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PREFACE

It is perhaps natural that some degree of apprehension prevails whenever a new major endeavor is undertaken. Such has been the case with the launching of the *Annual Review of Entomology*. In this instance there was no question that the job needed to be done, and our concern was limited to the best choice of methods for doing it. One estimate shows that there is appearing in world scientific literature well over 4000 papers in entomology each year. There is reason to believe that the actual number is considerably greater than this, and that it will continue to grow. Some of this literature is scattered and inaccessible, and much of it appears in journals not primarily concerned with insects. In some branches of entomology (e.g., insect biochemistry) approximately 90 per cent of the pertinent papers appear in non-entomological journals. Clearly, the mass of literature accumulating in all of the various fields of entomology is beyond the ability of any one individual to obtain readily, to read thoroughly, and to appraise critically. There has, in recent years, been a growing realization of this fact among entomologists generally. One of the solutions to the problem is to call upon specialists in the various branches of entomology to prepare for their fellow entomologists authoritative and scholarly reviews of the literature in their particular specialties.

In 1953 a committee of the Entomological Society of America was appointed to examine the problem of providing adequate reviews of entomological literature. After an exhaustive study, this committee recommended that the present needs of entomology would best be met by a review publication of the type published by the nonprofit organization, Annual Reviews, Inc., whose well-known publications already cover many fields in which the situation was similar to that now facing entomologists. This organization was approached on the matter, and, after an appraisal of its own, it also concluded that there was a real need for a review publication in the field of entomology, and it agreed to undertake the publication of an *Annual Review of Entomology*. The Entomological Society of America, in turn, agreed to assist and to give its support in a number of matters incident to the organization and publication of the *Review*.

The primary objective of the *Annual Review of Entomology* is to publish authoritative and concise treatments of definitive subjects of current interest. It is expected that the more active fields of research will require critical reviews annually while the less active areas may be summarized and evaluated as developments require. These reviews will be solicited judiciously from leaders in the fields concerned. It is our hope that each review will present a critical analysis of recent literature and, insofar as is feasible, an appraisal of the present status of the subject. We realize that such a policy may necessitate the omission of many papers that may be of

more than passing interest. Furthermore, it is not unlikely that the reviews may engender controversy because of the personal opinions and interpretations of the reviewers. However, by presenting divergent viewpoints in successive years, a well-rounded treatment of the subject as a whole should eventually be attained. It is hoped that the reviews will pursue a middle course which avoids the extremes of the personal advocacy of a restricted field on the one hand, and a mere concatenation of bibliographic summaries or abstracts on the other. The Editors and Editorial Committee invite and will always welcome suggestions for improvements.

All who read and profit from this *Review* owe a debt of thanks to Dr. J. Murray Luck and the other officers of Annual Reviews, Inc. whose unselfish interest in the needs of entomology for a review publication made it possible. Similar gratitude is due the Entomological Society of America for generously agreeing to aid in supporting the *Review* at least during its initial and formative stages. The Editors and Editorial Committee are especially grateful to Mrs. Lillian Rutherford for her skillful and invaluable aid in the editorial work. We also wish to thank the George Banta Company, Inc., for their splendid co-operation in the production of the volume. Our deepest thanks, of course, go to those who have joined in this undertaking by painstakingly preparing the reviews herein presented.

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THE PHYSIOLOGY AND BIOCHEMISTRY OF DIAPAUSE¹

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The term diapause refers to the state of arrested growth or reproduction that is typical of many hibernating or aestivating arthropods. Although adverse conditions of various kinds may lead to the failure of growth, it is often helpful to distinguish "quiescence" attributable to such causes, from "diapause" in its more limited sense. Despite the existence of borderline examples, certain physiological mechanisms can be recognised in the diapausing insect which are absent in the quiescent. During the past decade there have been notable advances in our knowledge of these mechanisms. The role of "token" stimuli from the environment in controlling the onset and termination of diapause, the endocrinology of growth arrests, and the biochemical changes associated with dormancy are all lines of enquiry that have proved particularly fruitful. The present article is concerned especially with these topics. General reviews in which the ecological and phenological, as well as the physiological aspects of diapause are discussed, include those of Bonnemaison (7), Andrewartha (2), and Lees (62).

THE INDUCTION OF DIAPAUSE

Photoperiod.—Recent investigations have shown that some form of response to length of day is extremely common among arthropods possessing a facultative diapause. In the majority of species long day lengths or permanent illumination prevent diapause while 8 or 12 hr. days induce diapause. Very short photoperiods or permanent darkness often cause uninterrupted growth. This general pattern of response has now been observed in the Lepidoptera *Acronyia* (18), *Grapholitha* (25), *Cydia* (25), *Polychrosis* (53), *Diataraxia* (101), *Antheraea* (94, 95), *Pieris* (21), *Harrisina* (92), and *Araschnia* (18, 67), as well as in the Colorado beetle *Leptinotarsa* (103) and the red mite *Metatetranychus* (60). The photoperiodic response is also of this "long day" type in certain Lepidoptera which hibernate as larvae. But there are important differences. In *Dendrolimus* (Lasiocampidae) larval feeding and moulting are soon arrested in short days, irrespective of the instar. But, unlike the species mentioned above, *Dendrolimus* remains susceptible to day length throughout the period of hibernation, so that growth is resumed a week or two after exposing the larvae to a long photoperiod (37, 38). Gayaspitz has also shown that the larvae of *Euproctis chrysorrhoea* (Linnaeus) and other lymantriid moths are sensitive to photoperiod, notwithstanding their strict univoltine rhythm in nature. But diapause is

¹ The survey of the literature pertaining to this review was completed in May, 1955.

only prevented by photoperiods corresponding to extreme long-day conditions (17 to 22 hr. days in the case of a Leningrad population). In this instance the absence of light, and even permanent illumination, causes the larvae to become dormant. Postdiapause growth is also facilitated by an optimal photoperiod of about 20 hr., but it is less certain whether the larvae are still photosensitive when fully dormant. The silkworm *Bombyx* is exceptional in that the direction of the response is reversed, short day lengths preventing, and long day lengths inducing diapause (49). This reversal is associated with the fact that the eggs are influenced by illumination almost immediately after development is resumed in spring. Under natural light conditions, therefore, the first generation moths of bivoltine strains lay non-diapause eggs in summer and the second generation diapause eggs in early autumn.

The mode of action of light has been examined in several species. *Grapholitha* and *Metatetranychus* are known to take account of day length as such (25, 60). But there is some evidence that the dragonfly *Anax* responds to changes in day length. Increasing photoperiods cause the last stage nymphs to metamorphose promptly, whereas decreasing or constant long photoperiods induce diapause (16). The light reaction itself seems always to be independent of intensity, provided the latter is not subliminal. The threshold is as low as 0.01 ft-c in the eggs of *Bombyx* (49) and about 1 to 2 ft-c in the deutonymphs of *Metatetranychus* (60). *Grapholitha* responds to a light intensity of 1 to 3 ft-c falling on the outside of the apples in which the larvae are tunneling (25). Although accurate action spectra are not yet available, the blue and blue-green regions of the spectrum are known to be especially effective in *Bombyx*, *Grapholitha*, and *Metatetranychus*, all three species being virtually insensitive to red light. The nature of the photosensitive pigment is still obscure.

Both the light and dark phases of the cycle of illumination are involved in the control of diapause. The role of the dark phase has been demonstrated in *Acronycta* by Danilyevsky & Glinyanaya (22, 23) who have found that diapause pupae are only formed if the dark period is longer than 9 hr. and shorter than 48 hr. In *Antherasa* the pupae are always of the diapause type if the dark phase exceeds 11 hr., apparently regardless of the duration of the light period (95, 96). However, the mode of action of the rhythm of illumination has been more closely studied in *Grapholitha* (25) and *Metatetranychus* (61). In the first species the conditions which evoke diapause are extremely limited: the duration of the light phase must fall between 7 and 15 hr. and that of the dark phase between 11 and 16 hr. All cycles in which either component is longer or shorter than these values cause the larvae to pupate without diapause. The conditions which lead to the production of females laying diapause winter eggs are much less restricted in *Metatetranychus*. The type of egg laid appears to be determined by the interaction of antagonistic diapause-preventing (light phase) and diapause-inducing (dark phase) proc-

esses. The light and dark phases both become more effective with time, the latter showing a particularly dramatic gain in effectiveness between 8 and 12 hr. Nevertheless, both reactions are slow to start, and for this reason diapause is not influenced by the inclusion of short light breaks within an effective dark period. This is also true of *Grapholita*. Indeed, in this respect, as in others, the photoperiodic reactions of arthropods seem to differ materially from those in plants. As a first approximation, it is tempting to conclude that some active product is synthesised in the light or dark and removed during the complementary phase. Since the number of effective cycles that fall within the sensitive period of development exert a cumulative effect (60), there must also be some means of transferring the substance from one cycle to the next.

It has been possible to show in *Diataraxia* and *Metatetranychus* that diapause is not governed by photoperiodic reactions set up in the food plant (60, 101). Yet although the action of light is evidently direct, the site of photoreception has still to be identified. Since Tanaka (95) has found that the lateral ocelli are not the receptors in the larvae of *Antheraea*, it may well be that light affects an internal organ, perhaps the central nervous system itself. Some indirect information on this question is provided by studies of the sensitive period.

Photoperiod often operates on the insect long before growth is finally arrested. The timing of the sensitive period varies considerably according to species. In *Bombyx* it precedes the stage of arrest by almost an entire generation, the type of egg being decided by the conditions experienced by the moth during late embryonic development (49). In *Polychrosis* the pupal diapause is also largely determined in the egg stage (53), while in *Araschnia* the fate of the pupae is not decided until the fourth and fifth larval instars (18). *Leptinotarsa* will still respond to a long photoperiod up to the time when it is entering the soil to hibernate (103). And red mites laying summer or winter eggs can be induced to switch over to eggs of the opposing type by exposure to an antagonistic photoperiod (60). The duration of the sensitive period is also a variable feature. In *Diataraxia* it occupies no more than two days during the "moulting sleep" of the penultimate instar (101); in contrast, all the larval instars of *Antheraea* show some sensitivity although the last two are probably more critical, as can be demonstrated by rearing the other instars in a "neutral" or intermediate day length (93, 94).

Since the interval between the sensitive period and the stage of arrest does not bridge the early stages of embryogenesis in any of these species, it need not be assumed that the effect of photoperiod is transmitted through the cytoplasm of the egg. This is true even of *Bombyx* where diapause is essentially a maternal character (p. 8). These results are therefore compatible with the view that some organ system, such as the central nervous system, is concerned in transmitting the stimulus. Nevertheless, it should be noted that in the pteromalid *Spalangia* and the blowfly *Lucilia*, there is

some evidence that the larval progeny is influenced by physical factors acting on the maternal generation (17, 90).

Temperature.—Diapause is seldom independent of temperature except in species like *Antheraea* (93) and *Harrisina* (92) where photoperiod has assumed a dominant role. As a rule, diapause is suppressed by high temperatures and induced by low. This response has been recorded in *Diataraxia* (101), *Chilo* (29), *Orgyia gonostigma* Linnaeus (54), *Eurydema* (8), *Metatetranychus* (60), and in many other arthropods. It is interesting that in *Bombyx* high temperatures and long photoperiods also act in unison, but the direction of the response is reversed (49).

Food.—There is little evidence that diapause is often brought on by changes in the diet. The low water and high fat content of the ripening cotton boll may be of some significance in *Platyedra* (28). The onset of diapause in *Euproctis chrysorrhoea* (Linnaeus) has been attributed to the age of the foliage (41). But this now appears doubtful as more recent researches have shown that day length, and not the larval food, is the dominant factor in this species (38). Nevertheless, diet exercises a marked effect on *Metatetranychus*. When the food consists of yellowing, senescent leaves or "bronzed" foliage (i.e., leaves damaged by the feeding punctures of other mites) winter eggs are laid, even though the conditions of temperature and photoperiod are such as to prevent diapause strongly. The effect may be one of simple starvation (60).

THE TERMINATION OF DIAPAUSE

It has long been recognised that the release from diapause is often favoured by a long exposure to temperatures that are too low to permit morphogenesis. When the rates of completion of diapause are compared with rates of growth, certain points of resemblance emerge: both processes take place only within a certain temperature range and proceed most rapidly at a well-defined temperature optimum. These considerations have led Andrewartha (2) to coin the term "diapause development" to describe the gradual process of physiological development which he believes must take place as a prerequisite to the resumption of growth. This concept is clearly of considerable utility even if it should eventually transpire that the mechanism involves nothing more than the synthesis of a comparatively simple series of chemical substances.

The temperature requirements for diapause development differ to a remarkable extent. The connection with geographical distribution has recently been emphasised by Danilyevsky (19). In most saturniid moths, for example, the temperature range compatible with morphogenesis is roughly the same (ca. 15 to 32°C.). But in the Palaearctic *Saturnia pavonia* Linnaeus the range which is favourable for diapause development extends from 7°C. down to almost -15°C., so that this species can never develop in constant temperature conditions. Diapause is completed at rather higher tem-

peratures in *Antheraea pernyi* Guérin (112), and in the subtropical species *Philosamia cynthia* (Drury) the ranges for diapause development and growth overlap broadly but are still by no means coincident. It is now clear that the temperature optimum is often relatively low in species from cold or temperate climates. The optimum is 7°C. in *Bombyx* (27, 68, 114), 10°C. in *Cephus* (78), *Epistrophe* (82), and *Aporia* (113). And approximately the same temperatures are effective in *Melanoplus bivittatus* (Say) (15) and many European Lepidoptera (19, 55). Species from warmer environments require correspondingly higher temperatures. The optimum in the Australian cricket *Gryllulus* is 13°C. (10), in the beetle *Anthrenus verbasci* (Linnaeus) nearly 20°C. (57). Other species with high optima include *Locustana* (66), *Leptinotarsa* (103), *Harrisina* (92), and the subtropical silkmoth *Eriogyna* (52). These requirements are usually satisfied during the winter or cool season, although, if the winters are severe, autumn and spring may be more favourable for diapause development (112). However, when the temperature optimum is relatively high, and diapause of no great intensity, the insect may be released from dormancy in autumn instead of the following spring. This aberrant type of life cycle is found in the winter moth *Operophtera* (56).

The duration of diapause is also variable. It is quite transient in the pentatomid *Eurydema*, disappearing after only 9 days at a temperature of 8°C. (8). In *Bombyx* 60 days at 5°C. suffice (68), while *Metatetranychus* requires 150 to 200 days (60). Many Lepidoptera with an intense diapause may lie dormant for several years (20). And the gall midge *Sitodiplosis* sometimes passes up to 12 winters in the soil (3). Another interesting feature is that the responsiveness to chilling often depends on the stage of morphological or physiological development. This is particularly evident in insect eggs. Thus the *Gryllulus* egg is most sensitive some days before the embryo has actually developed to the diapause stage (9). In contrast, diapause disappears most rapidly in the *Locusta* egg if the period of chilling comes after about 60 days of high temperature (that is, 50 days after embryonic development has ceased) (59). These observations show that the temperature optimum sometimes changes during the course of "diapause development." Nevertheless, very little is known about the mechanism itself. Since one would not expect that any chemical reactions catalyzed by enzymes would possess a negative temperature coefficient, it is necessary to assume that "diapause development" involves the interaction of two or more processes, perhaps competing for the same substrate.

The role of water.—Many orthopteran eggs, as well as hibernating larvae and adult insects, cannot begin their postdiapause growth until moisture has been taken up from their surroundings. When water is lacking, diapause is often prolonged by a period of quiescence. In such cases it is often difficult to decide whether the processes controlling water uptake form an integral part of the diapause mechanism. Nevertheless, if this were so, one might expect that active uptake would remain in abeyance until diapause develop-

ment was completed. This appears to hold good in *Locustana*, for eggs of the diapause type will replace any water lost by evaporation, thereby restoring their turgor; but they will not take up sufficient water to stretch the membranes until diapause has disappeared (66). In *Melanoplus differentialis* (Thomas) the entry of water is cut off at the beginning of the diapause period by the deposition of a waxy layer over the hydropyle, so that diapause can be artificially ruptured by immersing the egg briefly in xylol (91). Indeed Bucklin (12) has shown that dormant embryos, when removed from their membranes, will even develop in Ringer's solution. It is therefore reasonable to assume that the limiting factor in these eggs is water lack and that the resumption of growth is dependent on the active water-absorbing properties of the extra-embryonic tissues. The eggs of *Doclostaurus* possibly provide a further example of this type of relationship (4). Nevertheless, a similar interpretation cannot always be applied. If the freshly laid eggs of *Gryllulus* are incubated in moist conditions, almost all the water is imbibed in the first few days so that the eggs enter diapause in a fully hydrated condition (11). Water absorption is also virtually complete when the almost fully developed embryos of *M. bivittatus* become dormant (79, 80).

Similar differences are found among larval and adult insects. In the borer *Chilo* no water at all is taken in until diapause development has been completed (50, 51). Yet diapausing larvae of the sawfly *Cephus* absorb water whenever it is available. In the usual way uptake proceeds steadily during the 100 or so days of chilling that are needed to end diapause. But if the larvae are chilled without access to water the entire amount can be taken up during the postdiapause period. Diapause development in *Cephus* is not retarded by dehydration (13). Contact water is also necessary for prompt development in the gall midges *Mayetiola* (111), *Schizomyia* (69), and *Contarinia* (40), as well as in the weevil *Rhynchites* (43). However, diapause mechanisms seem to be lacking except perhaps in the first species. The physiology of these types of arrest has not yet been studied in detail, but it seems probable that dehydration inhibits the secretory activity of some component of the endocrine system, perhaps the prothoracic glands in the case of larvae.

THE INHERITANCE OF DIAPAUSE

Strains differing in the character of their diapause have been recognised in many arthropods. The inherited differences always appear to involve the response to the many agencies which elicit or terminate diapause. For example, geographical strains of *Tetranychus* respond to slightly different critical photoperiods (6, 60, 62); the northern Japanese race of *Chilo simplex* Butler has a more intense diapause than the southern (110); the West Australian race of *Austroicetes* has a rather higher temperature optimum for diapause development than the South Australian race (2). A more far-reaching adjustment to the climatic conditions prevailing within the area of dis-

tribution is seen in species, such as *Pieris napi* (Linnaeus), which are represented by races with facultative and obligatory diapause. Peterson (74) has found that obligatory diapause, and a univoltine life cycle, predominates in northern Scandinavia, whereas genotypes conferring facultative diapause become increasingly frequent towards the south as the favourable season becomes longer. The same is probably true of populations of *Pyrausta* in the Lake States (U.S.A.) (70, 109). Subtropical populations of *Locusta migratoria* Linnaeus show no form of arrest, but an egg diapause has appeared in the subspecies *gallica* from the Bordeaux region and in other isolated populations near the limits of distribution (58, 59). Nevertheless, diapause races are sometimes associated with ecological rather than geographical isolation. For example, in the mite *Bryobia* strains without diapause and others with facultative and obligatory diapause have developed in association with different host plants (65).

The genetics of diapause has been examined only in *Bombyx* (98). Several genes, both sex-linked and autosomal, affect the voltinism. They have been assigned different "hibernating values" which are recognised by the influence of temperature on the induction of diapause. By suitable recombination experiments it is possible to prepare a series of stocks showing a graded response to temperature. These range from multivoltines (no apparent diapause), through bivoltines to univoltines (virtually obligatory diapause). As all the intermediate grades are represented, it is quite clear that the genotype modifies and shifts the response of the "receptor mechanism" to environmental factors such as temperature (62). There is no doubt also that the extreme types should be regarded as responding to the environment; in the case of an obligatory arrest it is merely that the range of stimuli that are diapause-inducing has become so broad that the insect can rarely escape this condition. Selection experiments with species such as *Ephesia* (100), *Locusta* (59), and *Antheraea* (97) have also thrown light on this question.

DIAPAUSE IN PARASITIC INSECTS

The synchronous development of insects and their parasites is achieved in different ways. One type of relationship has recently been studied by Schneider (83, 84). The eggs of *Diplazon fissorius* Grav. (Ichneumonidae) are deposited in young syrphid larvae, but although they soon hatch, the first instar larvae undergo no further development until the host forms the puparium. In the multivoltine syrphid, *Epistrophe balteata* Deg. the delay lasts only a few days, but in the univoltine species *E. bifasciata* Fabricius which has a nine-months larval diapause, the parasite also overwinters as a young larva. It is certain that the limiting factor is not the actual development of the host as the parasite is unaffected by the larval moults. It is rather some event (presumably of a chemical or humoral nature) which is peculiar to pupation. As the parasite larvae are very rapidly activated or immobilised

when transplanted into the appropriate hosts, this state of arrest resembles "quiescence" rather than diapause.

Many parasites exhibit a second form of arrest, a definitive diapause which supervenes at the close of the last larval instar after the host has been consumed. The assumption has often been made that some "diapause substance" is ingested and that this in turn inhibits the growth of the parasite. However, recent work by Gayspitz & Kyao (39) suggests that the braconid *Apanteles glomeratus* (Linnaeus) responds independently to length of day when developing in *Pieris brassicae* (Linnaeus). Both parasite and host are "long-day" insects, but, in order to suppress diapause, *Apanteles* requires slightly longer photoperiods than *Pieris*. When reared at this critical photoperiod, therefore, the parasites escape diapause although most of the hosts would enter diapause if they survived. A more direct proof is furnished by the fact that dormancy can still be prevented by exposing the larvae of *Apanteles* to long days immediately after they have left the host, even though the parasitized *Pieris* larvae have previously received short-day treatment. Day length is also involved in releasing the scelionid egg-parasite *Telenomus* from diapause.

It is well known that certain Diptera which normally overwinter as diapausing third instar larvae, form their puparia prematurely in autumn when invaded by hymenopterous parasites. Implantation experiments with the ichneumonid *Diplazon pectoratorius* (Thunb.) have revealed that the parasite does not activate the host's endocrine centres; nor is the wound puncture of any significance. Induced pupation is a result of the direct action of some substance secreted by the parasite. This may either be saliva or, more probably, the moulting hormone which diffuses out through the body wall of the parasite (84).

THE HORMONAL REGULATION OF DIAPAUSE

It now appears probable that humoral controlling mechanisms are implicated in all forms of diapause, whether embryonic, larval, pupal, or imaginal; but the endocrine systems differ according to the stage of arrest. The long series of investigations by Fukuda (30 to 36) and Hasegawa (44) on *Bombyx* has shown that the type of egg is decided by a secretion liberated from the suboesophageal ganglion. In the presence of this hormone, which is presumably derived from neurosecretory cells, diapause egg batches are laid; in its absence nondiapause batches are laid. Although the voltinism is normally determined by the environment acting on the late embryo, the hormone is not secreted until the pupal stage. A pupa initially determined for the production of nondiapause eggs will, therefore, develop into a moth laying diapause eggs if a suboesophageal ganglion is implanted. The suboesophageal ganglion is itself controlled by the brain through the circumoesophageal commissures. In the insect determined as a nondiapause egg-producer the brain seems to inhibit the secretion of the hormone. This restraint disappears

when the connectives are cut. It follows that suboesophageal ganglia from either diapause or nondiapause donors are capable of converting the eggs in a "nondiapause" recipient to the diapause condition. It is less certain, however, whether the brain merely ceases to inhibit the ganglion in the diapause egg-producer or whether it actually stimulates the synthesis or release of the active product. Suboesophageal ganglia from insects belonging to different races all have the same potentialities when isolated. The difference arises from the behaviour of the brain: in multivoltine insects the brain inhibits, and in univoltine insects activates, the suboesophageal ganglion without apparent regard to the previous environmental conditions (see, however, p. 7). A similar hormone is released by the suboesophageal ganglion of the male *Bombyx*, and even by those of certain species (e.g., *Antheraea pernyi*) with a pupal diapause.

Despite this clear evidence of regulation by the maternal endocrine system, the more immediate reason for the growth failure in the *Bombyx* egg remains uncertain. In *Melanoplus differentialis* the cause of the arrest does not reside within the yolk or even within the embryo itself, for mitotic activity is immediately resumed when diapausing half-embryos or even isolated limb rudiments are cultured *in vitro* (12). In this egg the growth failure seems to be attributable to a physical factor, namely an insufficiency of water (p. 5). Possible ways of reconciling this apparent contradiction are discussed later (p. 12).

It is well known that moulting and growth are controlled by an endocrine system which includes the brain and prothoracic glands. Researches by Williams (104 to 107) have shown that the pupal diapause in *Platysamia* is the result of the failure by the neurosecretory cells of the brain to secrete the hormone which is required for the activation of the prothoracic glands. There is no reason to attribute the growth arrest to the presence of an inhibitory principle, for when an intact diapausing pupa is joined in parabiosis with a developing pupa both members of the pair develop promptly. These conclusions have been confirmed in *Actias selene* Hübner (107) and *Luehdorfia* (47), as well as in certain insects with a diapause in the larval stage such as in *Gryllus* (88) and *Cephus* (14). And cytological evidence suggests that neurosecretion is lacking during the dormant period of the sawfly *Lophyrus* (45). Nevertheless, the brain is not invariably responsible for the interruption in the cycle of endocrine activity. In *Sialis* and the swallowtail *Papilio xuthus* Linnaeus the prothoracic glands apparently fail to activate the tissues (71, 77). The evidence is considered below.

The action of temperature on this endocrine system is particularly important in the present context. Like many other insects, *Platysamia* requires an adequate exposure to low temperature before development can be resumed. There is little doubt that the site of action is the brain itself. Thus unchilled brains that are transplanted into brainless diapausing pupae acquire the ability to secrete the neurohormone after the "host" pupae have

been chilled; at the same time unchilled brains do not become competent after transplantation into chilled brainless pupae [Williams (personal communication)]. This must mean that the normal afferent nerve supply to the brain is not an essential part of the mechanism; nor is the brain activated by diffusible substances liberated by other chilled tissues. The action of temperature on the brain is not fully understood, but it is helpful to distinguish between the gradual development of competence to secrete the neurohormone (this is essentially the process of "diapause development") and the subsequent release of the active principle into the haemolymph: the first process often requires a low temperature, the second a much higher temperature (108).

The organs responsive to chilling in *Sialis* and *Papilio* seem to be the prothoracic glands. Chilled larvae of *Sialis* develop promptly even after brain removal. Apparently the prothoracic glands require a stimulus from the brain, just as in other insects, but this takes place before the larvae have entered diapause (77). Decapitated diapausing pupae of *Papilio* will not develop at high temperatures, but they respond in the normal way to chilling (71). An interesting temperature effect, which has been noted in *Cephus*, relates to the re-establishment of diapause when adequately chilled larvae are exposed for short periods to a high temperature of 35° or 40°C. It seems that this treatment halts the secretion or release of the prothoracic gland hormone and thereby permits the brain neurohormone to be dissipated (14).

Reproductive diapause in *Dytiscus* (48), *Leptinotarsa* (103), and *Anopheles* (24) is known to be associated with the absence of the gonadotrophic hormones that are necessary for the full maturation of the ovaries. Although the hormone secreted by the corpus allatum is the immediate agent, a more remote control is probably exercised by the brain in the case of *Dytiscus* (48) and *Leptinotarsa* (42).

METABOLISM AND DIAPAUSE

Oxygen consumption during hibernation often falls to little more than one-tenth of the value in the growing or reproducing insect. These trends in the intensity of respiration have recently been followed in the *Platysamia* pupa (85) and in the tenebrionid beetles *Anatolica* and *Opatrum* (26). The level of this "maintenance metabolism" is probably lowest in species with an intense diapause: this results in the slow utilization of the food reserves and lengthy survival (20). The initial pathways of oxidative metabolism during growth and diapause may well be alike. It is true that extremely low respiratory quotients have sometimes been recorded in dormant insects; and this has led to the suggestion that fat is converted into carbohydrate (1). Nevertheless, it is now known that many hibernating larvae and pupae conserve their water supplies by opening the spiracles intermittently. Carbon dioxide is therefore accumulated and only released in "bursts" every few hours (76). After allowance had been made for this circumstance a respira-