



Review

Eco-physiological phases of insect diapause

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Abstract

Insect diapause is a dynamic process consisting of several successive phases. The conception and naming of the phases is unsettled and, sometimes, ambiguous in the literature. In this paper, the ontogeny of diapause was reviewed and the most often used terms and the best substantiated phases were highlighted, explained and re-defined. The aim was to propose relatively simple and generally applicable terminological system. The phases of diapause induction, preparation, initiation, maintenance, termination and post-diapause quiescence were distinguished. The specific progression through diapause phases in each species, population (genotype), or even individual, is based on (thus far largely unknown) physiological processes, the actual expression of which is significantly modified by diverse environmental factors. Thus, such phases are eco-physiological in their nature.

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1. Introduction-objectives

The ability to pass through adverse periods in diapause helps insects to exploit seasonally fluctuating resources, to

diversify in tropical habitats, and allows them to colonize temperate and polar regions. Understanding of diapause as *a process*, rather than as *a status*, is now widely accepted by the research communities working not only with insects (Danilevsky, 1961; Danilevsky et al., 1970; Tauber et al., 1986; Danks, 1987, 1994; Hodek and Hodková, 1988; Hodek, 1996, 2002; Denlinger, 2000, 2002), but also with

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other invertebrate organisms such as rotifers (Hand, 1991; Ricci, 2001; Gilbert and Schröder, 2004), nematodes (Sommerville and Davey, 2002; McSorley, 2003), earthworms (Lee, 1985; Jiménez et al., 2000), crustaceans (Brendonck, 1996; Clegg, 2001; Gyllström and Hansson, 2004), or terrestrial gastropods (Storey, 2002; Attia, 2004).

In insects, this dynamic approach to diapause was pioneered by Andrewartha (1952), who coined the term “physiogenesis”, to distinguish the progression of physiological changes occurring during diapause from the “morphogenesis” during direct development. The dynamism during diapause is manifested in the changing responses to temperature, photoperiod, humidity, hormonal treatment and other factors—as observed in numerous laboratory and field experiments (Lefevre and de Kort, 1989; Okuda, 1990; Gomi and Takeda, 1992; Sawyer et al., 1993; Tzanakakis and Verman, 1994; Shindo and Masaki, 1995; Nakai and Takeda, 1995; Wipking et al., 1995; Glitho et al., 1996; Johnsen et al., 1997; Nakamura and Numata, 1997; Xue et al., 1997, 2001; Kroon et al., 1998; Koveos and Broufas, 1999; Harada et al., 2000; Košťál et al., 2000, 2004a; Nomura and Ishikawa, 2000; Tanaka, 2000; Gray et al., 2001; Broufas, 2002; Singtripop et al., 2002a, b; Fantinou et al., 2003; Numata, 2004; Higaki and Ando, 2005; for more examples from older literature see: Tauber and Tauber, 1976; Tauber et al., 1986, pp. 111–160; Danks, 1987, pp. 133–159; Hodek, 1983; Hodek and Hodková, 1988).

In contrast to almost unison agreement over the fact that the insect organism gradually changes as it proceeds through diapause, there has been much less consensus among the various authors on the terminology for the successive phases of this process. The selection of terms used by different authors for various diapause phases was presented by Danks (1987, pp. 10–11) in his monograph on insect dormancy. According to Danks (1987), two main difficulties hinder attempts to define useful terms: (a) missing overt markers for intrinsic changes and (b) attempts to arbitrarily subdivide those phenomena that essentially are continuous. The former obstacle stems from the limited level of knowledge which is currently available on the physiological/molecular basis of diapause (for recent reviews see: Denlinger, 2000, 2002). The later obstacle reflects general methodological problem: dividing complex (and essentially continuous) phenomena (such as whole ontogeny or diapause as a part of it) into more or less artificial fragments (such as stages or phases, respectively) is often useful, or even necessary, for the effective experimental research. This review has two main objectives:

1.1. Rectification and simplification of terminology

Several earlier authors have recognized the problem of unsettled terminology in use for diapause and its phases. For example, Mansingh (1971) wrote in his review paper on the classification of insect dormancies: “Attempts by

ecologists and physiologists to describe ... dormancy ... have led to introduction of undefined and confused terminologies...”; additionally, Tauber and Tauber (1976) stated in their review on insect seasonality: “When it is (insect seasonality) discussed, many statements and assumptions ... are erroneous or the concepts outdated ... one particularly misunderstood area is the seasonal progression of diapause and its termination in nature”; yet the harshest assessment of the situation probably came from Jungreis (1978): “The study of insect dormancies is a study of misstatements and misunderstandings”. Though competent discussions of diapause were published in the two most influential monographs (from the author’s point of view) by Tauber et al. (1986) and Danks (1987), the non-standardized usage of various terms has continued up until the present (for a discussion see: Hodek, 1996, 1999, 2002, 2003).

If the problem were only semantic, writing this paper would have had little meaning. The correct characterization and description of the particular phase of diapause, however, is critical for the interpretation of physiological and molecular data, which increasingly frequently appear with the current methodological progress. The purpose of this paper is not to introduce new terms but, rather, to re-establish, and sometimes re-define, the old ones in an attempt to propose a terminological system that would pragmatically cover the events during the whole ontogeny, including the diapause phase. The aim is to suggest relatively simple and generally applicable terminology. The reviews of Tauber et al. (1986) and Danks (1987) served as the basis, and discussions of older literature can also be found in these two monographs. In this paper, literature quotations are mostly limited to papers published after 1986–87. Although this review is focused on insects, examples from other taxa will be shown, to document the general nature of diapause(-like) responses in invertebrates.

1.2. Providing a background for advanced physiological and ecological studies

The introduction of powerful modern techniques in analytical biochemistry and molecular genetics have provided the tools for “opening the black box” hiding the regulatory mechanisms of diapause (Saunders et al., 2004). During the last decade, a wealth of new studies have emerged which share one common theme: searching for the mechanistic basis of the diapause processes at a molecular level (for review see: Denlinger et al., 1995; Flannagan et al., 1998; Denlinger, 2000, 2002). Thus, diapause-specific expression patterns were observed in various genes: (a) encoding heat shock proteins (Yocum et al., 1998; Yocum, 2001; Goto et al., 1998; Goto and Kimura, 2004; Rinehart et al., 2000; Hayward et al., 2005; Tachibana et al., 2005; Yocum et al., 2005); (b) involved in energy metabolism or energy storage (Blitvich et al., 2001; Lewis et al., 2002; Levin et al., 2003; Uno et al., 2004); (c) affecting hormonal regulation (Yamashita, 1996; Vermunt et al., 1999;

Rinehart et al., 2001; Xu and Denlinger, 2003, 2004; Huybrechts et al., 2004; Zhang et al., 2004 a, b; Wei et al., 2005); (d) encoding clock proteins with influence on diapause induction (Saunders et al., 1989; Shimada, 1999; Košťál and Shimada, 2001; Goto and Denlinger, 2002a; Pavelka et al., 2003; Hodková et al., 2003; Syrová et al., 2003; Spieth et al., 2004; Doležel et al., 2005), or (e) with some other functions (Lee et al., 1998a; Daibo et al., 2001; Goto and Denlinger, 2002b; Ramos et al., 2003; Tanaka et al., 1998; Yocum, 2004; Chen et al., 2004; Tanaka and Suzuki, 2005). With the increasing availability of genomic microarray analyses, further expansion of the studies comparing diapause vs. non-diapause gene expression patterns may shortly be expected. Any such comparison should be based on the crucial knowledge obtained in earlier studies: *the diapausing organism gradually changes as it proceeds through successive phases of diapause*.

Diapause represents an important part of the life-cycle in many species of invertebrates. As such, it is considered in ecological studies with the aim to model and predict population responses to the environment which changes either seasonally or linearly, on an evolutionary scale (Hanski, 1988; Taylor and Spalding, 1989; Sawyer et al., 1993; Jeffree and Jeffree, 1994; Hoffmann and Blows, 1994; Lawton, 1995; Easterling and Ellner, 2000; Fiksen 2000; Bale et al., 2002; Parmesan and Yohe, 2003; Thomas et al., 2004). This direction of research will undoubtedly profit from the increasing precision in the knowledge of how the responses to environmental factors change at an individual ontogenetic level.

2. Diapause as a specific sub-type of dormancy

A brief introduction of the term diapause and related terms is pertinent here. In this paper, slightly modified terminology, as proposed by Shelford (1929) and later recommended by Lees (1955) and Danks (1987), will be retained:

Dormancy	Is a generic term covering any state of suppressed development (developmental arrest), which is adaptive (that is ecologically or evolutionarily meaningful and not just artificially induced), and usually accompanied with metabolic suppression.
Quiescence	An immediate response (without central regulation) to a decline of any limiting environmental factor(s) below the physiological thresholds with immediate resumption of the processes if the factor(s) rise above them.
Diapause	A more profound, endogenously and centrally mediated interruption that routes the developmental programme away from direct morphogenesis into an alternative diapause programme of succession of

physiological events; the start of diapause usually precedes the advent of adverse conditions and the end of diapause need not coincide with the end of adversity.

Classifying dormancies in only two broad categories (quiescence and diapause) is relatively simple and widely accepted. Where the decision about the appropriate category cannot be made with certainty, the general term “dormancy” should be preferred. More elaborate classification systems, as those proposed by several authors (Müller, 1965; Mansingh, 1971; Ushatinskaya, 1976; Witsack, 1981), appear not to be viable (for a discussion see: Danks, 1987, pp. 12–16).

The term *cryptobiosis* is related to the (extreme) depth of metabolic suppression: it is defined as “a peculiar state of biological organization when the organism shows no visible signs of life and when its metabolic activity becomes hardly measurable, or comes reversibly to a standstill” (Keilin, 1959; Clegg, 2001). Thus, a cryptobiotic period within the animals’ life cycle may represent either an extreme case of quiescence, or form a distinct period/phase within diapause. Representatives of many invertebrate taxa (some crustaceans, rotifers, nematodes, tardigrades, collembolans and insects) are capable of becoming cryptobiotic in embryonic, larval and/or adult stages upon dehydration, exposure to sub-zero temperatures, or the lack of oxygen (for a current review see: Clegg, 2001; Jönsson, 2001; Wright, 2001; Watanabe et al., 2002).

The stage of developmental arrest in which diapause proceeds may take very different forms. On one side there are various immobile stages such as diapausing embryos, cocooned mature larvae, pre-pupae and pupae which do not accept any food and display deep metabolic suppression, even if hydrated at relatively high temperatures. On the other side, diapausing free-living larvae and adults can move and their metabolic suppression is usually less deep. And there are also extreme cases, where the developmental arrest takes place in otherwise active specimens. For instance, diapausing 4th instar larvae of the nematoceran *Chironomus riparius* continue feeding and growing during winter, while the morphogenetic development of primordial adult structures (known as imaginal discs) is stopped at a specific stage IV 4–5a (Goddeeris et al., 2001). Similarly, diapausing larvae of the Mediterranean corn stalk borer *Sesamia nonagrioides* continue to feed, grow and even moult with several supernumerary instars. The larval development is thus prolonged but, importantly, the rates of feeding are low (so that the growth practically stops) and the morphogenetic development of imaginal discs is completely blocked (Lavenseau and Hilal, 1990; López et al., 1995). Similar diapauses have been observed in other lepidopteran and coleopteran larvae. Larvae of some species do not accept any food while continuing supernumerary larval moults, which results in a decrease of size and weight (sometimes called “retrograde development”)

(Oku, 1984; Gadenne et al., 1989; Shintani et al., 1996; Munyiri and Ishikawa, 2004). Such diversity in diapause expression (for current reviews see: Danks, 1991a; Danks, 1994; Danks, 2001; Danks, 2002) complicates the effort to find general principles. In the following text, the ontogeny that includes diapause will be divided into three main phases: (1) pre-diapause; (2) diapause; and (3) post-diapause. Each phase may comprise some sub-phases, expression of which depends not only on genotype-driven physiological changes but is also influenced by environmental conditions. Thus, the term *eco-physiological phases* will be used to reflect the fact that progression through phases is regulated by the interaction between endogenous and exogenous factors.

3. Pre-diapause

During the pre-diapause phase, direct ontogenetic development (morphogenesis) continues but, in response to specific environmental signals/conditions, the individual becomes destined for later entry into the diapause phase (endogenous developmental arrest).

3.1. Induction phase

Diapause is induced in advance of the advent of the environmental adversity. Diapause-inducing stimuli (or cues) are perceived during a fixed and specific *sensitive period*, which is genetically determined, and it ranges from various periods within the parental generation through different stages of embryonal, larval and pupal development to the adult individual. The inducing cues are *signalling* for the coming deterioration of environmental conditions, and the term *token stimuli* (Lees, 1955) is used in the literature to distinguish them from direct effects of other environmental factors on the rate of physiological processes.

The sensitivity to token stimuli may persist during further phases, where it takes on different roles, e.g. in the diapause maintenance or termination (this will be discussed later). Other environmental factors usually modify, and sometimes even revert or overwhelm, the effect of token stimuli (for reviews see: Tauber et al., 1986, pp.43–47; Danks, 1987, pp. 104–132). The signalling nature of token stimuli is best understood in the case of photoperiod. When a population sample of individuals is exposed to a *critical photoperiod* at their sensitive stage, half of them will enter diapause and the other half will continue in direct development. In insects, receptors for photoperiodic signal are localized in various parts of brain or the compound eyes (for a review see: Numata et al., 1997), and the pathways by which this signal is transduced into a developmental programme (direct or diapause development) have recently been investigated (Saunders et al., 1989; Saunders, 2005; Shimada, 1999; Košťál and Shimada, 2001; Goto and Denlinger, 2002a; Pavelka et al., 2003; Hodková et al., 2003; Syrová et al., 2003; Doležel et al., 2005; Danks, 2005).

Molecules of specific chemicals may serve as token stimuli, as well. Formation of the diapausing “dauer” stage during larval development in the nematode *Caenorhabditis elegans* in response to pheromonal signal (chemical signal released by conspecific organisms) is the case best understood. A constitutively produced pheromonal substance reaches a critical concentration in crowded conditions, which signals for the possible depletion of food resources in the future. Some individuals then arrest their development and form morphologically and physiologically distinct 3rd instar larvae, called the dauer stage. The signalling pathway, leading from the perception of the sensory information to the selection of an appropriate developmental programme, is being studied at the molecular level (Hekimi et al., 1998; Gerisch et al., 2001; Houthoofd et al., 2004; Matyash et al., 2004).

In some freshwater branchiopods and copepods, the production of diapausing eggs is induced by allelochemical substances (chemical signals released by other species), contained in exudates released into the water by their predators (Hairston, 1987; Słusarczyk, 1995). The induction of reproductive diapause in the desert locust *Schistocerca gregaria* by missing giberellin or eugenol in their diet may also exemplify the role of allelochemicals as a token stimuli (Ellis et al., 1965). In the tropics, changes in food quality may serve as a widespread token stimulus for diapause induction (Denlinger, 1986). In theory, even the environmental factors such as temperature or oxygen level might adopt the role of principal token stimulus in those habitats where they seasonally change in a predictable and sufficiently slow manner, and where photoperiodic or other token signals are less distinct or available (some tropical habitats, soil, caves, deeper layers in large water reservoirs, decaying wood).

In the less common case of *obligatory diapause*, the initiation of developmental arrest needs no external cues because it represents a fixed component of the ontogenetic programme and is expressed regardless of the environmental conditions. Token stimuli are utilized to induce more widespread *facultative diapauses*, where individuals can switch between two ontogenetic alternatives, i.e. direct development or diapause. Following is the general definition of the induction phase:

Induction phase	Occurs during genotype specific ontogenetic stage(s) (sensitive period) when cues from the environment are perceived and transduced into switching the ontogenetic pathway from direct development to diapause when the token stimuli reach some critical level (the response may be modified by other environmental factors).
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3.2. Preparation phase

The phases of induction and initiation may be either: (a) more or less separated within the same generation (or even

between generations) by a preparation phase or, (b) immediately successive (or even overlapping). The preparation phase is best documented in those organisms where the mother exerts control over the developmental fate of her progeny (for reviews on insects see: Mousseau and Dingle, 1991). Two relatively well understood cases of maternally induced diapause: the egg diapause in the silkworm *Bombyx mori* and the pupal diapause in the flesh fly *Sarcophaga bullata*, clearly show that diapause induction leads to specific alterations in gene transcription, neuroendocrine milieu and metabolic pathways and that the individual is destined for later entry into a developmental arrest (Yamashita, 1996; Denlinger, 1998). The information about developmental destiny is “stored” during the preparation phase. The preparation phase may be also characterized by different behavioural activities or physiological processes such as migration, location of suitable micro-habitats, aggregation, or the building-up of energy reserves before the final moult/transition into the diapause stage. Denlinger (2002) stated that events seen during the preparation phase “are surely reflected in diapause-related expression patterns of select genes, but the molecular events governing most of these prediapause characteristics remain unidentified”. Collectively:

Preparation phase	Occurs where the phases of diapause induction and initiation are separated by a period of direct development during which the individual is covertly programmed for later expression of diapause. Behavioural and physiological preparations for diapause may take place.
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4. Diapause

During this phase, direct development (morphogenesis) is endogenously arrested and an alternative programme of (so-far mostly unknown) physiological events proceeds, which is significantly modulated by changing environmental conditions. This phase corresponds to the period of *physiogenesis* or *diapause development sensu* Adrewartha (1952). Although the term diapause development is used by many authors, others point out its contradictory (oxymoron) nature and avoid using it (Mansingh, 1971). Different phases were distinguished during diapause by different authors (for some of them see: Danks, 1987, pp. 10–11). The least consensus has been reached in the understanding of the termination of diapause (for recent discussions see: Hodek, 1996, 2002). The effort to further sub-divide the diapause phase was motivated by frequent observations of changing responses to various environmental conditions (most often temperature) or to hormonal stimulation during diapause (see above for citations). This effort, however, suffers from limited knowledge that has been reached on the physiological nature of diapause processes so far (Denlinger, 2000, 2002). An attempt will be

presented in this review to explain diapause as a succession of three eco-physiological sub-phases: (1) initiation, (2) maintenance and (3) termination.

4.1. Initiation

The existence of a characteristic and distinct phase during the early part of diapause is widely recognized by different authors, although it has received many different names (e.g. entry, onset, initiation, beginning, start, fixation, intensification; see Danks, 1987, p. 10). Considering morphological criteria, the initiation phase begins when the ontogenetic stage is reached, at which direct development (morphogenesis) ceases. In some cases, this moment can be relatively easily distinguished, e.g. by moulting into the specific diapause stage with characteristic colour or shape or by formation of a cocoon (for review see: Danks, 1987, pp. 19–24). Morphological determination of the transition to diapause may require a more detailed examination such as: staging of embryonic development (Bell, 1989; Suzuki et al., 1990), dissecting primordial adult structures in larvae (Košťál et al., 2000; Goddeeris et al., 2001), opening pupal cases (Denlinger, 1981), staging of ovarian development in adult insects (Schopf, 1989; Spurgeon et al., 2003). It is a challenge for insect physiologists to identify more precisely the moment of diapause start in individual species by revealing, at cellular and molecular levels, what is the sequence of events which precede the cessation of morphogenesis. In general, either regulatory factors (unknown upstream factors → neuropeptides → hormones), or competency of target tissues (hormonal receptors → members of signalling cascades → cell-cycle regulators →, etc.), or both, might be involved. While different functions of hormones in this transition has already been postulated (for reviews see: Denlinger, 2000, 2002), the roles of other factors, such as heat shock proteins, have also received attention recently (Hayward et al., 2005).

In addition to cessation of direct development, the initiation phase of diapause is characterized by some other processes which allow it to be distinguished from subsequent phases. The regulated decrease of metabolic rate probably represents the most general feature of the initiation phase (Tauber et al., 1986, p. 50; Varjas and Sáring, 1998). Metabolic suppression represents a complex process, which requires concerted changes in phosphorylation state of metabolic enzymes, function of biological membranes and gene expression (Hochachka, 1985; Connett, 1988; Storey and Storey, 1990; Guppy et al., 1994; Brand, 1997). In many insects diapausing in mobile stages, a relatively slow decrease of metabolic rate is observed during the initiation phase. Although the developmental processes are blocked, high metabolic activity is required to support specific behavioural and physiological activities. Free living larvae and adults may continue accepting food, which is converted into energy reserves in the form of triacylglycerols, glycogen or hexameric proteins

(numerous examples may be found in Tauber et al., 1986 and Danks, 1987). They may also actively seek suitable microhabitats. For instance, the freshly moulted adult chrysomelid beetles *Colaphellus bowringi* undergo a period of intense feeding before they dig into the soil for summer or winter diapause (Xue et al., 2002). The continental-scale migration of diapausing monarch butterflies to their overwintering sites probably represents the most conspicuous case of behavioural activity connected to the initiation phase (Urquhart and Urquhart, 1978; Goehring and Oberhauser, 2002). Physiological preparations for the period of adversity may also take place during this phase (Danks, 1991b; Denlinger, 1991; Storey, 2002). In many cases, stress tolerance mechanisms (typically cold-hardening) may only become potentiated during the initiation phase; and they are overtly expressed later, in response to a specific stimulus (cold) (Hodková et al., 2002; Hodková and Hodek, 2004; Košťál et al., 2004a, b). Such a vigorous physiological and, sometimes, behavioural activity may be accomplished only at relatively high temperature and when the other factors are permissive, as well. Examples in the literature either confirm that the initiation phase has a relatively high temperature optimum (Johnsen et al., 1997), or they show that relatively higher temperatures during this phase result in developing a more intense diapause of longer duration and with higher survival rate after its termination (for references see Tauber et al., 1986, pp. 141–142 and Danks, 1987, pp. 146–151). It should be noted that the accumulation of energy reserves and also behavioural activities such as migration or seeking suitable microhabitat may fall into the preparation phase in those species, which undergo diapause in early embryonic or pupal stages; or which moult into a morphologically distinct (larval or pre-pupal) diapause stage.

The increase of diapause intensity has been reported in some insects during the initiation phase of diapause (for examples see: Hodek, 1983; Danks, 1987, pp. 134–135; Košťál et al., 2000; Košťál and Šimek, 2000; Singtripop et al., 2002b). In some other insects, “intensification” has never been observed. For instance, in the larvae of the moths *Ostrinia nubilalis* and *Sesamia nonagrioides* diapause intensity appears to be at its maximum from the moment of diapause start (Beck, 1989; Fantinou et al., 2003). The *diapause intensity* is measured as relative *duration* of developmental arrest (diapause) at a given moment and under given environmental conditions (Vino-gradova, 1974). Most often, the time-requirement for reaching the overt resumption of direct development when exposed to specific diapause-terminating conditions was assessed. The initial or maximum level of diapause intensity varies both within and between the populations, which can be attributed to different genetic backgrounds, and it is often considerably influenced by the conditions experienced during the induction and preparation phases (for references see: Danks, 1987, pp. 133–138; Wipking, 1995; Varjas and Sáringer, 1998; Nakamura and Numata, 2000).

Based on the above points, a definition of the initiation phase may be derived:

Initiation phase	Direct development (morphogenesis) ceases, which is usually followed by regulated metabolic suppression. Mobile diapause stages may continue accepting food, building of energy reserves and seeking suitable microhabitat. Physiological preparations for the period of adversity may take place and intensity of diapause may increase.
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4.2. Maintenance

Despite the fact that environmental conditions after the initiation phase of diapause are usually still permissive for continuation of direct development (and, indeed, non-diapause individuals of the same genotype *do* continue their development under such conditions), diapause individuals remain locked in developmental arrest. The metabolic rate is held relatively low and constant and the individuals *maintain* their diapause and ensure that the arrest persists over the period of several weeks – months before the diapause is terminated by a combination of: (a) unknown endogenous processes and, (b) specific change of environmental conditions (usually linked to the advent of environmental adversity or change in token signal). In the field, the insects usually initiate winter diapause (hibernation-type) when it is still summer and maintain it during the warm summer/autumn (Tauber and Tauber, 1976). Similarly, insects with summer (aestivation-type) and tropical diapauses initiate and maintain their diapause before the adversity-period comes (the habitat either dries out or is flooded; the food resource becomes limited/changes in quality; or the activities of competitors/predators increase) (Masaki, 1980; Denlinger, 1986; Godfrey and Hassell, 1987; Wolda, 1988; Topp, 1990; Tanaka, 2000; Adis and Junk, 2002). The period of maintenance may extend to several years or even decades in some species and specific cases (for review see: Hanski, 1988; Powell, 2001; Menu and Desouhant, 2002; Sandberg and Stewart, 2004; for an alternative view of “repeated diapause” see: Soula and Menu, 2005).

Although the maintenance phase represents the most “true” phase of diapause, practically nothing is known about its physiological nature. Basic processes, such as energy-store depletion and somatic aging, likely contribute to gradual change of the physiological state during maintenance. Most importantly, some poorly understood (sequence of) change(s) proceeds during this phase, which is overtly manifested as gradually decreasing diapause intensity and/or increasing sensitivity to diapause-terminating conditions (Tauber and Tauber, 1976; Hodek, 1983; Sawyer et al., 1993). Specific token stimuli (e.g. long-day photoperiod in many winter diapauses) may help to maintain diapause (Tauber and Tauber, 1976). A period

of relative “refractoriness” to diapause-terminating conditions was also reported in the early phase of diapause of the eggs of rotifers (Gilbert and Schröder, 2004), crustaceans (Arnott and Yan, 2002), and in diapausing nematodes (Sommerville and Davey, 2002). Such observations led some authors to name this phase as “refractory” (Mansingh, 1971; Watson and Smallman, 1971).

The definition suggested here is:

Maintenance phase Endogenous developmental arrest persists while the environmental conditions are favourable for direct development. Specific token stimuli may help to maintain diapause (prevent its termination). Metabolic rate is relatively low and constant. Unknown physiological process(es) lead to more or less gradual decrease of diapause intensity and increase of sensitivity to diapause terminating conditions.

4.3. Termination

Our understanding of how diapause ends is still very incomplete. It is recognized that diapause maintenance may culminate in *spontaneous termination* and resumption of direct development in many insects and mites which are kept under *constant* laboratory conditions (Gomi and Takeda, 1992; Veerman, 1994; Tzanakakis and Verman, 1994; Wipking, 1995; Musolin and Saulich, 1996; Nakamura and Numata, 1997, 1999, 2000; Fantinou et al., 1998; Košťál et al., 1998; Tachibana and Numata, 2004; for other examples see: Danks, 1987, pp. 154–155; Hodek and Hodková, 1988; Hodek, 2002). Similarly, spontaneous hatching of diapause eggs or excystment from resting (diapausing) cysts was observed in the planktonic rotifers *Brachionus* sp. (Gilbert and Schröder, 2004) and ciliates *Pelagostrombidium* sp. (Müller, 2002), respectively. In such cases, no distinct termination *phase* can be recognized and diapause is simply maintained until it ends.

In many other species, however, the requirement for specific diapause-terminating conditions (*sensu* Tauber and Tauber, 1976) is strict and/or fitness is considerably compromised without their intervening effect (for discussion see: Hodek, 1996, 2002, 2003). For instance, the maintenance phase, under constant laboratory conditions that were used for diapause induction and initiation, will continue until all larvae of the fly *Chymomyza costata* die, while the termination may proceed only at low temperatures (Košťál et al., 2000). In the laboratory, the maintenance and termination phases can be clearly separated in some insects by specific settings of the environmental conditions. In the field, complexity, fluctuations and linear changes of environmental conditions make the distinction more difficult. Nevertheless, it has been shown that specific conditions/stimuli often *do participate* in the termination of diapause in the field, even if they *are*

not strictly required in the laboratory. This is ecologically meaningful because the initiation of diapause may take place during very different periods of the year in different individuals of the same population. Each individual then maintains the diapause for a different time before the advent of the adversity period (or of a reliable token signal of it), which then serves as synchronizing stimulus and prevents untimely (premature) termination of diapause. Termination then takes the form of a distinct *ecophysiological* phase, during which diapause intensity decreases to its minimum level and subsequent resumption of direct development is enabled (but need not be realized). Numerous examples of the effects of diapause-terminating conditions are reported in the literature. Chilling is the most common factor terminating many winter diapauses in the field (Tauber et al., 1986, pp. 146–148; Hodek, 1996, 2002). Tanno (1970) found that freezing (formation of ice crystals) was a necessary factor for termination of prepupal diapause in the Japanese poplar sawfly *Trichiocampus populi*, both in the field and laboratory. Most of the summer diapauses and, perhaps, even some rare cases of winter diapauses, are terminated in the field by the change of photoperiodic signal (for examples see: Masaki, 1980; Tauber et al., 1986, pp. 131–133; Ito, 1988). Contact with water was reported to serve as the terminating factor for summer diapauses of the larvae of the stem borer *Busseola fusca* (Okuda, 1990), and of the eggs of the chrysomelid beetle *Homichloda barkeri* (Nahrung and Merritt, 1999) (but see also the discussions in: Tauber et al., 1998; Hodek, 2003). In some crustaceans, drying of the sediment increases emergence from diapausing eggs upon re-hydration (Arnott and Yan, 2002).

Approximately synonymous terms for the termination phase have been suggested such as: “reactivation” (Danilevsky, 1961), “restoration” (Ushatinskaya, 1976), “activation process” (Mansingh, 1971), or “diapause ending processes” (Wipking, 1995) (for some other synonyms see Danks, 1987, p. 10). All these terms indicate that the potentiality for further continuation of direct development returns during this phase. Hodek (1983) suggested distinguishing between “horotelic” (evolving at the standard rate) and “tachytelic” (evolving at a rate faster than the standard) ways of diapause termination. In its original meaning, the term horotelic was used as a synonym of natural diapause termination in the field and the term tachytely designated artificial activation of diapausing individual by various environmental stimuli. The most salient fact noticed by Hodek (1968, 1983) is that the individuals that terminated their diapause by horotelic and tachytelic processes differ qualitatively. Thus, diapausing adults of the bug *Pyrrhocoris apterus* brought to reproduction by tachytelic photoperiodic activation (exposure to long-day photoperiod at high temperature) remained responsive to photoperiod, while the adults that terminated diapause in a horotelic process (in the field, or by exposure to low temperatures) lost their photoperiodic sensitivity. It has been known for a long time that diapause in insects or

other organisms may be precociously terminated, or interrupted (?), by various artificial stimuli such as mechanical shaking, electric or temperature shocks, injury, infection, or treatment with solvents and other chemicals (Clegg et al., 1996; for other examples see: Denlinger et al., 1980; Danks, 1987, p. 155). How these factors operate, and if the post-termination state after such precocious termination differs from the state after horotelic termination, is not known.

The process of diapause termination eventually leads to either the overt resumption of direct development (if the conditions are permissive) or the covert return of potentiality for direct development (if the conditions are not permissive). Such understanding of diapause “end” is in accordance with the view of Tauber et al. (1976, 1986); Danks (1987) and Hodek (1983, 1996, 2002). Photoperiodic termination of summer diapause in the prepupae of the moth *Cymbalophora pudica*, which is immediately followed by pupation and pupal development (Košťál and Hodek, 1997), exemplifies the case when the end of diapause merges with the resumption of direct development. However, winter diapauses of insects inhabiting temperate regions usually end during early or mid winter when the ambient temperatures attain their seasonal minimum and the other environmental conditions are also far from favourable (Hodek, 1983, 1996, 2002). Similarly, termination of summer and some tropical diapauses may be accomplished during the dry period, which prevents further development (Tauber et al., 1998; Hodek, 2003).

Characterizing the termination and the end of diapause in physiological terms is a future goal for students of diapause. Hypothetically, diapause is a complex of processes (some may run in parallel while others may run in succession), which are variously interlocked. If one of the processes (or some sub-set of processes) differs in its requirement for environmental conditions/stimuli from the preceding processes, the progress of diapause (diapause development) is inhibited (either slowed down or stopped) until the new conditions are reached. Reaching the diapause-terminating conditions stimulates (either accelerates or resumes) diapause development and thus marks the beginning of termination phase, which proceeds until the end of diapause. The end of diapause is linked to the return of potentiality for biosynthesis, release and transport of regulatory factors (hormones etc.) and to the return of the competence of target organs to respond to these factors (Khan and Buma, 1985; Endo et al., 1997; Matsuo et al., 1997; Readio et al., 1999; for review see: Denlinger, 1985, 2000, 2002). Sensitivity of the target tissues is likely regulated by the presence/absence of hormone receptors. It has been shown that ecdysone receptor (EcR), or its dimerization partner ultraspiracle (USP), are down-regulated during pupal diapause, and further that expression of their genes rapidly reappears upon the resumption of direct development in the tobacco hornworm *Manduca sexta* (Fujiwara et al., 1995); or spontaneously, at the time coinciding with diapause end,

in the flesh fly *Sarcophaga crassipalpis* (Rinehart et al., 2001), respectively. Some other genes are known to start their expression only after passage of a specific time-period of diapause and their products may thus participate in the processes of diapause termination (Niimi et al., 1993; Lee et al., 1998b). In a long series of papers on the cold termination of diapause in the eggs of the silkworm *Bombyx mori*, the physiological mechanism of this process was attributed to the conformational change of a specific protein named Time-Interval-Measuring-Enzyme (TIME), which is regulated by the time-holding peptide (PIN) (Kai and Nishi, 1976; Kai et al., 1987, 1995; Ti et al., 2004).

The current lack of clear markers for diapause termination and its (covert) end led to the development of an alternative view (Mansingh, 1971) where the end of diapause is linked to overt resumption of direct development. Some authors prefer this alternative view (Bell, 1994; Gillot, 1995; Irwin et al., 2001; Nahrung and Allen, 2004; Teixeira and Polavarapu, 2005).

Here, the definition is suggested, which links the termination phase to specific termination conditions/stimuli:

Termination phase	Specific changes in environmental conditions stimulate (accelerate or resume) the decrease of diapause intensity to its minimum level and thus synchronize individuals within a population. By the end of the termination phase, a physiological state is reached in which direct development may overtly resume (if the conditions are permissive) or covert potentiality for direct development is restored but not realized (if the conditions are not permissive).
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5. Post-diapause

The environmental conditions favoring diapause termination may differ from those favoring resumption of direct development. The organism then remains exogenously locked in the state of *post-diapause quiescence* (note difference from the endogenous lock during diapause). By the end of post-diapause quiescence, changes in limiting factors allow the organism to continue in direct development. Thus, post-diapause *resumption* of direct development is postponed to the vernal rise of temperatures in winter-diapausing insects (for references see: Lees, 1955; Lees, 1956; Tauber et al., 1986; Danks, 1987; Hodek, 1983, 1996, 2002; Régniere, 1990), and summer-diapausing insects must usually wait for the increase of humidity, or presence of liquid water (for recent review see: Tauber et al., 1998; Hodek, 2003). Similarly, the resumption of direct development in the resting eggs of freshwater zooplanktonic rotifers and crustaceans is commonly

influenced by a variety of environmental factors such as the rise of temperature and oxygen levels or exposure to light (Ricci, 2001; Gyllström and Hansson, 2004; Vanderkerkhove et al., 2005). In some cases, specific biotic factors, such as seasonal change of the biochemistry of the host plant or appearance of a food source signaled by allelochemicals, may stimulate the resumption of direct development (Wolda, 1988; Denlinger, 1986). The individuals which went through diapause may differ qualitatively from those, which reached the same ontogenetic stage through direct development only. For example, sensitivity to diapause-inducing/maintaining photoperiod is usually lost during cold-termination, but this loss may be only transient in the case of “recurrent photoperiodic response” (Hodek, 1971, 1979). The rotifer females that hatch from resting (diapause) eggs differ in many morphological and physiological aspects from the genetically identical (parthenogenetic) females of subsequent generations (King and Serra, 1998; Gilbert and Schröder, 2004).

The fact that the competency of the organism for direct development is already fully restored during the post-diapause quiescence is also recognized by those authors, who prefer to include this period of externally driven developmental arrest in the diapause phase. The terms “activated phase” or “competent phase” have sometimes been used for this period (Mansingh, 1971; Watson and Smallman, 1971). The definition suggested here is:

Post-diapause quiescence Exogenously imposed inhibition of development and metabolism, which follows the termination of diapause when conditions are not favourable for resumption of direct development.

6. Summary

The concept of insect diapause as a dynamic process consisting of several successive phases was reviewed in this paper. The study was motivated by the widespread and persisting ambiguities in the usage of various terms to describe diapause. No new terms or phases were created here. Rather, the most often used terms and the best substantiated phases were highlighted, explained and re-defined, where necessary. Not all the phases must necessarily be found in all species and situations.

The proposed terminological system is diagrammatically presented in Fig. 1 (it should be stressed that the presentation is highly schematic). During the *induction* phase (late embryonal and early larval stages here), token stimuli are perceived and, when they reach a critical level, the information is transduced into the decision for inclusion of a diapause phase into the developmental programme. During the *preparation* phase, direct development (morphogenesis) continues, but the information about diapause destiny is stored and physiological preparations for the period of developmental arrest may take place. A preparation phase is not present in species in which the initiation phase immediately follows the phase of induction. The *start* of diapause means reaching the specific ontogenetic stage, in which direct development ceases. During the *initiation* phase, metabolic rate drops relatively rapidly, diapause intensity is at its maximum level, or may even increase. In those species with no distinct preparation phase, specific behavioural and physiological activities take place during initiation, which serve to secure survival through the period of developmental and metabolic arrest and environmental adversity (migration, seeking suitable microhabitat, feeding, building energy reserves, etc.). The *maintenance* phase is characterized by

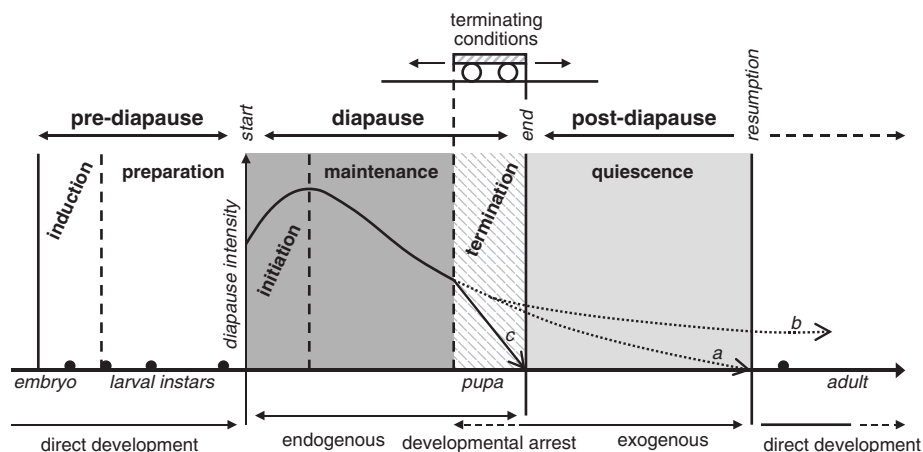


Fig. 1. Schematic depiction of the terms as they were defined in this paper. Thick line with arrowhead in the lower part of the picture indicates the passage of time starting from formation of zygota to the death of one hypothetical insect individual. The points on the line delineate major ontogenetic stages (different staging must be considered in different species). Three major phases, namely pre-diapause, diapause and post-diapause, are distinguished during the diapause-including ontogeny. Further division to sub-phases, namely induction, preparation, initiation, maintenance, termination and quiescence, is indicated by vertical lines (not all the phases must necessarily be found in all species and situations). Changes in diapause intensity are schematically presented: dotted branches (a and b) apply to the constant conditions, while solid branch (c) applies to the change of environmental conditions (specific terminating conditions/stimuli coming at different physiological times—movable carriage). Detailed explanation of all terms is in the text.

continuing developmental arrest and a relatively low and constant metabolic rate, despite the fact that environmental conditions are still favourable for physiological and morphogenetic processes. Unknown (sequence of) process(es) is (are) responsible for the decrease in diapause intensity. The curve showing development of diapause intensity splits into three trajectories in Fig. 1. Dotted trajectories (a and b) display two possible ways of development under constant conditions (the same as those during induction, initiation and maintenance). Trajectory (a): in some species, diapause may reach its end spontaneously and resumption of direct development follows immediately. Trajectory (b): other species cannot terminate diapause under constant conditions (finally they die). In the field situation, trajectory (c) applies: specific diapause-terminating conditions/stimuli, which are either strictly required (b) or intervening (a), stimulate diapause progression to its end during the *termination* phase. The “carriage” with terminating conditions symbolizes that such conditions may come at different physiological times to different individuals of the same population (and also at different seasonal times in successive years). The *end* of diapause is linked to the full return of potentiality for direct development. Such potentiality may be either immediately realized when the conditions are permissive or, as it is shown in Fig. 1, its realization is exogenously inhibited by adverse conditions during the phase of post-diapause *quiescence*. In this later case, direct development *resumes* only upon the onset of permissive environmental conditions. The individuals which had passed through diapause may differ from those that had reached the same ontogenetic stage through direct development only.

The above described phases are based on (thus far largely unknown) physiological processes, the actual expression of which is significantly modified by diverse environmental factors. Thus, such phases are *eco-physiological* in their nature. Despite the enormous diversity of diapause responses, a relatively simple terminology, as suggested in this paper, should be sufficient to cover major phases that appear during the diapause-including ontogeny of invertebrates.

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