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MINI REVIEW

# Diapause research in insects: historical review and recent work perspectives

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**Abstract**

All organisms on Earth have evolved biological rhythms to face alternation of periods of favorable and unfavorable environmental conditions, at various temporal scales. Diapause is a state of seasonal dormancy adapted to recurring periods of adverse environmental conditions and triggered by biotic and abiotic factors that precede the arrival of these conditions. Several monographs already review the mechanisms of diapause expression in arthropods, from initiation to termination phases. Rather than adding another review to the literature on this topic, this paper primarily aims to link past concepts on seasonal strategies with new perspective on diapause research in arthropods. By focusing on insects, I examine the legacy of diapause history research in terrestrial arthropods since antiquity but mostly over the past 3 centuries, its contribution to the understanding of insect seasonal ecology, and I explore some of the reasons why it is still relevant to study diapause. I highlight some of the topical issues on which current work focuses to better understand and integrate arthropod diapause with their ecology, especially in the climate change context and for the provision of ecosystem services.

## Introduction

Most aspects of organismal physiology, metabolism, and behavior are clock-controlled and result in daily or seasonal strategies (e.g., sleep or hibernation). Measurement of photoperiodic changes at various time-scales serves as basis for the functioning of such clocks. Circadian rhythms have evolved to match a 24-h light-dark periodicity, corresponding to Earth rotation around its own axis, whereas seasonal life cycles, from plant blossoming to mammal hibernation, have been shaped by environmental changes occurring over the year.

Arthropod adaptations to seasonal environmental changes are remarkable and by far the most studied, although literature has been mostly insect-focused. Most arthropods, as small poikilothermic animals, are particularly sensitive to increases or decreases in temperatures above or below their optimum, to frost and drought conditions, and to decreases in resource availability (Bale, 2002; Speight et al., 2008). From all latitudes, they have evolved seasonal strategies to face recurrent changes, mostly in temperature and moisture (Tauber et al., 1986; Leather et al., 1993). Tropical regions are typically less variable than temperate areas, although dry and wet seasons follow one another. In temperate areas, the need to survive winter has a particularly significant impact on an organisms' life cycles.

One of the strategies evolved by arthropods to overwinter is diapause, which is a dynamic state of low metabolic activity, genetically determined, with the neuro-hormonal system as mediator (Denlinger, 2002). It is characterized by behavioral inactivity, morphogenesis and reproductive functions arrest, and slowing growth (Danks, 1987). Diapause occurs at a species-specific stage of ontogenesis and its expression is regulated by various environmental signals that precede and reliably predict the arrival of unfavorable conditions (token stimuli). The cause-effect relationship between diapause and cold-resistance in arthropods is still debated, and both phenomena may not be directly related depending on species or populations (for a review on these links, see Hodkova & Hodek, 2004). The main stimulus inducing winter diapause in arthropods is the day length decrease after summer. Once induced, diapause cannot be immediately terminated even if favorable conditions for development appear (Tauber et al., 1986). Seasonal adaptations in insects have been the subject of many syntheses (e.g., Tauber et al., 1986; Danks, 1987, 2007). Although other types or degrees of dormancy

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do exist (e.g., summer diapause, aestivation, quiescence. . .), winter diapause is the strategy that has received most attention (Masaki, 1980; Leather et al., 1993).

In this brief historical review, I consider the evolution of the concepts and the semantics that led to the current definition of dormancy and diapause and its implications for modern research. As a perspective, I present topical issues on arthropod seasonal polyphenism and the most recent advances in the study of diapause.

## History of diapause study

The study of biological rhythms is fascinating, especially because humans are also strongly influenced by circadian cycles and the alternation of seasons in our biology and activities (Stevenson et al., 2015). Since the Neolithic era, with the appearance of agriculture and livestock breeding, humans have had to understand and master the natural cycles of plants and animals to exploit them efficiently throughout the year.

The scientific study of the effects of daily photoperiodism began in plants with the sensitive *Mimosa pudica* L., which opens and closes its leaves on a 24 h cycle, clearly expressing a rhythmicity linked to day and night alternation (De Mairan, 1729). Concerning seasonal photoperiodism, long before the term 'diapause' was introduced, naturalists were already interested in understanding how animals spent the winter, in what forms, what behaviors were adopted, and how long was their inactivity during the unfavorable season. The French naturalist René-Antoine Ferchault de Réaumur, a member of the Royal Society of London and director of the 'Académie Royale des Sciences', commented for the first time a detailed study on insect behavior and physiology during winter, in a work of several volumes (De Réaumur, 1734). He mentions in particular, his research on the overwintering of honey bees and, without mentioning it as such, De Réaumur makes here the first description of dormancy in insects:

> 'I know of no insects to which heat is so necessary. They perish with cold, in an air temperature which appears good enough to all other insects of our climate. The cold, which stops plant growth, which causes our prairies and fields to lose their flowers, puts the bees into a state in which food ceases to be necessary to them; it holds them in a sort of numbness, during which there is stop sweating or, at least, during which the quantity of what they sweat is not considerable that it may not be repaired by food, without their life running at risk. In winter, while it freezes, the hives without transparent walls can be considered without fear; for they can be laid on the side, or even turned upside down, without putting any bees in motion. They are seen piled up and pressed very closely together; they do not need a lot of room, they are usually between the cells toward their lower part, or toward the middle of the top of the hive. If thaw arrives, if the temperature softens, and especially if sunrays hit the hive and warm it up, the honey-flies emerge from their kind of lethargy; they wave their wings, they set in motion, and activity is restored to them'. [Translated from old French]

Diapause was first defined by analogy with the hibernation in mammals such as in hedgehogs, a phenomenon that was well known since antiquity (e.g., the naturalist writings of Pliny the Elder or of Aristotle; Bostock & Riley, 1855). The term 'hibernation' was used in the 19th century to describe winter dormancy in insects (Rennie, 1857). Dormancy is a recurring period in the life of an organism during which development and reproduction are slowed, and may result in a simple slowing of growth, quiescence, or diapause, depending on the predictability of the environment (Danks, 1987). By studying the silkworm, Duclaux (1869) differentiated for the first time the simple torpor due to low temperatures from extended dormancy. The term 'resurrection' appears several times in the early literature to refer to anabiosis, a return to life after a period of cryptobiosis, i.e., complete metabolic, developmental, and behavioral inactivity (Preyer, 1891). The term 'diapause' was introduced for the first time by Wheeler (1893) to describe the developmental stage of locust eggs during the winter. The term 'quiescence' or 'pseudo-diapause' was introduced a few years later by Shelford (1929) and Roubaud (1930) in an attempt to differentiate these phenomenon from 'true diapause'.

From the 1910s to the mid-20th century, driven by the development of ecology and evolutionary sciences, there was a revival of scientific interest in the overwintering of insects and their ability to resist low temperatures (Sanderson, 1908; Bodine, 1923; Holmquist, 1928; Salt, 1936); notably by studying cryoprotective compounds. For a review of the history of research on cold tolerance of insects, see Sømme (2000). During the 1920s and 1930s, the first chronobiology laboratories were established and began to study the effect of photoperiod on plants, mammals, birds, and insects. Beling (1929) discovered that bees can be habituated to search for food at a particular time of the day, corresponding to flowers opening and nectar production that are also based on circadian rhythms. Therefore, the adaptive and ecological significance of insect clocks was beginning to emerge. As seasonal activity patterns are correlated with changes in temperatures over the year, it was first assumed that they were due to this

particular factor, although some authors did not feel diapause was adaptive and attributed it to a physiological maladjustment during development (e.g., Simmonds, 1946). First discovered in plants, the use of photoperiod as a proxy for environmental changes was proposed for insects in a study on aphid seasonal polyphenism and migration (Marcovitch, 1924). The study of dormancy in insects has been since strongly linked to the study of photoperiodism and clock mechanisms, and extended to all associated traits: sexual morph production, changes in body coloration, physiology, metamorphosis, diet, etc. It was also at this time that Bünning (1936) proposed a link between the photoperiodic system inducing diapause and the circadian system. Bünning (1936) also proposed two distinct mechanisms of photoperiodic time measurement in plants, then extended to insect photoperiodism for diapause induction (Bünning, 1960): an endogenous circadian oscillator which coincides with external variations in photoperiod, and an hourglass which measures day- or night-length and their relative duration. The diversity of insect clocks, especially in regard to photoperiodism is reviewed and discussed in Saunders (2002).

Andrewartha (1952) made the first synthesis of what insect diapause and phenology imply with regard to their ecology, an issue that is still far from being resolved. Lees (1955) described diapause from an ecophysiological point of view and highlights the importance of studying the seasonal cycles of insects, paving the way to the first research on endocrine control and the genetic basis of diapause (Lees, 1956; Salt, 1961). For instance, Williams (1946) observed that diapause in the silkworm *Antheraea pernyi* Guérin-Méneville was hormonally controlled. First reports of transgenerational effects on diapause and of maternally induced diapause in insects were also written (Simmonds, 1946, 1948; Schneiderman & Horwitz, 1958; Saunders, 1965). At the end of this work, ecologists and entomologists produced a definition and above all a clear classification of what diapause is. Indeed, there is then much confusion about the nature of the various types of dormancy in insects. There is a gradient from simple behavioral inactivity to deep diapause, and detangling the expression of these responses inherent to insect seasonal ecology was all but simple. A new classification system for dormancy types was produced in the second half of the 20th century in a will to produce a set of clearly defined terms, particularly in order to dissociate programmed arrest of development (photoperiodism) to immediate, direct, physiological responses to environmental conditions (Danilevskii, 1965; Müller, 1970; Mansingh, 1971; Thiele, 1973; Beck, 1980). Important insights were provided into the role of token (anticipatory) cues regulating diapause in arthropods. In particular, based on these classics, a description of the main factors inducing, maintaining, and terminating diapause was developed, the terms diapause, torpor, dormancy, rest, and quiescence were clearly defined and dissociated, and the notions of obligatory vs. facultative diapause appeared.

The monographs of Tauber et al. (1986) and Danks (1987), two classics of the discipline, reviewed insect adaptations to seasonal events and provided a framework on studies of insect dormancy, seasonal cycles, biological clocks, and photoperiodism. The work pursued from the 1980s to the edge of the new century was successful at linking internal processes governing diapause (timers, internal clocks, hormonal regulation, physiological responses to induction and termination cues) to its ecological significance. Research articles and reviews produced in the past 30 years strove to synthetize discoveries on the diversity of biological contexts involved in insect dormancy, in addition to strictly photoperiodic responses. Still, the evolutionary origins of winter diapause remain rather unclear, because there is a gradient of dormancy strategies ranging from temporary slowing of growth to deep diapause. Winter diapause was first viewed as a recent acquisition in insects, which would only have appeared after the colonization of temperate environments following the last glaciation (Levins, 1969). This hypothesis does not seem very likely as the ability to enter diapause also exists in tropical arthropods, although it is often more difficult to detect than in temperate environments (Tauber & Tauber, 1981). More likely, diapause would have a tropical origin and insects would not have acquired de novo the ability to enter diapause after the last glaciation (Tauber & Tauber, 1981). In particular, due to the 'anticipatory' aspect of diapause, its origin would be related to evolutionary changes in the ability to measure stimuli indicating the approach of seasonal changes (Tauber et al., 1986; Saunders, 2002). As insects colonized higher latitudes, they would have developed abilities to measure seasonal photoperiod changes from pre-existing circadian clocks (Meuti & Denlinger, 2013). Natural selection would have acted on these characteristics of pre-existing photoperiodism and dormancy in tropical species until they adapted to environmental changes that occur in temperate environments (Tauber & Tauber, 1981). One can therefore conclude that diapause is a phenomenon phylogenetically ancient in arthropods.

Recent advances examined endocrine and molecular control of diapause (Denlinger, 2002) as well as energetic demand of overwintering strategies (Hahn & Denlinger, 2011). Studies focused on the integration of ecological and physiological phases of diapause (Hodek, 1996, 1999; Koštál, 2006), on geographic clines in diapause expression (Saunders & Hayward, 1998; Hut et al., 2013), on the links

with seasonal polymorphisms in life cycles (Danks, 1994; Nylin, 2013), on trade-offs between insect diapause and life-history traits or life-history strategies (Ellers & van Alphen, 2002; Danks, 2007), on developmental plasticity (Gotthard & Berger, 2010), on diapause inheritability (Winterhalter & Mousseau, 2007; Han & Denlinger, 2009), and on implications for community level interactions (Boivin, 1994; Lalonde, 2004; van Nouhuys & Lei, 2004). The importance of summer diapause as a response to stressful summer conditions and constraining for arthropod activity, mostly neglected until then, also appeared in the literature (Masaki, 1980; Butler et al., 1985; Koštál & Hodek, 1997). Relationship among photoperiodism, diapause, and cold tolerance was introduced as an important facet of insect overwintering strategies (Denlinger & Lee, 1991; Hodkova & Hodek, 2004). More recently, study of diapause is also dealing with evolutionary insights such as phenology evolution in a context of rapid changing environments (Bradshaw & Holzapfel, 2001; Bale & Hayward, 2010). Therefore, from first observations in antiquity to the present day, diapause study is a rich, diversified, and dynamic field of research which is now succeeding at integrating organismal biology with insect ecology and evolution.

## Pursuing studies on diapause

There are numerous reasons to pursue both fundamental and applied work on diapause (Denlinger, 2008). Although the neuro-endocrinal and physiological mechanisms involved in diapause expression from its initiation to its termination are now quite well understood, the following questions remain to be answered more clearly. (1) Through which molecular processes do environmental stimuli act on diapause and its evolution? (2) Will diapause expression be subject to modifications in the context of a rapidly changing environment? And (3) what could be the consequences of such changes for ecosystem functioning and the provision of ecosystem services?

### Genetics of diapause

Genetic basis of diapause expression in insects is emerging as an important facet of recent studies on seasonal polyphenism. Key molecular processes governing diapause have been identified in numerous species from various clades (e.g., Mori et al., 2007; Tyukmaeva et al., 2015; Zhao et al., 2016). The regulation of seasonal photoperiodism is strongly related to the system governing circadian rhythms in insects (Bünning, 1960; Goto, 2013; Dolezel, 2015). Recently, RNA interference approaches have demonstrated the role of some circadian clock genes in diapause expression of *Nasonia vitripennis* (Walker) (Mukai & Goto, 2016). In the pea aphid, *Acyrthosiphon pisum* (Harris), it has been demonstrated that the genes involved in the circadian rhythms – in particular *per*, *Clock*, *cycle*, and *timeless* – were also involved in the photoperiodic control of the induction of sexual morphs, that lay overwintering diapausing eggs (Cortés et al., 2010).

An increasing number of studies is examining latitudinal variation in diapause expression in many species of insects with broad geographic repartition (e.g., Paolucci et al., 2013; Lehmann et al., 2015; Posledovich et al., 2015). *Drosophila melanogaster* Meigen has been used as a model organism to study the genetic bases of clines in reproductive diapause expression across latitudes (Schmidt et al., 2005). For example, Zhao et al. (2016) showed genetic polymorphism and various transcriptome profiles along clinal variation of diapause expression in *D. melanogaster*. By performing QTL analyzes, Paolucci et al. (2016) found that differences in diapause expression between a Corsica (France) population of *N. vitripennis* and a population from Finland were caused by two genomic regions on which *period* and *cycle* clock genes are located. These results support the long-lasting hypothesis that clinal variations in diapause expression represent adaptations to local climatic conditions. The recent development of genome editing technologies such as CRISPR-Cas9 offers new avenues to genetically manipulate diapause expression.

Finally, the bases of diapause heritability are still poorly understood in most insect species, but may be keys to understanding the evolution of diapause. For example, *Ostrinia furnacalis* (Guenée) displays incomplete genetic dominance in photoperiodic control of diapause. The crossing between a strain which enters high diapause levels and a strain which expresses almost no diapause under the same abiotic conditions forms a hybrid strain which expresses diapause in an intermediate fashion (Xia et al., 2012). Some insect strains within a population may also be more sensitive than others to signals of diapause induction or termination (Roff & Bradford, 2000). For example, some individuals of *Diabrotica barberi* Smith & Lawrence, an important maize pest, express a prolonged diapause as an adaptation to the variability of crop cycles. French et al. (2014) demonstrated that this prolonged diapause was highly inheritable ($h^2 = 0.70$), and that there was a strong polymorphism of diapause expression in the population. To better encompass diapause heritability issues, information on the sex of the parent transmitting the diapause characters is required in most species (e.g., Pruisscher et al., 2017).

### Epigenetic mechanisms

The role that epigenetics plays in diapause expression has so far received little attention, in particular because the

genetic basis of diapause was itself little known – the biological models in which diapause and epigenetics are studied are often different (Bewick et al., 2017). Epigenetic regulation of insect diapause could act through DNA methylation, histone modifications, and small RNA interference (Reynolds, 2017). In some insect species, there is a non-photo/thermo-sensible generation in which it is impossible to induce diapause. Such inhibition is potentially based on an epigenetic counter and would prevent the induction of a maladaptive diapause phenotype in spring where environmental conditions are similar as in fall (Henrich & Denlinger, 1982; Reznik & Samartsev, 2015). Recently, in the parasitoid *N. vitripennis*, for which diapause is under maternal regulation, Pegoraro et al. (2016) demonstrated that females exposed to short photoperiods had a very different genome methylation profile than females exposed to long days, which influenced the diapause of their offspring. It remains to be seen whether insects in which no direct maternal effect on diapause is known also show signs of DNA methylation that could, for example, modify their thermal tolerance or other features associated with the diapause syndrome (Powell & Bale, 2008; Reznik & Samartsev, 2015). Poupardin et al. (2015) showed some genes to be downregulated in short-day conditions in the fly *Chymomyza costata* (Zetterstedt). One of these genes (*dpy-30*) is important for histone modification in animals, including insects, which may control the switch from direct development to diapause. In the same fly species, reduced activity of the small-interfering-RNA pathway may be important for initiating diapause (Poupardin et al., 2015). In *Sarcophaga bullata* Parker, an established model for epigenetic studies in insects, microRNAs are differentially regulated in diapausing insects compared to their non-diapausing counterparts and may thus be involved in numerous pathways associated with the various phases of diapause expression (Reynolds et al., 2017). The most recent advances concerning the implication of epigenetics in the diapause phenomenon have been synthesized by Reynolds (2017).

#### Diapause expression in a climate change context

As seasonality is impacting human populations, ecosystems, and agriculture, a better understanding of disruption of seasonal events through climate change is needed (Stevenson et al., 2015). Insect adaptations observed along climatic gradients make it possible to predict that the photoperiodic response (e.g., the critical day length inducing diapause) could be susceptible to modifications by climate change. An analogy can be established – populations that are locally experiencing higher temperatures should have similar responses to populations that migrate toward the south or to milder climates (Hut et al., 2013). Photoperiod will not be modified by climate change at a given latitude, but temperature will, thus modifying environmental pressures that maintain diapause expression within insect populations. This could lead to rapid plastic or evolutionary (genetic) responses of insect photoperiodism and phenology to adapt to new seasonal conditions (Bale & Hayward, 2010; Tougeron et al., 2017).

Although some genes that are over- or under-expressed during the phase of diapause emergence have been identified in some insects (see discussion in Denlinger, 2002), the ecological, hormonal, and genetic mechanisms associated with the end of diapause require deeper research in the majority of species (Koštál, 2006). Investigating the environmental and endogenous causes of diapause cessation is particularly important in the context of climate change, especially in species that require a period of frost to trigger or accelerate the end of diapause (Hodek, 1996; Mehrnejad & Copland, 2005; Lehmann et al., 2017b). In insects, neural mechanisms associated with the detection of photoperiodism could be involved in measuring the amount of time elapsed since the onset of diapause (Saunders, 2012). Recently, Lehmann et al. (2017a) demonstrated that in the butterfly *Pieris napi* (L.), the sensory structures linked to vision are well developed in pupae in diapause, unlike other cerebral structures. These results, although preliminary, suggest that these structures may play a role in maintaining and terminating diapause (Lehmann et al., 2017a). More in-depth exploring of the role of insulin signaling pathway in diapause regulation would also be necessary to better understand diapause termination mechanisms in insects (Sim & Denlinger, 2013). Finally, overwintering insects are on a tight energy budget and are incapable to compensate any energy deficiency during diapause which may be challenging in the context of global warming. Some insects can evaluate the current state of their energy stores and use this information to terminate diapause prematurely, although the mechanism of energy-sensing remains poorly known (Hahn & Denlinger, 2011).

There is a consensus in the recent literature that climate warming has positive effects on insects from temperate climates (Bale et al., 2002; Deutsch et al., 2008; Altermatt, 2010). In absolute terms, fitness could increase in winter because higher temperatures allow better survival and increased activity, reproduction, and resource foraging. On the other hand, in predictive models on the consequences of global changes, species are often considered as single entities, which is ecologically incorrect. In particular, thermal optima differ among species within trophic networks (Berg et al., 2010) and phenological responses to climate change vary among taxa (Thackeray et al., 2016). Yet, changes in phenology within a food web (such as

changes in diapause expression) can ultimately translate into modifications in strength, occurrence, and frequency of the multitrophic interactions (Davis et al., 1998; Thomson et al., 2010; Gilbert et al., 2014). Outstanding questions currently concern potential outcomes of shifts in species interactions after a change in phenology on food-web functioning as well as on the efficiency of ecosystem services such as biological pest control or pollination (Gilman et al., 2010; Valiente-Banuet et al., 2015).

#### Implications for pest control

Interesting perspectives appear for the study of diapause if a particular focus is made on insect pests and their natural enemies, such as insect parasitoids. Indeed, climate warming is expected to lead to more important pest outbreaks (Björkman & Niemelä, 2015) and the longer growing period generated by rising temperatures may lead to presence of crop pests throughout winter, as it has already been documented for some aphid species (Dedryver et al., 2008). Among parasitoids, temperature has a strong impact on diapause expression (Li et al., 2008; Tougeron et al., 2017) but also on host-parasitoid interactions, such as parasitoid attack rates and virulence, host defensive behavior, and immune responses (Cayetano & Vorburger, 2013; Le Lann et al., 2014; Delava et al., 2016; Wu et al., 2016). Thus, potential modifications in overwintering strategies, either of the pests or their natural enemies, can destabilize food webs and modify (positively or negatively) the efficiency of biological control (Thomson et al., 2010; Furlong & Zalucki, 2017).

From an applied point of view, being able to manipulate diapause is an important challenge for the future of biological control, especially in the context of mass rearing and insect cold-storage (Colinet & Boivin, 2011). It is difficult to manipulate diapause for insect storage because of high mortality levels under artificial environments (van Lenteren & Tommasini, 1999), because cold storage generally has negative effects on life histories (van Baaren et al., 2005; Colinet & Boivin, 2011; Ismail et al., 2014), and because diapause does not necessarily increase insect cold tolerance (Hodkova & Hodek, 2004). Despite these difficulties, many successes have been reported in this area and some biological control species can be cold-stored for several weeks before mass release, in diapause, without strong fitness impairments (e.g., Garcia et al., 2002; Hun et al., 2004). Thus, research currently focuses on improving storage methods in order to produce effective natural enemies whilst balancing production costs. Zhang et al. (2018) recently showed that *Trichogramma dendrolimi* Matsumura benefits from the diapause state in terms of quality of long-term cold storage and parasitism efficiency on the Asian corn borer, *O. furnacalis*, during mass releases. Fundamental research will help improve such methods by focusing on costs of diapause, on diapause induction and termination signals, and on getting a better knowledge of diapause heritability. Moreover, new bio-engineering methods may serve at improving the use of diapause in a biological control context. For example, a recent study using RNAi approaches showed that diapause can be induced under diapause-averting photoperiod by silencing the *cycle* gene in the true bug *Riptortus pedestris* (Fabricius) (Ikeno et al., 2010).

Finally, as diapause is under strong endocrine control (Denlinger et al., 2012), it is possible to inhibit or induce it by exposing insects to various synthetic hormones that mimic natural ones, such as juvenile hormones, ecdysteroids, or other molecules specifically involved in the diapause syndrome (Corbitt & Hardie, 1985). For example, in *Aphidius matricariae* Haliday and *Aphidius ervi* Haliday, ecdysteroid application induces diapause independently of other environmental stimuli that the parasitoid receives (Christiansen-Weniger & Hardie, 1999). By using these hormones, it could be possible to control diapause for cold-storage, but also to force its initiation or termination at specific periods of the year to control crop pests (discussed in Denlinger, 2008). These methods of diapause control are difficult to apply in the field, although some trials have already been conducted (Ždárek et al., 2000) – they are paving the way to future studies.

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