DIAPAUSE AND QUIESCENCE AS TWO MAIN KINDS OF DORMANCY AND THEIR SIGNIFICANCE IN LIFE CYCLES OF MITES AND TICS (CHELICERATA: ARACHNIDA: ACARI). PART 2. PARASITIFORMES

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ABSTRACT: Concerning the problem of life history and such an important its aspect as seasonality of life cycles and their control enabled by dormant stages, the parasitiform mites reveal the obvious similarity with the acariform mites. This concerns the presence of both main kinds of dormancy (diapause and quiescence). The great importance in the seasonal control of life cycles in some parasitiform mites, like in acariform mites, belongs also for combinations of diapause with non-diapause arrests, particularly with the post-diapause quiescence (PDQ). This type of quiescence evoked after termination of diapause and enabling more accurate time-adjustment in recommencement of active development, is characteristic of both lineages of the Parasitiformes — Ixodida and Mesostigmata (particularly Gamasida). The available data show that in ixodid ticks the PDQ may be resulted similarly after developmental and behavioral diapause. Reproductive diapause combined with the PDQ is characteristic of some gamasid mites (particularly the family Phytoseiidae), while most gamasid and uropodid mites with phoretic dispersal reveal the dormant state (apparently of diapause nature) at the deutonymphal stage. The uncertainty between diapause and non-diapause dormancy is retained in some many cases (even in ixodid ticks and phytoseiid mites), and the necessity of further thorough study of different forms of diapause and non-diapause arrests in representatives of the Acari is noted therefore.

KEY WORDS: Parasitiform mites, Ixodida, Mesostigmata, life history, life cycle control, dormant stages, diapause, quiescence, post-diapause quiescence, phoresy

INTRODUCTION

The paper presents an extention of analytical reviews concerning the dormant stages in life cycles of representatives of the complex group of chelicerate arthropods, named the Acari or Acarina. The previous reviews were devoted to the comparative and evolutionary aspects of dormant stages distribution in life cycles of mites and ticks in comparison to mandibulate arthropods — insects and crustaceans (Belozerov 2006, 2007), and to the diapause and quiescence as two main kinds of dormancy and their significance in life cycles of the acariform mites — Oribatida, Astigmata and Prostigmata (Belozerov 2008). In general, the mentioned papers (together with the presented new one) take into account and are based mainly on the results and conclusions of my many-years experimental studies on ecophysiology of mites and ticks, which were begun fifty years ago with gamasid mites (Belozerov 1957, 1958 etc.), and thereafter, five years later, with ixodid ticks in regard to diapause and photoperiodic control of their life cycles (Belozerov 1963, 1964a etc.).

In the last review on diapause and quiescence in life cycles of the acariform mites (Belozerov 2008) it was shown that both main functions concerning their seasonality, namely the survival of mite populations during periods of adverse conditions (mainly by means of increased individual resistance), and the seasonal control of their life cycles (through special population adaptations) are enabled in the acariform mites by both kinds of dormancy controlled either endogenously (diapause), or exogenously (quiescence), and also in both ways (through the combination of diapause and quiescence). The latter version is expressed in most obvious way by combinations of diapause and post-diapause quiescence attributed recently in insects (Hodek 1996; Koštal 2006), though the constitutive role of combinations of diapause, quiescence and growth rate in the control of complex insect life cycles was emphasized in special paper of Danks (1991) after preliminary approaching these questions in comprehensive fundamental monographs by Tauber et al. (1986) and Danks (1987).

Of special importance in the mentioned paper of Belozerov (2008) is the conclusion that the combination of diapause and post-diapause quiescence ascertained not only in insects, but in many extant acariform mites also, corresponds to the initial ancestral state of dormancy for adaptations of mites and other arthropods to adverse environmental changes, both predictable (seasonal), and non-predictable (irregular). Such a hypothesis, being of definite interest not only for acarologists, gives reasonable explanation also for the retention of such adaptation in extant acariform mites (Prostigmata and Astigmata) from their ancestors, and particularly for possible presence of the same combined seasonal dormancy in extant oribatid mites, as representatives of acariform mites with especially full set of plesiotypic traits (in spite of currently existing controversial interpretations of their nature, either quiescence, or diapause).

Here, as it follows from the title of the paper, I concern the same aspects of life history in the
Parasitiformes (Anactinotrichida), the second superordinal lineage in the Acari, comprising four orders, two of which (Opilioacarida and Holothyrida) have basal position, but are scanty in species number and badly studied biologically, while two others — Mesostigmata (Gamasida) and Metastigmata (Ixodida) are studied much better (due to their medical, veterinary and agricultural importance) and present therefore more or less appropriate material for the analysis of dormant stages in regard to the control of life cycles in these arachnids. The Parasitiformes includes about 80 families (73 of which are within Mesostigmata) and more than 12500 described species (Walter and Proctor 1999), but in regard to the great majority of them (excluding parasitic Ixodida and the plant-inhabiting predaceous phytoseiid mites from Mesostigmata) we have extremely limited information concerning their life history, seasonal cycles, dormant stages and other related features.

According to morphological, ontogenetic, and other essential traits, both two lineages of Acari, Acariformes and the target group Parasitiformes, represent separate taxa (Zachvatkin 1952, Lindquist 1984, Lehtinen 1991, Norton et al. 1993, etc.), which monophyly is strongly confirmed now by the special nuclear rRNA analysis (Klompen et al. 2007). However it is still unclear, if Parasitiformes differ from or similar to Acariformes in regard to such essential traits of life history as properties and features of dormant stages in their life cycles. In regard to ontogeny, it is well known, that life cycles in Parasitiformes (in contrast to Acariformes) are characterized by the absence of preralval instar, that nymphal phase in Mesostigmata has only two instars (PN and DN), while representatives of the family Ixodidae (among Ixodida) have the single nymphal instar, and the single gonotrophic cycle in adult females (all these traits reflect the processes of oligomerization in their ontogenesis), while the family Argasidae is characterized in general by the opposite processes of polymerization, i.e. by an increased number of nymphal instars and by repeated gonotrophic cycles.

In the phylogenetic trees of Acari and non-mite arachnids, made on the basis of cladistic rRNA analysis (Klompen et al. 2007), the Ixodida with their two main subtaxons (ixodid and argasid ticks) have the position intermediate between acariform and other parasitiform mites, showing that basal Ixodida phylogenetically are younger than Acariformes, but older than Mesostigmata. This situation is consistent with data on changes in the rates of rRNA sequence evolution, occurring from relatively low in most non-mite arachnid lineages (Palpigradi, Araneae, Solifugae, etc.), to intermediate in Acariformes, Opilioacarida, Holothyrida, and Ixodida, and to high in the Mesostigmata (Klompen et al. 2007). These data correspond to the results of Murrell et al. (2005) that the rates of evolution in Mesostigmata (in regard to rRNA) are significantly higher than in other Parasitiformes (and in Acariformes also).

If to follow the taxonomic and evolutionary sequence used in the presentation of materials on Acariformes (Belozerov 2008), it is logically to start the consideration of diapause and quiescence in Parasitiformes not from Mesostigmata, but from Ixodida that have evolved earlier, and are peculiar now by tight combination of both plesiotypic (primitive) and apotypic (specialized) features.

**IXODIDA**

The order Ixodida includes the single superfamilly Ixodoidea comprising about 713 ixodid species, 185 argasid species, and one nutalliellid species, all of which are high-specialized temporary parasites of terrestrial vertebrates (Balashov 2009). Due to great medical and veterinary importance (as blood-sucking parasites and vectors of many human and animal pathogens), Ixodida presents now one of the best investigated group of arthropods (Balashov 1967, 1998, 2009; Sonenshine 1991, 1993, etc.), though in regard to seasonal adaptations in their life cycles considered in the above mentioned monographs and in special reviews (Belozerov 1976a, 1981, 1988, 1991, 1999; Sonenshine 1988, etc.), as well as in numerous ichnological publications, our knowledge is never-

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1 As in my previous paper (Belozerov 2008), I follow here the system of the Acari used by G. Evans (1992), and therefore increase the taxonomic range up to the superordinal level for Parasitiformes and up to the ordinal level for Ixodida and Mesostigmata (unlike Klompen et al. 2007, and many other acarologists, who consider these taxa as the order and suborders respectively).

2 The mentioned terms (oligomerization and polymerization) were introduced by V.A. Dogiel (1954) for two main pathways of morphological evolution, and used by V.N. Beklemishev (1970) for evolutionary events in biological systems of cyclical character (ontogenesis, life cycles etc.). The role of oligomerization in transformation of life cycles in ticks is considered in my paper (Belozerov 1977) published in the collected articles devoted to V.A. Dogiel.
Diapause and quiescence as two main kinds of dormancy in mites and ticks

...theless still limited, and many ixodologists (Drummond 1967, Wright 1969, Vail et al. 1994; Fujimoto 2003, etc.), as well as other zoologists (Brendonck 1996, etc.), had to note the uncertainty concerning the nature of dormancy (diapause or quiescence?) in objects of their study. The approach to the study of dormant states in ticks is quite one-sided also, being directed (as well as in insects) almost on diapause, the most important kind of dormancy in arthropods. This approach was characteristic also for my studies with main attention to different types of tick diapause (developmental, reproductive, behavioral and pre-engorgement), their regulatory mechanisms and eco-physiological significance (Belozerov 1982, 1988, 1999). Even recently (Belozerov 2007) ixodoid ticks were not considered as respects to quiescence, the non-diapause dormancy of great importance (Belozerov 1982, 1988, 1991) as an adaptation to increased temperature and dryness were ascertained in the soft ticks, Argas reflexus from Europe (Dautel and Knülle 1998) and Ornithodoros guerneyi, the australian Kangaroo tick (Doube 1975). The same kind of quiescence enforced by low humidity and increased temperature is quite probable in unfed larvae and nymphs of the hard tick Ixodes ricinus (Randolph 2004). Besides that, Randolph et al. (2000) expressed a meaning about the presence of cold-dependent quiescence in unfed hibernating larvae of I. ricinus (though with equating it to ‘behavioral diapause’). The usual winter non-activity of unfed I. ricinus nymphs and adults is considered by Dautel et al. (2008) as quiescence rather than a behavioral diapause. Thus, such type of consecutive, non-diapause dormancy (Müller 1970; Ushatinskaya 1976) enforced by adverse conditions (particularly by high or low temperatures), and considered by ecologists usually as the common arrest arising through the direct response to constraining factors, and terminated just after their elimination, is usual for ixodid ticks as specific representatives of Parasitiformes.

It is mentioned above that the most important feature in tick life history is characterized by the regular alternation of free-living and parasitic periods of their life during each postembryonic stage (larval, nymphal and adult) with their functionally specific, successive steps of post-hatching and post-molting maturing, of host-seeking activity in unfed ticks, their attachment and feeding on hosts, followed after detachment by development and molting in engorged immatures or oogenesis and egg-laying in engorged adult females (see periodization of tick development by Balashov 1959, 1967, 1998). In many tick species the normal realization of these functions is delayed or interrupted by an adaptive arrest of these vitally important events — by morphogenetic diapause in oviposited eggs, engorged larvae, nymphs and adult females; by behavioral diapause with blocking some links in host-seeking activity of unfed ticks, and by pre-engorgement diapause with feeding delays at parasitic stage (Alfeev 1948, Belozerov 1976a, 1982). These arrests may be obligatory (genetically fixed) or facultative (cued by external token factors). It is known also, that numerous diapausing arrests of different types are characteristic of ticks with plesiotypically long (perennial and biennial) life cycles, while mono- or polyvolute ticks with apotypic cycles of shorter duration have limited number of such adaptive arrests (Belozerov 1977, 1981, 1982, 1988, 1991). Now it is possible to add that greater importance in seasonality of life cycles in ticks, like in acariform mites, belongs not only for diapause, but also for combinations of diapause with non-diapause arrests (the post-diapause quiescence and others). This problem approaching two main kinds of tick diapause (morphogenetic and behavioral), and their relationships with post-diapause quiescence in time-adjustment of separate ontogenetic stages and of the whole phenology in tick populations, is considered below in the next two sections.

Combinations of developmental diapause and post-diapause quiescence in seasonal adaptations of ixodid ticks

The re-checking of available data on seasonal dormancy in ixodid ticks (with taking into consideration the results of analyses conducted for Acariformes) has allowed ascertaining obvious traits of the post-diapause quiescence (PDQ) among...
some representatives of ixodid ticks. This kind of non-diapause dormancy, known in insects (Danks 1987, 1991, 1999) and well attributed by Czech entomologists Hodek (1996) and Koštal (2006), is rather common in acariform mites (Belozerov 2008), and can be acknowledged for ixodid ticks also. The presence of PDQ first of all concerns prostriate ticks (subfam. Ixodinae), the most pleiotypic group from the family Ixodidae (Table 1). For instance, the termination of developmental (morphogenetic) diapause in overwintering eggs of the European forest tick *Ixodes ricinus*, is followed by real PDQ, which has the same properties and adaptive significance for “fine” time-adjustment of development in ticks, as well as in the acariform spider mites emphasized earlier by Veerman (1985).

**Diapausing eggs of Ixodes ricinus** oviposited in late summer (Serdyukova 1951; Randolph et al. 2002) by adult females affected in unfed state by summer LD-photoperiods and high temperature, are characterized by obvious PDQ displayed in winter after egg reactivation and termination of diapause (Belozerov 1973, 1990). Both diapausing and quiescent eggs have no traits of embryonic events during hibernation. The arrest of development in state of PDQ retains until the end of unfavorable cold season. The potentiality for further embryonic development obtained after diapause termination may be realized under favorable increase of temperature in spring, but egg hatch occurs only by late summer and early autumn, due to the slow egg development rate in this tick (see Randolph et al. 2002). There are no doubts that ixodine ticks and acariform mites are principally similar in regard to PDQ acquired after termination of egg diapause (Belozerov 2008).

In general, the same traits concern a combination of diapause and PDQ in **hibernating engorged nymphs of I. ricinus**, though related processes are more complex here, being dependent on peculiarities in nymphal photoperiodic control. Firstly, the control of development is enabled here by the so-called two-step photoperiodic reaction of short-day/long-day (SD-LD) type, and is based on continuous and uninterrupted photoperiodic sensitivity in unfed, feeding and engorged nymphs (Belozerov 1966, 1995a, 1998). The option between developmental diapause and its lack can be determined therefore in unfed nymphs according to the norms of SD-reaction (when LD evokes covert diapause state, while opposite SD-impact favors the further non-diapause development), or in engorged nymphs, where the result of photoperiodic impact corresponds the norms of LD-reaction (when LD evokes development, but SD initiates and maintains its arrest followed by reactivation). These, not simple regularities were ascertained by means of many special experiments (Loew 1964; Belozerov 1966, 1967, 1968, 1970, 1971, 1972, 1988, 1995a, 1998; Babenko 1970; Belozerov and Il‘yin 1974, 1981) with attention both to the initial and terminal phases of diapause development. The covert diapause evoked by LD-photoperiods in unfed nymphs, displays later (after their engorgement) an obvious arrest at SD-conditions, which enable simultaneously two opposite events — diapause maintenance and its elimination followed by PDQ appearance. The reactions of this type are detected not only in *I. ricinus*, but also in related species of *Ixodes ricinus*-complex, namely in the so called Taiga tick *I. persulcatus* from Eurasia (Belozerov 1985a, 1995b, 1998; Belozerov et al. 2003), and in the deer tick *I. scapularis* from North America (Belozerov and Naumov 2002; Belozerov et al 2003; Ogden et al. 2004). The same dependence upon photoperiods is quite probable also for the Central Asian tick *I. kazakstani* (Babenko and Gal’chenko 1976), and even for the South African tick *I. rubicundus* (Belozerov et al. 1996; Fourie et al. 2001; Belozerov et al 2003).

The presence of two alternative reactions in mechanisms of photoperiodic control of developmental events in these ticks made to believe initially (Belozerov 1988, 1995a), that they provide the induction of two different nymphal developmental diapause (of LD- and SD-types), both of which reveal similar arrest of development after engorgement (through preventing stimulation of apolysis as the initial step of molting types), but differ by mechanisms evoking and terminating the developmental arrest. However, the results of analysis concerning dormancy in acariform mites (Belozerov 2008) changed this meaning and allowed a new interpretation for one of these two arrests in nymphal *Ixodes* ticks.

The developmental arrest in engorged nymphs induced by LD-action before their feeding, and retained covert until their engorgement, presents the **proper LD-diapause**, displayed in fed nymphs

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1. **LD** — long-day and **SD** — short-day photoperiods, i.e. longer or shorter than threshold (critical) photoperiod.
### Table 1. Morphogenetic diapause and its termination followed by post-diapause quiescence in some representatives of ixodine and amblyommine ixodid ticks (Ixodidae)

<table>
<thead>
<tr>
<th>Species</th>
<th>Stage of developmental arrest</th>
<th>Induction</th>
<th>Maintenance</th>
<th>Termination</th>
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</thead>
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<td><em>Ixodes ricinus</em></td>
<td>European forest tick with perennial life cycle.</td>
<td>Hibernation of unfed and engorged La, Ny and Ad, as well as eggs</td>
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<td>Pre-and post-feeding SD-impact. Opposite LD-type response plays the main role in determining the development of diapause, and after larval or nymphal feeding, is affected by additional component of SD-type that modifies LD-response through impact of increased temperature (PDQ).</td>
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<td>Larval diapause is similar with photoperiod-dependent quiescence, but is temperature-dependent.</td>
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<td>Post-diapause PDQ: Realization of acquired developmental potency after impact of increased temperature.</td>
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<td>Overwintered diapause eggs have typical PDQ and hatch next year (in 9–11 months after oviposition), while non-overwintered females hatch the same year (in 2–3 months after oviposition).</td>
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<td>Retention of photoperiodic and temperature sensitivity ensures the termination of diapause (by impact of LD and increased temperature). The PDQ is not discovered, but probable.</td>
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<td>SD-reactivation enables PDQ with recovering ability for LD-response.</td>
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### Ixodes ricinus

**Ad females** engorged

- Ability of engorged females for hibernation is determined by LD-impact onto unfed females
- Temperate and cold conditions (with no photoperiodic effect) as in egg diapause
- Reactivation during first winter month, enabling the development of gonads by spring

| Ability of engorged females for hibernation is determined by LD-impact onto unfed females | Temperate and cold conditions (with no photoperiodic effect) as in egg diapause | Reactivation during first winter month, enabling the development of gonads by spring | PDQ is quite probable (with rather low temperature threshold) | SD-females begin oviposition (non-diapause eggs) in 11–12 days, while LD-females (diapause eggs) — in 15–16 days after engorgement (at 18°C). | Belozerov et al. 1966 |

**Ixodes persulcatus**

- Eurasian forest tick with perennials life cycle, hibernation of engorged La and Ny (together with unfed La, Ny and Ad)
- La and Ny engorged

- Control of development in nymphs is determined by two-step SD-LD reaction as in *I. ricinus*. Winter dormancy in La as in *I. ricinus*.
- Nymphal diapause is maintained by the same conditions as in *I. ricinus*. Winter dormancy in La as in *I. ricinus*.
- Reactivation during first winter month, enabling PDQ and potentiality for development after diapause termination in La and Ny.
- PDQ is obvious

| The combination of LD- and SD-responses was observed in larvae also, as well as the modifying effect of increased temperature for diapause response in unfed larvae. | Belenko, Platonova 1965; Babenko 1967, 1970; Filipova 1985; Belozerov 1985a, 1995b, 1998; Balashov 1998; Fujimoto, 1993 |

**Ixodes scapularis**

- N. American tick with perennial life cycle and hibernation of most stages in unfed and engorged state
- La, Ny and female engorged

- Control of development in nymphs is determined by two-step SD-LD reaction as in both previous *Ixodes* species.
- Diapause of engorged nymphs is maintained by SD (together with temperate or low temperatures). These conditions ensure SD-reactivation in diapausing nymphs with requiring development potentiality as in *I. ricinus*.
- The overt diapausal arrest in engorged nymphs is replaced by PDQ after SD-reactivation. The stage, sensitive to day-length in nymphs, ends not with diapause onset, but after stimulation of morphogenetic events.
- PDQ is obvious in engorged nymphs (with recovering potentiality for development after reactivation). They may molt soon after transfer into LD and permissive temperature.

| Life cycle is completed in 2–4 years. All unfed postembryonic stages have bimodal host-seeking activity and the ability to overwinter. This ability is peculiar for engorged quiescent La and Ad females, and for engorged Ny in the state of developmental diapause. | Yuval, Spielman 1990; Lord 1995; Lindsay et al. 1995; Belozerov, Naumov 2002; Ogden et al. 2004 |

**Haemaphysalis concinna**

- Eurasian forest-steppe tick with perennial life cycle
- La, Ny engorged and Eggs

- Development of La and Ny is ensured by LD-impact to unfed and engorged ticks, while their developmental diapause is a result of SD-impact both before and after feeding also
- Diapause is maintained by SD- and cold-conditions.
- Termination of diapause occurs after cold reactivation followed by PDQ, which is broken in warm and LD-conditions.
- PDQ is probable, but not investigated

| Increase of temperature from 18 to 25°C (in unfed nymphs under SD-conditions) evokes increasing their development time after feeding from 25–28 up to 55–70 days (under LD-conditions) that evidences modifying effect of hidden SD-response on basic LD-reaction. | Zhmaeva, 1948; Belozerov 1969, 1974; Belyaeva, Ryabova 1971 |
### Diapause and quiescence as two main kinds of dormancy in mites and ticks

<table>
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<tr>
<th><strong>Dermacentor marginatus</strong></th>
<th>Adult females (overwinter together with unfed adult ticks)</th>
<th>Reproductive diapause of engorged females is induced before their feeding by thermostabile LD-reaction with long sensitivity and adequate changes of covert diapause state in unfed female, displayed after engorgement.</th>
<th>Cold reactivation of engorged females (with overt ovary arrest) and of unfed females (in covert diapause state) is necessary during 2 months to ensure diapause termination and onset of cold-dependent PDQ with further gonad development under effect of temperate/high temperature. Reactivation of unfed females (in the state of covert reproductive diapause) is possible through SD-impact also.</th>
<th>PDQ enables time-adjustment of oviposition in spring to ensure the development of summer transitory stages (eggs, La and Ny) by autumn and accumulation of adult ticks capable for hibernation.</th>
<th>The proper PDQ in engorged females begins after their cold reactivation and terminated in permissive conditions after cold constraints elimination. The same features of seasonal adaptations with reproductive winter diapause of engorged females and respective PDQ is characteristic apparently of <em>D. reticulatus</em> (Razumova 1965).</th>
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<td><strong>Dermacentor silvarum</strong></td>
<td>Adult males and females (attached to host)</td>
<td>A delay of feeding in adult ticks attached to their hosts in winter is determined by impact of summer temperatures and LD on unfed ticks.</td>
<td>The delay of engorgement is maintained by low temperature and SD, which produce simultaneously reactivating effect.</td>
<td>Cold and SD-reactivation of attached hibernating ticks ensures the termination of pre-engorgement diapause (apparently with onset of PDQ resulting engorgement and rapid oviposition of detached females in permissive conditions).</td>
<td>This type of winter dormancy presents not a quiescence enforced by cold, but diapause (Alfeev 1948) followed by cold-dependent PDQ. According to Liu et al. (2005) adult ticks in North China overwinter usually off hosts, but reveal feeding delays and reproductive diapause in summer. Probably it is a confusion with other species, similar biologically with <em>D. marginatus</em>.</td>
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### Table 1. Continued
| *Amblyomma triguttatum*  
| ---  
| **Parasite of marsupials in Eastern Australia**  
| Engorged and unfed Ny  
| The diapause of engorged nymphs is determined by winter SD-impact on ticks before and after feeding  
| Developmental arrest is maintained by SD and increased temperature  
| The termination of diapause is enabled by action of LD on engorged nymphs in spring  
| Modifying effects in unfed Ny are not observed.  
| Guglielmone 1994; Guglielmone and Moorhouse 1986  

| *Amblyomma variegatum*  
| ---  
| **Monovoltine tick from Southern Africa**  
| Engorged females  
| Reproductive diapause of engorged females is induced by SD-impact to unfed adult ticks  
| A delay in gonad development of engorged females is maintained by high (28°C) temperature  
| Termination of diapause is enabled by short exposure to low temperature with subsequent transfer to high or temperate temperature  
| PDQ is hardly characteristic of seasonal control in this tick  
| *A. variegatum* has only one generation per year. Females engorged in August to October reveal reproductive diapause displayed in an increase of pre-ovipositional period (35–63 days against 15–16 days in females engorged from November to March) due to delays of oogenesis.  
| Pegram et al. 1988  

Notes: PDQ — post-diapause quiescence; LD — long-day and SD — short-day photoperiods.
Diapause and quiescence as two main kinds of dormancy in mites and ticks

(even under SD-conditions, which enable both its maintenance and termination through simultaneous reactivating effect of the same SD-photoperiods) with obtaining PDQ and potentiality for further development. The realization of this potentiality in reactivated nymphs is enabled through LD-stimulation of apolysis, the start-point of molting events. Thus, alike to some acariform mites with their combination of diapause and PDQ, nymphs of the mentioned *Ixodes* species really possess the same type of combined seasonal adaptation with similar sequence of photoperiodic events, comprising LD-induction of the proper diapause (1), its termination through cold- or SD-reactivation with acquiring the state of quiescence (PDQ) and potentiality for further development (2), which is realized by LD-stimulation of developmental events after constraint’s elimination (3). Thus, the whole cycle of proper diapause development includes the necessity in threefold change of photoperiods (LD-SD-LD) for evoking and eliminating the developmental arrest. Reactivation (either cold- or SD-dependent) enables an inversion of day length response in nymphs of *I. ricinus* (recovery of sensitivity to LD-photoperiods). These relationships were confirmed in *I. ricinus* (Belozerov 1988, 1995a), *I. persulcatus* (Belozerov 1995b, 1998) and *I. scapularis* (Belozerov and Naumov 2002), in which LD-diapausing nymphs maintained after engorgement under reactivating SD-regimes, reveal the rapid synchronous molt, being transferred into LD-regimen.

In contrast, the so-called “SD-diapause” of engorged nymphs is resulted from their direct response to autumn SD-action, and reminds in many traits the *photoperiodic quiescence* and *photoperiodic oligopause* (see Müller 1992) enforced by SD-impact and terminated after replacement of SD-for LD-regime. The same situation is characteristic of *I. ricinus larvae*, which dormancy is evoked and maintained by SD-impact, and terminated as a rule by LD and increased temperature. It was noted above that dormant state in hibernating (though unfed) larvae of *I. ricinus*, is considered by Randolph et al. (2002) as a quiescence. I can recognize that the same situation in this species may be characteristic of its engorged larvae and nymphs, which overwinter apparently in the state of quiescence enforced by autumn SD and decreased temperature. The temperature as the usual constraining factor affecting quiescence (through its initiation, maintenance and termination), seems to be supplemented in both immature stages of *I. ricinus* by the photoperiod, since they possess sensitivity to day length during the whole their life. A paper by Ogden et al. (2004) emphasizing the difference between engorged overwintering La and Ny of *I. scapularis* in regard to dependence of their development largely on temperature (in La) or on temperature-independent diapause (in Ny), gives an essential support for considering the larval developmental arrest (as well as the SD-determined nymphal developmental arrest) as a quiescence rather than a developmental diapause, while the nymphal developmental arrest induced in unfed nymphs by LD-impact must be considered as a real diapause. Nevertheless some more investigations and discussions are necessary, of course, to ascertain the peculiarities of this photoperiodic SD-arrest at larval and nymphal stages of *I. ricinus* (and other mentioned species of *Ixodes*), and to determine, if they are really SD-quiescence or SD-diapause.

Thus, the time-adjustment of nymphal development in the mentioned prostriate ticks may be controlled in two ways, either by proper LD-diapause and PDQ depending in both cases on photoperiod and temperature, or by photoperiod/temperature-dependent arrest with traits of SD-quiescence.

Evident examples of PDQ that enables together with developmental diapause the accurate time-adjustment of seasonal events in tick life cycles is presented not only in Ixodinae, but also in another tick subfamily, Amblyomminae (Table 1). Life cycle seasonality of amblyomminic ticks is studied rather well [see the review in Chapter VI of Balashov (1998) monograph], in contrast to mechanisms of life-cycle control, which need much more attention in ecophysiological study of dormant stages (especially at their terminal phases) in these ticks.

Within the genus *Haemaphysalis*, the most primitive among amblyomminic ticks, the traits of PDQ are characteristic of overwintering engorged nymphs of *H. concinna*, the biologically plesiotypic forest species with photoperiodic control of nymphal developmental diapause induced by SD-impact and reinforced by 25°C before feeding (Table 1). This tick has perennial or semivoltine life cycles with numerous stages revealing dormancy in unfed and engorged specimens. Similar plesiotypic traits are characteristic of many Eurasian species of *Haemaphysalis* (*H. japonica douglasi*, *H. flava*, *H. inermis*, *H. punctata*, *H. pospelovashtromi* and others), which seasonal
control is ensured undoubtedly by combination of developmental diapause and quiescence (PDQ) in La, Ny and Ad females (as well as by behavioral diapause at all these stages).

The genus *Dermacentor* is remarkable for surprising difference between Eurasian (with rather apotypic traits of monovoltine development controlled at adult stage only) and American species (with rather pleiotypic cycles controlled at several dormant stages). It is of interest that only Eurasian species possess the adult diapause of morphogenetic (reproductive) type, while the seasonal control in almost all American species is ensured by behavioral diapause. The obvious case with combination of reproductive diapause and cold-dependent PDQ is known from studies of the spring steppe Eurasian tick *D. marginatus* (Belozerov 1963, 1964b, Belozerov and Kvitko 1965; Belozerov and Lamanova 1967) revealing 6–7-month diapause delay of gonad development (induced by the late summer LD-impact on unfed adult females), while after cold reactivation of overwintering unfed females in the state of covert diapause (or of engorged females in the state of overt diapause) the oviposition begins in 1–2 weeks. Undoubtedly, the termination of morphogenetic diapause in *D. marginatus* females (as well as in *I. ricinus* nymphs), results the occurrence of real state of PDQ that continues in field until cessation of constraining factors, such as low temperatures in *D. marginatus* (due to the lack of photosensitivity in its engorged females) or SD-photoperiods in *I. ricinus* (due to retention of photoperiodic sensitivity in its diapausing nymphs). Though *D. marginatus* presents still the only known representative of this genus, which alike to ixodine ticks possess the complex ancestral adaptation (combined from diapause and PDQ), there are no doubts that some species of this genus (the Eurasian *D. reticulatus* and *D. niveus*, the South Asian *D. auratus*, etc.) have adaptations of the same kind also.

Among representatives of the genus *Hyalomma* evolved in open arid landscapes of Asia (Pomerantzev 1948a), the Camel tick *H. dromedarii* is one of the most primitive and generalized species of this genus (Pomerantzev 1950) characterized by especially full set of seasonal adaptations (autumn diapause delays in eggs, unfed and engorged La, Ny and Ad), some of which seem to be followed by PDQ. In more specialized species (*H. asiaticum, H. anatolicum*) some stages lose regulatory functions, and seasonal control is enabled in them by engorged nymphs and females with diapause arrests of development, and by unfed adult ticks with behavioral diapause. The regulation of seasonal events through photoperiodic response is recorded only for *H. anatolicum* (Mourad, Belozerov 1976; Belozerov, Mourad 1977), the inhabitant of arid sub tropics in the Central and West Asia, including North Africa. Diapause of nymphs and females is determined by SD-effects only. Due to the thresholds of photoperiodic reaction, adult females of *H. anatolicum* begin to diapause one month earlier (August), than nymphs (the middle of September), as shown by Berdyev (1974). Though the events of diapause termination in *H. anatolicum* were studied less thoroughly, it seems probable that developmental diapause in nymphs and reproductive diapause in females of this species are followed by PDQ (due to early beginning of its diapauses and rather strong climate seasonality in its area). This complex ancestral adaptation is characteristic apparently for some other species of this genus.

The genus *Amblyomma* (together with representatives of the deleted genus *Aponomma*) is presented by parasites of tropical and subtropical vertebrates (particularly of different reptilians). They reveal definite life-cycle seasonality enabled by different kinds of dormancy under the day-length control according to other investigated ixodid ticks. For instance, the Australian tick *A. triguttatum* parasitizing on large marsupials, has a photoperiod-dependent diapause of engorged nymphs (Guglielmone, Moorhouse 1986; Guglielmone 1994). Its nymphs are sensitive to day-length both before and after feeding, and have photoperiodic reaction of LD-type, due to that their diapause is induced by SD, but is terminated by LD-impact. In this regard they are similar with nymphs and adults of palearctic *Hyalomma anatolicum* (Mourad, Belozerov 1976; Belozerov, Mourad 1977), particularly in regard to possible presence of PDQ. An African monovoltine tick *A. variegatum* has some developmental arrests in eggs and engorged females (Hoogstraal 1956; Pegram et al. 1988). Perhaps, the acclimatization of this African tick in Antilles, where it was introduced in some last decades (Estrada-Peña et al. 2007), might get possible by means of combined diapause/PDQ ad-
aptation. However, many Amblyomma have photoperiodic control of behavior in unfed ticks, as larvae of *A. cajennense* in Brazil (Labruna et al. 2003), nymphs and adults of *A. americanum* and *A. maculatum* in southern parts of USA (Sonenshine 1991), as well as the same stages of *A. hebraeum* in Africa (Norval 1977a,b).

The phylogenetically young genus *Rhipicephalus* (comprising one-host ticks from the former genus *Boophilus*) in contrast to all other mentioned ixodids has no diapause arrests of morphogenetic type. The seasonal control of life cycles in its species is enabled only by behavioural diapause (Table 2) of either unfed adults, as in *R. turanicus* (Berdyev 1973, Belozerov 1976b), or unfed larvae, as in *R. schulzei* (Nel’zina, Danilova 1960), in both cases with monovoltine development. Monovoltinism is well common in *Rhipicephalus* ticks from Africa, where this genus has evolved (Pomerantzhev 1948a; Walker et al. 2000), and most species possess there behavioural diapause at adult stage. The widely distributed in E.Africa tick *R. appendiculatus* is typical in this regards (Rechav 1981; Short, Norval 1981; Berkvens et al. 1995; Randolph 1993, 1997, 2004, 2008; Madder et al. 1999; Randolph, Rogers 1997; Speybroeck et al 2002) being dependent upon seasonal changes of vital factors (dry and rainy seasons), and controlled by token factors (day length). Its behavioural diapause is followed by PDQ (Speybroeck et al. 2006), likely to developmental diapause in some other ixodid ticks.

Thus, the presence of PDQ after morphogenetic diapause is not unusual phenomenon among ixodid ticks. It is ascertainment at least in three species of prostriate ticks related to *Ixodes ricinus*-complex (*I. ricinus*, *I. persulcatus* and *I. scapularis*), and for sure in one species of amblyomminine ticks (*Dermacentor marginatus*), though the same combined seasonal adaptations seem function in some other ixodid ticks also.

**Combinations of behavioral diapause and post-diapause quiescence in seasonal adaptations of ixodid ticks**

Most ixodid ticks are characterized by the presence of seasonal adaptations both in unfed specimens (behavioral dormancy), and in engorged specimens (arrests of development and reproduction). Since the above-considered data have concerned the combination of quiescence (PDQ) with developmental diapause, it is of interest to learn, if quiescence may exist in association with behavioral diapause also. This seems quite possible, inasmuch as both types of diapause are similar in their ecological functions and results.

Unfortunately, our knowledge about connections of quiescence (particularly PDQ) with behavioral diapause (Table 2) is very limited, though this type of diapause is quite common in ixodid ticks, being the only kind of diapause in the genus *Rhipicephalus*, and this diapause is of great importance due to its influence on dynamics of seasonal questing activity of ticks as vectors of animal and human diseases. If the presence of PDQ in Ixodida is real both after developmental and behavioral diapause, this gives important evidence in regard to ancestral character of this complex adaptation in life-cycle adjustment of the Acari.

The only essential support of an assumption on the reality of PDQ after behavioral diapause is given recently by a group of parasitologists and mathematicians from the Institute of Tropical Medicine (Antwerpen, Belgium) in studies of life cycles and analysis of behavioral diapause in African tick *Rhipicephalus appendiculatus* (Speybroeck et al. 2006). By using different mathematician methods, particularly such advanced techniques as generalized auto-regression models and hidden Markov chains (MacDonald, Zucchini 1997), they revealed the sequence of some “hidden” stages during diapause arrest and post-diapause events in *R. appendiculatus* adult ticks evidencing an accordance of behavioral diapause to developmental diapause (covert events of their induction and termination with transformation into post-diapause quiescence).

In the model suggested by Speybroeck et al. (2006), three successive phases of diapause development with “hidden” states of behavioral diapause were ascertained, namely a **non-responsive dormant phase** of deep diapause (1), a **responsive dormant phase**, most comparable with a quiescence, when a tick responds to favorable and unfavorable conditions by becoming active or returning to a dormant state (2), and, at last, a **non-dormant phase**, in which ticks react to microclimatic conditions (3). These phases reveal some correlation with phases of diapause development attributed by Hodek (1996) and Koštál (2006) for developmental diapause in insects (Table 3). Undoubtedly, the authors of this model have taken into consideration the conception of PDQ in diapause development of insects introduced by I. Hodek, who participated in some studies of the Belgian group on *R. appendiculatus* diapause
<table>
<thead>
<tr>
<th>Species</th>
<th>Stage of behavioral diapause</th>
<th>Induction</th>
<th>Maintenance</th>
<th>Termination</th>
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<tbody>
<tr>
<td><em>Ixodes ricinus</em></td>
<td>Unfed <em>La, Ny, Ad</em></td>
<td>BD in all life-cycle stages is facultative and induced by SD-impact</td>
<td>By SD and cold conditions</td>
<td>By SD and cold conditions</td>
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<td>After reactivating impact by cold and SD</td>
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<td><em>Ixodes persulcatus</em></td>
<td>Unfed <em>La, Ny, Ad</em></td>
<td>BD in <em>La</em> and <em>Ny</em> is facultative and induced by SD-impact</td>
<td>By SD and cold conditions</td>
<td>After reactivating impact by cold and SD</td>
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<td><em>Ixodes scapularis</em></td>
<td>Unfed <em>La, Ny, (Ad)</em></td>
<td>BD in <em>La</em> and <em>Ny</em> is facultative and induced by SD-impact</td>
<td>By SD and cold conditions</td>
<td>After reactivating impact by cold and SD</td>
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<td><em>Haemaphysalis concinna</em></td>
<td>Unfed <em>La, Ny, Ad</em></td>
<td>BD in <em>La</em> and <em>Ny</em> and (Ad) is facultative and induced by SD-impact</td>
<td>By SD and cold conditions</td>
<td>After reactivating impact by cold and SD</td>
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<td><em>Haemaphysalis longicornis</em></td>
<td>Unfed <em>La, Ny</em></td>
<td>BD in <em>La</em> and <em>Ny</em> is facultative and induced by SD-impact</td>
<td>By SD and cold conditions</td>
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**Remarks:**
- Acquiescence is the state of diapause that is induced by SD-impact and followed by cold-dependent PDQ (post-diapause quiescence).
- BD in *Ad* stage is facultative and induced by SD-impact. The stability of obligatory BD in *Ad* is rather low, and its short duration is supplemented by cold-dependent PDQ in unfed adults.
- The nature of dormancy in unfed ticks needs more thorough study.
- Moreover, the dependence of activity and BD upon day length (according to norms of LD-reaction) and some traits of development (seasonal changes in development) are different between populations of *I. ricinus* in northern and southern geographic regions.
- Besides the dependence of activity and BD upon day length (according to norms of LD-reaction), some traits of development and development of engorged *La* are different between populations of *I. ricinus* in northern and southern geographic regions.
<table>
<thead>
<tr>
<th>Species</th>
<th>Stage(s)</th>
<th>Developmental Diapause</th>
<th>Photoperiodic Impact</th>
<th>Dormancy in Engorged Ticks</th>
<th>Remarks</th>
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<tbody>
<tr>
<td><em>Diapause and quiescence as two main kinds of dormancy in mites and ticks</em></td>
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<tr>
<td><em>Haemaphysalis parva</em> (= <em>otophila</em>)</td>
<td>Unfed Ad</td>
<td>Summer BD of Ad ticks is induced by LD (similar with winter reproductive diapause)</td>
<td>PDQ is not known, but probable.</td>
<td>Eggs, La and Ny are fast-developing summer stages not capable for dormancy</td>
<td>In contrast to LD-induced developmental diapause, the autumn activity of unfed adult ticks is determined by SD photoperiodic impact.</td>
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<td>Monovoltine 3-host tick from N. Caucasus</td>
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<td>Belozerov 1995c</td>
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<tr>
<td><em>Dermacentor variabilis</em></td>
<td>Unfed La, Ny (Ad)</td>
<td>Facultative BD of unfed La and Ny is induced by SD, while their activity (especially in Ny) by increased temperature. No dormancy in engorged ticks.</td>
<td>See remarks</td>
<td>See remarks</td>
<td>BD after its termination by winter cold reactivation may be substituted for temperature-dependent PDQ. PhPR is necessary not for La and Ny activation in spring (this is enabled by increase of temperature), but for maintenance of active state in summer (by LD-impact), and mainly for production of winter BD (by SD-impact), and its change into cold PDQ. Adult ticks do not react to day-length.</td>
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<td>3-host tick from eastern USA with biennial cycle, hibernation of unfed ticks at all stages</td>
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<td>Smith, Cole 1941; Sonenshine 1972; Burg 2001</td>
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<tr>
<td><em>Dermacentor andersoni</em></td>
<td>Unfed (La), Ny and Ad</td>
<td>Adult ticks have obligatory BD. Traits of diapause induction in La and Ny are not revealed. No dormancy in engorged ticks.</td>
<td>Maintenance of adult diapause and its elimination is ensured only by cold conditions with no photoperiodic impact.</td>
<td>Activation of cold-reactivated adult ticks is enabled by increase of temperature.</td>
<td>Seasonal controlling functions of La and Ny are probable, but not investigated. In some traits of feeding delays on their hosts, <em>D. andersoni</em> adult ticks have similarity with Asian <em>D. silvarum</em>.</td>
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<tr>
<td>Prairie’s tick from western USA, biennial, hibernation of unfed ticks at all stages</td>
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<td>Wilkinson 1968, 1973</td>
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<tr>
<td><em>Dermacentor albipictus</em></td>
<td>Unfed La and attached Ny</td>
<td>Summer BD of unfed La determined by LD-impact, and pre-engorgement winter diapause of Ny attached to host</td>
<td>Long nymphal stage on moose may function to synchronize development of engorged females with favourable conditions for reproduction in spring. Engorged female dropped from late February to mid-May (the peak in late March). These seasonal patterns may be influenced by photoperiod.</td>
<td>By 2–3 weeks of attachment most larvae on infested moose molt to Ny, which dominate the tick population from October to mid-February, and adults from February to May. The peak of host disengagement by engorged females is late March.</td>
<td>The delay between hatching and ascension of vegetation by La has been referred to as a resting period (Bishopp, Wood 1913), dormancy (Cameron, Fulton 1926), an inactive state (Howell 1939), quiescence (Drummond 1967), and diapause (Wright 1968). Unfed larvae ascend vegetation in autumn in response to decrease of day-length. Their number increases from early September to early October and decreases to zero by December. La develop to Ny and Ad on moose during winter and early spring. By mid- to late-May moose are tick-free.</td>
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<td>One-host winter parasite of moose in USA and Canada with monovoltine life cycle</td>
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<td>Wright 1968, 1971; Drew, Samuel 1985, 1989; Patrick, Hair 1977</td>
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### Table 2. Continued

| *Rhipicephalus appendiculatus* | Unfed Ad | BD is induced by SD-impact on unfed Ad. No dormancy in engorged ticks. | BD is maintained by SD and cold conditions. | Termination of BD is enabled by wet and warm conditions. | A generic population model with attention to specific patterns of life cycle and BD in its unfed adult ticks (Randolph, Rogers 1997; Randolph 2008) and a model of BD development and its termination with PDQ (Spaybroeck et al. 2006) explain essential events in life cycle control of *R. appendiculatus*. | BD is peculiar to unfed adult ticks, which emerge in southern Africa after July and do not start questing during cold dry season until November, thus the egg-to-larva development occurs during the warm wet season (December–May). | Rechav 1981; Short, Norval 1981; Randolph 1993, 1997; Madder et al. 1999; Spaybroeck et al. 2002 |
|-------------------------------|----------|-----------------------------------------------------------------------|---------------------------------------------|--------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------| Belozerov 1976; Berdyev 1980; Balashov 1998 |
| *Rhipicephalus turanicus* 3-host tick from arid landscapes of Central Asia, Africa and southern Europe | Unfed Ad | Monovoltine development synchronized mainly by BD of unfed Ad ticks | Strong dormant state of unfed Ad after their molt from Ny is induced by SD-impact under 25°C. In field conditions this corresponds to autumn season when new Ad cohort reveals traits of hibernal dormancy. | BD of unfed Ad is maintained by SD-impact under 18–25°C. Activating and reactivating effect on unfed Ad ticks is enabled by LD. | The hibernating reserve presented by Ad ticks is supplemented by few engorged Ny, which molt may be delayed through modifying effect of autumn SD under increased temperature (see remarks for other tick species). | Belozerov 1976; Berdyev 1980; Balashov 1998 |
| *Rhipicephalus pumilio* 3-host tick from steppe and semi-desert landscapes of Central and Eastern Asia | Unfed La, Ny, Ad | Biennial and perennial development controlled by BD of unfed La and Ny. No adaptive dormancy in engorged ticks. | Development of this tick (with or without BD) is determined by LD-reaction enabling hibernation of unfed La and Ny. | BD of unfed La and Ny is maintained by SD-impact under 18–25°C. Activating and reactivating effect on unfed La and Ny is enabled by LD (above 15 hr of light p.d.) under 18–25°C. | Perennial life cycle (2–3 years) with bimodal questing activity of La, Ny (before and after their over-wintering), and Ad. Presence of PDQ after BD is quite possible. | Belozerov 1985; Balashov 1998 |
| *Rhipicephalus schulzei* Parasite of suslik *Citellus pygmaeus* inhabiting its borrows | Unfed La | Monovoltine or biennial development determined mainly by larval BD, which is probably facultative. | Mechanism of larval BD is unknown | Maintenance of larval BD is ensured apparently by a decrease of temperature. | Cold reactivation of diapausing La is probable | Life cycle of *R. schulzei* is considered as monovoltine with hibernation of only unfed La (1) or as biennial with hibernation of unfed La, Ny and Ad (2). The first pathway seems to be a basic one supplemented by the second. | (1) Nel’zina, Danilova 1960; (2) Balashov 1998 |

Notes: BD — behavioral diapause, PDQ — post-diapause quiescence; PhPR — photoperiodic response; LD — long-day and SD — short-day photoperiods.
Comparison of successive events in diapause development for morphogenetic diapause of an abstract insect (after Koštal 2006) and for behavioral diapause of an African tick *Rhipicephalus appendiculatus* Neum. (after Speybroeck et al. 2006)

<table>
<thead>
<tr>
<th>Sequence of events during development of morphogenetic diapause in an insect (according to Koštal 2006)</th>
<th>Pre-diapause</th>
<th>Diapause</th>
<th>Transitional state</th>
<th>Post-diapause quiescence</th>
<th>Active life</th>
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<tbody>
<tr>
<td>Induction (as a covert event) and preparation (as a first overt event) of diapause</td>
<td>Initiation and maintenance of the arrest as an induced response to endogenous and exogenous impacts.</td>
<td>Termination of diapause as a result of reactivation.</td>
<td>Exogenous arrest enforced by adverse conditions and terminated in permissive conditions.</td>
<td>Active life until the death due to exhausting food reserves.</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sequence of events during development of behavioral diapause in a tick (according to Speybroeck et al. 2006)</th>
<th>Non-diapause direct development</th>
<th>Diapause</th>
<th>Responsive dormant phase</th>
<th>Post-diapause non-dormant phase</th>
<th>Active life</th>
</tr>
</thead>
<tbody>
<tr>
<td>Active life in permissive conditions</td>
<td>First hidden and non-responsive dormant phase enforced by onset of long day-length and drought, but supplemented by aging decrease of diapause state.</td>
<td>Second hidden phase with conversion to non-diapause behavior by means of response to token factors. It is a responsible state with capability of ticks to change their active or dormant state according to external conditions.</td>
<td>Third hidden phase of active state irrespective to existent conditions. A decrease of response to token factors (day-length), but an increase of ability to react to external vital factors (temperature, humidity).</td>
<td>Active life until the death or the repetition of the same patterns of life cycle.</td>
<td></td>
</tr>
</tbody>
</table>

### Table 3.

| Notes. The method of modeling diapause termination, elaborated by Speybroeck et al (2006), was suggested by them for analysing both behavioral and developmental diapause. |
Table 4.
Preliminary data on presence of developmental diapauses (with cases followed by PDQ marked by bold) in different genera of ixodid ticks

<table>
<thead>
<tr>
<th>Genus</th>
<th>Behavioural diapause</th>
<th>Developmental diapause</th>
<th>PDQ after developmental diapause</th>
<th>Nature of associated dormancy</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ixodes ~ 220 species</td>
<td>La +/- Ny +/- Ad +</td>
<td>Egg +/- La +/- Ny +/- Ad +/-</td>
<td>Egg – 1 La – 3 Ny – 3 (+2 ?) Ad –</td>
<td>LD-diapause + PDQ</td>
</tr>
<tr>
<td>Haemaphysal ~ 150 species</td>
<td>La +/- Ny +/- Ad +</td>
<td>Egg – La +/- Ny +/- Ad +/-</td>
<td>Egg – La – 1 (+?) Ny – 1 (+?) Ad –</td>
<td>–</td>
</tr>
<tr>
<td>Dermacentor ~ 30 species</td>
<td>La +/- Ny +/- Ad +</td>
<td>Egg – La +/- Ny +/- Ad +/-</td>
<td>Egg – La – Ny – Ad – 2 (+?)</td>
<td>–</td>
</tr>
<tr>
<td>Hyalomma ~ 30 species</td>
<td>La +/- Ny +/- Ad +</td>
<td>Egg + La – Ny – Ad +/-</td>
<td>Egg + La – Ny – Ad – 1 (+?)</td>
<td>LD-diapause + PDQ</td>
</tr>
<tr>
<td>Rhipicephalus ~ 54 species (+ Boophilus and Margaropus)</td>
<td>La +/- Ny +/- Ad +</td>
<td>Egg – La – Ny – Ad +</td>
<td>Egg – La – Ny – Ad –</td>
<td>No developmental diapause at stages of egg, La, Ny ad Ad</td>
</tr>
<tr>
<td>Amblyomma ~ 100 species (+ Bothriocroton?)</td>
<td>La +/- Ny +/- Ad +</td>
<td>Egg +/- La +/- Ny +/- Ad +/-</td>
<td>Egg ? La – 1 (+?) Ny – 1 (+?) Ad – 1 (+?)</td>
<td>SD-diapause</td>
</tr>
</tbody>
</table>

Notes. Marks +/- designate the presence of species in the respective genus with and without diapause (behavioral and developmental) at definite stages; marks + or – designate the ability or inability of respective stages to diapause. In the column “PDQ” the number of species revealing the post-diapause quiescence is shown for respective stages of the mentioned tick genera. In the first column the genera *Rhipicephalus* and *Amblyomma* do not include subordinated genera *Boophilus* and *Margaropus*, and *Aponomma* (deleted) and *Bothriocroton* respectively. Developmental and reproductive types of diapause are considered here as a common category of morphogenetic diapause.

(Madder et al. 2002). Some fitness in sequence of “hidden” (covert) phases during diapause development (of both kinds of diapause) evidences high probability of their resemblance (particularly in regard to PDQ), that was confirmed by Dr. Hodek (personal message) about his agreement that the 2nd hidden phase (= responsive dormant phase by Speybroeck et al. 2006) in ticks really is very similar to the post-diapause quiescence in insects.

For more clearness, I think to repeat the peculiarities of these successive “hidden” states, expounded by the authors (Speybroeck et al. 2006). These three different states relate to phases during the dynamic event of diapause development and post-diapause activity in the tick. The first hidden state could be defined as a non-responsive dormant phase, though in this state ticks may spontaneously terminate diapause as their age increases. The second hidden state is a responsive dormant state, during which the tick responds to unfavorable or favorable conditions by becoming active or returning to a dormant state. The third hidden state is a non-dormant state, in which ticks actively react to microclimatic conditions. The method of analysis based on the hidden Markov chains and other discrete-valued time series (MacDonald, Zuchini 1997), and applied for changes of behavioral events in a tropical tick, can be used, according to Speybroeck et al. (2006), for further learning the dynamic events of development in both behavioral and morphogenetic diapause of ticks. However, it is necessary to take into attention the meaning of S. Randolph (2004, p. 59) about generic models (like that of Randolph and Rogers 1997), which have given encouraging results for the more simple and tractable system of *R. appendiculatus* in Africa, but are not fully achieved for the complex system of *I. ricinus* in temperate regions (largely because of unresolved questions about diapause).
Thus, the association of diapause with quiescence may be considered as a common feature of life-history traits in ixodid ticks with developmental and behavioral diapause. The third type of diapausing dormancy expressed in delays of feeding and engorgement in host-attached ticks, known in some ixodids with winter parasitism (adults of *Dermacentor silvarum* in N.E.Asia, nymphs of *D. albipictus* in Canada and *Hyalomma scupense* in Russia, and some others), has taken in the present paper the term “pre-engorgement diapause”. Among these cases, only the data on *D. albipictus* (Drew, Samuel 1989) allow to suggest the presence of PDQ (associated with pre-engorgement diapause) and its time-adjustment function for early-spring synchrony in engorgement of nymphs and detachment of engorged females of this one-host winter parasite.

**Some notes on modifying effects of increased temperature in unfed immature ticks on quantitative peculiarities of their development after engorgement**

It is necessary to note, that interrelations of LD- and SD-components in the basic mechanism controlling development and diapause in *Ixodes* (and other ticks) may be modified by the effect of increased temperature on unfed immature ticks. The available data concerning these modifying effects are mentioned in the Table 1 and 2 (column “Remarks”). For instance, photoperiodic response attributable to unfed nymphs of *I. ricinus* is intensified by increased temperature about non-diapause development in reactivated nymphs, but promotes delays in diapause nymphs. Modifying effects were observed in monovoltine *Rhipicephalus turanicus*, larvae and nymphs of which were maintained in unfed state under SD-photoperiods and 25°C (though immatures of this species have no capability for adaptive forms of dormancy in contrast to *I. ricinus*). The modifying effect of increased pre-feeding temperature was observed also in nymphs of *Haemaphysalis concinna* (with developmental diapause) and in larvae of *H. longicornis* (without developmental diapause and with behavioral diapause only). Quite possible that similar modifying effects discovered in insects also (Saulich, Musolin 2007) will reveal their exact ecological significance after more thorough investigations, and will find the precise place in principal systems of developmental control in arachnids.

**MESOSTIGMATA**

As was mentioned above, mesostigmatid mites present most large (73 families from 80) and very diverse (morphologically and biologically) group of Parasitiformes comprising more than 10000 species. In most their traits concerning morphology, ontogeny, life history, ecology and other features, the Mesostigmata reveal obvious contrast to the Ixodida.

Mesostigmatid mites are small- and middle-sized creatures, living in soil, litter, manure, spunk and different other habitats of permanent and temporary character (as nests of insects, small vertebrates, etc.). Many representatives of this order retain the primary life type of soil/litter-dwelling predators-entomophags. However, a lot of them have passed to specialization to saprophagy, necrophagy, fungiphagy, phytophagy, as well as (particularly gamasid mites) to different forms of parasitism on terrestrial vertebrates. Gamasid mites reveal in this regard the widest diapason of adaptive biological radiation (Lange 1984; Radovsky 1994). They are known as facultative and obligatory hematophags in nests and other shelters of vertebrates, as off-shelter (“pasture”) temporary parasites of reptilians and rodents, as well as permanent ecto- and endoparasites of different vertebrates (Balashov 2009). However, ontogenetically both gamasid mites (the suborder Gamasina), and uropodid mites (the suborder Uropodina) are similar, in spite of different phylogenetic levels (Fig.1), and their life cycles comprise identically an egg
and four postembryonic stages (La, PN, DN and Ad). Some ontogenetic changes known in Gamasi-
na (embryonization of La and even PN, aphagry of 
La in most species and of nymphs in some spe-
cies) are resulted by usual regression at the first 
postembryonic instar and by transformations due
to parasitic adaptations at nymphal phase of their 
life cycles (Fig. 2).

Besides large-scale biological diversity,
gamasid mites are characterized by the obvious r-
selected traits of life history strategy revealed in 
rapid development of separate ontogenetic stages 
and short duration of the whole life cycle. Gamasid 
mites are obviously superior in this and many oth-
er regards to the more uniform suborder Uropodi-
da, the representatives of which are characterized 
in contrast by K-selected attributes of life history 
(being biologically similar in this regard to orib-
atid mites with their plesiotypic traits). Due to the 
more slow development, uropodid mites need 
much more time for the completion of their life 
cycles. The available information emphasizes that 
gamasid mites (both free-living and parasitic) are 
remarkable for rapid development with comple-
tion of their life-cycles during 1–3 weeks, due to 
that most species are characterized by polyvoltine 
development (Table 5), while development of 

uropodid mites takes 3–4 months, and has usually monovoltine or biennial character (Table 6).

The main direction in investigations of mes-
sostigmatid mites (particularly of gamasids) has 
concerned morphology and taxonomy (Zakhvat-
kin 1948, 1952; Bregetova 1956; Karg 1971, 1989; 
Gilyarov and Bregetova 1977, etc.), as well as 
problems of ecological and evolutionary parasitol-
ogy (Nel’zina 1961; Beklemishev 1970; Zemska-
ya 1973; Lange 1984; Radovsky 1994, etc.), while 
such important life history aspects, as seasonality 
of life cycles and their control, were studied much 
worse. The Gamasina, in spite of many investiga-
tions, presents a hard group for ascertaining and 
understanding the peculiarities and regularities of 
seasonality in their life cycles, and mechanisms of 
their control by dormant stages. This problem is 
connected not with great diversity of these mites, 
but firstly with obvious scarcity in data concerning 
their life-history traits connected with seasonality 
and related adaptations. The same situation is 
characteristic of the Uropodina also.

Our knowledge on phenology and dormant 
stages in Mesostigmata is extremely poor there-
fore. According to Table 5, the dormant stage in 
soil-dwelling gamasid mites with plesiotypic 
preyatory habits (such as parasitids Androlaelaps,
Diapause and quiescence as two main kinds of dormancy in mites and ticks

<table>
<thead>
<tr>
<th>Species</th>
<th>Genus</th>
<th>Family</th>
<th>Egg</th>
<th>L1</th>
<th>PN</th>
<th>DN</th>
<th>EG–AD</th>
<th>Dormant stage</th>
<th>Habitat</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctoseius semiscissus</td>
<td>Ascidae</td>
<td></td>
<td>3.3</td>
<td>2.0</td>
<td>1.4</td>
<td>1.2</td>
<td>7.9</td>
<td>Ad</td>
<td>Phoretic female</td>
<td>Soil-dwelling predatory mites in mushroom farm, phoretic on sciarid flies</td>
</tr>
<tr>
<td>Androlaelaps sp.</td>
<td>Stratiolaelaps sp.</td>
<td>Laelaptidae</td>
<td>4.9</td>
<td>2.0</td>
<td>8.1</td>
<td>30.2</td>
<td></td>
<td>Hibernal female</td>
<td>Soil-manure dwelling predatory mites with long-living adults</td>
<td>Mihm, Chiang 1976</td>
</tr>
<tr>
<td>Pergamasus crassipes</td>
<td>Parasitidae</td>
<td></td>
<td>1.5</td>
<td>2.0</td>
<td>7.0</td>
<td>11.5</td>
<td>22.0</td>
<td>Ad?</td>
<td>Litter-dwelling predaceous mite</td>
<td>Hartenstein 1962</td>
</tr>
<tr>
<td>Parasitellus fucorum</td>
<td>Parasitidae</td>
<td></td>
<td>2.8</td>
<td>2.2</td>
<td>4.5</td>
<td></td>
<td>12.0 and more</td>
<td>Phoretic resistant DN</td>
<td>Phoretic on bumblebees, reproduction in the nest</td>
<td>Koulianos, Schwarz 1999</td>
</tr>
<tr>
<td>Poecilochirus necrophori</td>
<td>Parasitidae</td>
<td></td>
<td>1–1.5</td>
<td>2.5–3</td>
<td>3–4</td>
<td>8–9 and more</td>
<td></td>
<td>Hibernal DN on adult beetles or their prepupa</td>
<td>Phoretic resistant DN with facultative diapause</td>
<td>Belpolova 1957, Belozero 1956, Schwarz 1951, Koulianos 1998</td>
</tr>
<tr>
<td>Macrocheles muscaedomesticae</td>
<td>Macrocheleidae</td>
<td></td>
<td>6–10</td>
<td>6–11</td>
<td>13–24</td>
<td>17–26</td>
<td>42–71 hours at 27°C</td>
<td>Phoretic Ad female</td>
<td>Phoretic on synanthropic flies and using fly eggs as food</td>
<td>Axtell 1967</td>
</tr>
<tr>
<td>Ornithonyssus bacoti</td>
<td>Dermanyssidae</td>
<td></td>
<td>1–2</td>
<td>0.5</td>
<td>3.5 up to 7.5</td>
<td>6–10</td>
<td>10–1.5</td>
<td>Quiescent PN and AD</td>
<td>Temporary ectoparasite of poultry in hen-farms</td>
<td>Nel’zina 1951, Bregetova 1956, Belozero 1958, Zemskaya 1951, Lange 1984</td>
</tr>
</tbody>
</table>

**Table 5.** Duration (in days) of life cycle stages in some Gamasina (at 18–25°C) with data on their dormant stages.
<table>
<thead>
<tr>
<th>Species</th>
<th>Egg (days)</th>
<th>La (days)</th>
<th>PN (days)</th>
<th>DN (days)</th>
<th>EG-AD (days)</th>
<th>Dormant stage</th>
<th>Habitat</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytoseiulus longipes, <em>Ph.</em> persimilis Phytoseiidae</td>
<td>2.2–3.7</td>
<td>0.7–1.0</td>
<td>1.21.8</td>
<td>1.2–2.1</td>
<td>5.3–8.5</td>
<td>Hibernal female diapause</td>
<td>S. African mites introduced in USA for control of spider mites</td>
<td>Badh, McMurtry 1984</td>
</tr>
<tr>
<td>Typhlodromus bambusae Phytoseiidae</td>
<td>1.7</td>
<td>1.0</td>
<td>0.8</td>
<td>0.8</td>
<td>4.2–7.5 6.1–7.3</td>
<td>Hibernal female diapause</td>
<td>Predator of spider mites from bamboo in China, Japan</td>
<td>Zhang et al. 1999; Saito 1990</td>
</tr>
<tr>
<td>Kampimodromus aberrans Phytoseiidae</td>
<td>2.3</td>
<td>0.9</td>
<td>1.2</td>
<td>2.6</td>
<td>6.9–7.1</td>
<td>Hibernal female diapause</td>
<td>Predator of gall and spider mites infesting different plants</td>
<td>Ozman-Sullivan 2006</td>
</tr>
</tbody>
</table>

**Table 5. Continued**

<table>
<thead>
<tr>
<th>Species</th>
<th>Egg</th>
<th>La</th>
<th>PN</th>
<th>DN</th>
<th>EG-AD</th>
<th>Dormant stage</th>
<th>Habitat</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trachyurodopa coccinea</td>
<td>8</td>
<td>20</td>
<td>26</td>
<td>44</td>
<td>98</td>
<td>DN</td>
<td>Rotting wood</td>
<td>Krasinskaya 1961</td>
</tr>
<tr>
<td>Uroplitella minitissima</td>
<td>19</td>
<td>20</td>
<td>34</td>
<td>69</td>
<td>142</td>
<td>DN</td>
<td>Rotting wood</td>
<td>Krasinskaya 1961</td>
</tr>
<tr>
<td>Urodonichys janeti</td>
<td>12</td>
<td>26</td>
<td>39</td>
<td>44</td>
<td>121</td>
<td>DN</td>
<td>Forest litter</td>
<td>Krasinskaya 1961</td>
</tr>
<tr>
<td>Uroobovella marginata</td>
<td>5–8</td>
<td>14–24</td>
<td>35</td>
<td>41</td>
<td>95–108</td>
<td>Phoretic + sedentary DN</td>
<td>Soil, manure and oligochet cultures</td>
<td>Krasinskaya 1961; Faash 1967</td>
</tr>
<tr>
<td>Leidinychus krameri</td>
<td>5.1–7.7</td>
<td>3.3–4.5</td>
<td>18.8–72.5</td>
<td>24.8–100</td>
<td>52–184</td>
<td>DN</td>
<td>Cosmopole pest of stored food</td>
<td>Radinovsky 1965</td>
</tr>
<tr>
<td>Chiropturopoda bakeri</td>
<td>2.7–3.2</td>
<td>3.3–7.0</td>
<td>3.2–4.0</td>
<td>4.0–4.8</td>
<td>13–30</td>
<td>DN</td>
<td>Cultivated soil and manure, Predatory and fungiforous mite.</td>
<td>Nawar et al. 1993</td>
</tr>
<tr>
<td>Janetiella pyriformis</td>
<td>9.5</td>
<td>17.6</td>
<td>25.8</td>
<td>29.5</td>
<td>82.2 53–135</td>
<td>Phoretic + sedentary DN</td>
<td>Soil- and manure- inhabitant with oligochets as food.</td>
<td>Athias-Binche, Habersaat 1988</td>
</tr>
<tr>
<td>Uropoda orbicularis</td>
<td>5</td>
<td>12</td>
<td>20</td>
<td>45</td>
<td>77</td>
<td>Phoretic DN</td>
<td>Soil-inhabitant. Predaceous on nematodes.</td>
<td>Radinovsky 1965</td>
</tr>
</tbody>
</table>

**Table 6.** Duration (in days) of life cycle stages in some Uropodina (at 18–25°C) and their dormant stages
Stratiolaelaps, Pergamasus, etc.) is presented usually by adult females. The dormancy in free-living mites dispersed by insects (some Macrochelidae, Ascidae, Parasitidae) is presented, as a rule, either by adult females, or by DN, combining phoresy with dormancy (apparently in state of diapause) during transportation on their carriers. Quite opposite dormant state, namely a quiescence at different stages of life cycle (PN, DN and AD), is characteristic of temporary ectoparasitic dermanyssid mites (Dermencyssus gallinae, Alldermanyssus sanguineus, Ornithonyssus bacoti), though some related species (D. hirundinis) hibernate as unfed PN in the state of behavioral diapause. These data, being rather fragmentary, need examinations, and hardly can be used as characteristics for definite gamasid families. The same picture concerns uropodid mites (Table 6), some representatives of which undoubtedly combine capability for phoresy and dormancy, though the function of dormancy can be based on different mechanisms (either diapause, or quiescence). The study of the Guano mite Uroobovella coprophila, inhabitant of Australian bat caves, gives good evidence for quiescence enforced by food constraints, since nymphs and adults of this cave mite become quiescent when fresh guano is absent, but return to the active development just after appearance of fresh food (Harris 1973). However, in Uropoda (Phaulodinychus) repleta dormant functions are enabled by diapausing adult mites and eggs (Weigmann 1996). This species from low salt marshes in North Germany is strongly monovoltine, with pre- and post-hibernation activity of adult mites, and rapid summer successive development of immatures. The related species, U. (Phaulodinychus) minor from upper dune zone, has bivoltine development and reveals less regular phenology, due to possible hibernal quiescence of its life-cycle stages.

There are no doubts that development of mesostigmatid mites virtually is impossible without stages that are capable for dormancy of any type. In many cases the dormant state is really combined with phoresy. The statement of Athias-Binche (1991) is of importance that a phoretic stage in any species of mites represents to a propagule, which is a resistant dormant instar and a dispersal agent. Though the phenomenon of phoresy in mites (both Parasitiformes, and Acariformes), is approached by many acarologists (see Athias-Binche 1991; Houck, O'Connor 1991; Evans 1992, etc.), its connection with dormancy was studied and analyzed quite insufficiently, and needs therefore further special investigations, firstly in regard to an onset and termination of dormant state in phoretic stages, followed by moulting in DN or reproduction in Ad. During these studies it is necessary to take into account the presence of two types of dormant DN (phoretic and sedentary). This property is equally common for Uropodina (among Parasitiformes) and Acaridia (among Acariformes). Essentially, that resistance of phoretic DN in both cases is much higher than that in sedentary dormant DN. For instance, the sedentary DN in Uroobovella marginata survive not more than 60 days, while phoretic DN (in U. marginata and Uropoda orbicularis) — up to 150 days. Phoronts are more resistant to starvation, dryness and other inappropriate impacts (Karg 1989).

In contrast to great uncertainty concerning nature of dormant stages, enabling life-cycle control in most gamasids and uropodid mites, as well as their survival during adverse seasons and passive dispersal to new habitats, one compact group among mesostigmatid acarines presented by plant-inhabiting, arboreal predatory mites (the family Phytoseiidae), reveals the strong determinacy in diapause nature of dormant stage. Practically all representatives of this family, which comprises not less than 560 species (Wainstein 1977), are characterized by reproductive hibernal diapause of adult females (Table 5), though there are some examples of phytoseiids in tropical and subtropical areas that have non-interrupted development without reproductive diapause, while some others from temperate areas have the winter quiescence at the adult stages or at every life-cycle stages (Veerman 1992). Phytoseiid mites are well known as active agents for control of spider mites (Acariformes: Tetranychidae) and four-legg mites (Acariformes: Eriophyoidae), extremely important agricultural plant pests. Besides numerous special publications concerning biology of different phytoseiid species, general information on ecological, physiological and applied aspects of seasonal adaptations in phytoseiid mites is given in reviews by Overmeer (1985), and especially full by Veerman (1992). Essential materials on these important agents of biocontrol are adduced in outstanding comprehensive two-volume book (Helle, Sabelis 1985) devoted to all aspects of taxonomy, biology and control of spider mites.

The family Phytoseiidae presents probably the single taxon among Acari, the seasonal development of which is controlled in almost all species by fertilized adult females in the state of faculta-
tive hibernal diapause. The main role in induction of their diapause belongs to the photoperiod that was ascertained by Putman (1962) on *Typhlodromus caudiglans* in Canada and by Sapozhnikova (1964) on *Amblyseius similis* in Russia, and confirmed for many other phytoseiids by different acarologists (Veerman 1992). This reproductive diapause enables the autumn/winter break of numerous summer generations, when diapausing females cease egg-laying in autumn, and leave the foliage in a search of shelters for hibernation on or out the tree. It is necessary to emphasize that in regards to physiological mechanisms of photoperiodic induction of diapause (Veerman 1992), phytoseiid mites reveal the great resemblance with spider mites (Tetranychioidea) and insects, and owing to rapid development they represent very convenient subject for experimental study of photoperiodism ecophysiology in arthropods. The resemblance of thermo-photoperiodic responses in phytoseiid and tetranychid mites enables the good coordination of their life cycles (especially of their escape from hibernation places) that makes phytoseiids to be very efficient control agents.

Due to the main aspects of our review dealing with different kinds of dormancy in the Acari, it is worth highlighting the resemblance of seasonal adaptations in phytoseiid and tetranychid mites concerning similar combinations of both types of dormancy (diapause and quiescence, namely the PDQ) in their resting stages, which enable the time-adjustment of their transition from seasonal developmental arrest to active development. The participation and importance of this dual mechanism (diapause + PDQ) in regulation of seasonal development of tetranychid mites (revealed by Zein-Eldin 1956 in *Petrolia apicalis* with aestivating eggs) was comprehensively reviewed and emphasized by Veerman (1985) for diapause in tetranychid mites, as well as in my previous paper on dormancy in the Acariformes (Belozerov 2008). Concerning the presence of the same complex mechanism in the control of seasonal arrests in phytoseiid mites, the reliable information is given in a paper of Broufas (2002) on induction and termination of hibernal reproductive diapause in adult females of *Euseius finlandicus* from northern Greece. The diapause in this mite is terminated by mid February. However its females stay in their overwintering sites until the second half of March under field conditions (due to the presence of cold-dependent post-diapause quiescence). According to references in Broufas (2002) paper, the maintenance of resting state through post-diapause quiescence after diapause termination has been reported earlier by different acarologists for some other phytoseiid mites (*Typhlodromus occidentalis*, *Amblyseius deleoni*, *A. longispinosus*, *A. andersoni* etc.).

**DISCUSSION AND CONCLUSION**

The materials of the present paper give conclusive evidences that mechanisms of life cycle control in representatives of the Parasitiformes can be based not only on opposite types of dormancy (either diapause, or quiescence), but also on their complexes, which enable more efficient time-adjustment of key events in seasonal development of parasitiform acarines. The presence of such complexes combined from diapause and post-diapause quiescence is quite usual in some representatives of Ixodida and Mesostigmata, like in already considered representatives of the Acariformes (Belozerov 2008), particularly Prostigmata and Astigmata, though only presumably for Oribatida. The ascertained resemblance of parasitiform and acariform mites allows further supporting the idea that the seasonal adaptations of such combined nature (diapause and post-diapause quiescence) are of plesiotypic character and could be taken by these arachnids from their ancestors.

The post-diapause quiescence (as a consecutive dormancy) associated with diapause (as a prospective dormancy) is characteristic of different arthropods — insects (Danks 1991, Hodek 1996, Koštal 2007), acarines (Veerman 1985, Belozerov 2008) and crustaceans (Brendonck 1996, etc.). This type of quiescence, as well as diapause, provides two important vital functions (time-adjustment of development and survival of resistant dormant instars). When diapause is completed, it is followed by quiescence that prolongs the dormant period until the onset of appropriate environmental conditions (Danks 1987, 1991). Besides the post-diapause quiescence that appears as a result of diapause termination, insects and other arthropods are known to possess some other types of quiescence — particularly the usual “stage-independent quiescence” (Gurney et al. 1991) as a direct response to constraining factors at any instar or stage, and the specific “stage-specific quiescence” (Gurney et al. 1994) resulted in insects at definite instar or stage due to special temperature thresholds of their development. The listed forms of quiescence have different relations to diapause and, respectively, unequal participation in season-
al control of life cycles (see Belozerov 2008, 2009). Only the usual (stage-independent) and post-diapause quiescence are known in the Acari.

According to Danks (1991), life cycles in arthropods may contain a large number of adaptive elements that act in combination. The life cycle might be timed (in one or several instars) by means of “a photoperiodically-controlled growth rate, followed by a photoperiodically-induced diapause, succeeded by a temperature-controlled quiescence”. Such complex systems with their main function to regulate life cycles in conditions of seasonal predictability of environmental changes, provide also remarkable flexibility to cope with environmental conditions that may differ “from place to place or year to year”, and these systems undoubtedly are more widespread than is realized now (Danks 1991). They may be termed as **multi-component systems of seasonal life-cycle control**. The necessity of detailed studies concerning the diversity and nature of the responses collaborating in life-cycle control noted in this regard by Danks (1991), is well accordant to a proposal of Russian ecologist Emme (1953) about the need of comparative research of different forms of non-diapause and diapause dormancy for further progress in ecological physiology of insects, mites and other arthropods. After Tauber et al. (1986) and Danks (1987), the diversity of these kinds of dormancy is considered in most comprehensive form by H.J. Müller (1992) in his monograph "Dormanz bei Arthropoden".

As it is clear from data approached in the presented and previous paper concerning the seasonality of life cycles and its control in representatives of the Parasitiformes and the Acariformes, the related traits of their life histories are quite similar and comparable. This concerns the diversity of mechanisms controlling life cycles through different types of diapause and quiescence, as well as by their combinations. The most significant and understandable example of such similarity is illustrated by a combination of diapause and post-diapause quiescence, the properties and adaptive significance of which for “fine” time-adjustment of life cycle patterns in ticks (Ixodida) and phytoseiid mites (Mesostigmata), alike in acariform mites, are quite comparable. However, many peculiarities of options and regularities of life cycle control in both lineages of the Acari need further experimental research (both in field and laboratory), as well as a comprehensive analysis and modeling this control with taking into account diapause and non-diapause forms of dormancy, as was noted earlier by Emme (1953) and Danks (1991). The real perspective of such approaches for Ixodida is demonstrated recently by experimental studies conducted by Randolph et al. (2002) in UK with *Ixodes ricinus* and by Ogden et al. (2004) in Canada with *I. scapularis*, by similar studies with an African tick *Rhipicephalus appendiculatus* (Randolph 1997; Speybroeck et al. 2002) and modeling its seasonal population dynamics (Randolph, Rogers 1997; Randolph 2004, 2008), as well as by modeling the respective population dynamics in *I. ricinus* (Randolph et al. 2002; Randolph 2004, 2008) and analyzing the behavior diapause development in *R. appendiculatus* (Speybroeck et al. 2006) also.

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