *Acta ent. bohemoslov.*, **65**, 422-435.

— 1970. Termination of diapause in two coccinellids [*Coleoptera*]. — *Acta ent. bohemoslov.*, **67**, 218-222.

Hodek, I. & Čerkasov, J. — 1958. A study of the imaginal hibernation of *Semiadalia undecimnotata* Schneid. [*Coccinellidae, Col.*] in the open. — *Acta Soc. Zool. Bohemoslov.*, **22**, 180-192.

— 1961. Prevention and artificial induction of imaginal diapause in *Coccinella septempunctata* L. [*Col.: Coccinellidae*]. — *Ent. exp. et appl.*, **4**, 179-190.

— 1963. Imaginal dormancy in *Semiadalia undecimnotata* Schneid. [*Coccinellidae, Col.*]. II. Changes in water, fat and glycogen content. — *Věstník Čs. spol. zool.*, **27**, 298-318.

Kiritani, K. — 1963. The change in reproductive system of the southern green stink bug, *Nezara viridula,* and its application to forecasting of the seasonal history. — *Japan. J. app. Ent. Zool.*, **7**, 327-337.

Le Berre, J. R. — 1965. Quelques considérations d'ordre écologique et physiologique sur la diapause du Doryphore *Leptinotarsa decemlineata* Say. — *C. R. Soc. biol.*, **159**, 2131-2135.

Lees, A. D. — 1955. The physiology of diapause in arthropods. — *Cambridge Univ. Press*, London, 151 pp.

Pantiukhov, G. A. — 1968. Issledovanie ekologii i fiziologii khishchnogo zhuka *Chilocorus rubidus* Hope [*Coleoptera, Coccinellidae*]. — *Zool. zhurnal*, **17**, 376-386., (russ.).

Precht, H. — 1963. Versuche mit der Schmalwanze *Ischnodemus sabuleti* Fall. Ein Beitrag zum Diapauseproblem. — *Zool. Anz.*, **171**, 13-28.

Sicker, W. — 1964. Die Abhängigkeit der Diapause von der Photoperiodizität bei *Tetrix undulata* (Sow.) [*Saltatoria, Tetrigidae*] (mit Beiträgen zur Biologie und Morphologie dieser Art). — *Z. Morph. Ökol. Tiere*, **54**, 107-140.

Stewart, R. K. — 1968. The biology of *Lygus rugulipennis* Poppius [*Hemiptera: Miridae*] in Scotland. — *Trans. R. ent. Soc. Lond.*, **120**, 437-457.

Strübing, H. — 1963. Zum Diapauseproblem in der Gattung *Stenocranus* [*Homoptera, Auchenorrhyncha*]. — *Zool. Beitr.*, **9**, 1-119.

Thiele, H. U. — 1966. Einflüsse der Photoperiode aud die Diapause von Carabiden. — *Z. angew. Ent.*, **58**, 143-149.

— 1969. The control of larval hibernation and of adult aestivation in the carabid beetles *Nebria brevicollis* F. and *Patrobus atrorufus* Stroem. — *Oecologia*, **2**, 347-361.

Tischler, W. — 1963. Weitere Untersuchungen zur Ökologie der Schmalwanze *Ischnodemus sabuleti* Fall. [*Hem., Lygaeidae*]. — *Zool. Anz.*, **171**, 339-349.

Zaslavski, V. A. & Bogdanova, T. P. — 1965. Osobennosti imaginal'noj diapauzy u dvukh vidov *Chilocorus* [*Coleoptera, Coccinellidae*]. — *Trudy Zool. inst. AN SSSR* (Ekol. vred. nasek. i entomof.), **36**, 89-95., (russ.).