Acarina 17 (1): 3–32

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

V. N. Belozerov

Biological Research Institute, St. Petersburg State University, Peterhof 198504, Russia;
e-mail: val.belozerov@mail.ru

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 began 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[1] 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 taxons (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 prelarval 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 gonotrofic cycle in adult females (all these traits reflect the processes of oligomerization[2] 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 gonotrofic 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 superfamily 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 ixodological publications, our knowledge is never-

---

[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 taxons 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.

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 ecophysiological 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 in the acariform mites (Belozerov 2008), since some real traits of post-diapause quiescence, particularly in *Ixodes ricinus* eggs and engorged nymphs, were overlooked by me in my dissertation on seasonal control of life cycles in ixodid ticks (Belozerov 1988).

There are no doubts that in ixodoid ticks, as well as in already analyzed acariform mites (Belozerov 2008), some kinds of non-diapause dormancy (quiescence) together with diapause play an essential role in adaptations to predictable and unpredictable environmental changes. The real cases of common quiescence (*i.e.* "the stage-independent quiescence" according to Gurney et al. 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 ixodoid 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 polyvoltine 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 great 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 plesiotypic group from the family Ixodidae (Table 1). For instance, the termination of developmental (morphogenetic) diapause in overwintering eggs and engorged nymphs 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[1] 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 Ranbdolph 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[2], 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 events), 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-diapaus**e, displayed in fed nymphs

---

[1] LD — long-day and SD — short-day photoperiods, i.e. longer or shorter than threshold (critical) photoperiod.

[2] Detailed consideration of the problem concerning two-step photoperiodic reactions in insects is given in publications by Zaslavsky (1972, 1974, 1984 and 1987).

Table 1.
Morphogenetic diapause and its termination followed by post-diapause quiescence in some representatives of ixodine and amblyommine ixodid ticks (Ixodidae)

Species	Stage of developmental arrest	Diapause			Post-diapause quiescence	Remarks	References
		Induction	Maintenance	Termination			
Ixodes ricinus European forest tick with perennial life cycle. Hibernation of unfed and engorged La, Ny and Ad, as well as eggs	**Egg** Hibernation in the state preceding the onset of embryogenesis.	Result of maternal LD-effect. Non-diapause eggs are laid by overwintered or lab. SD-females.	Temperate and cold conditions (with no photoperiodic effect).	Cold reactivation during first winter month with requiring the cold-dependent PDQ and potency for further development. Reactivation takes 1.5–2.5 months.	PDQ: Realization of aquired developmental potency after impact of increased temperature.	Overwintered diapause eggs have typical PDQ and hatch next year (in 9–11 months after oviposition), while non-diapause eggs laid in spring by overwintered females hatch the same year (in 2–3 months after oviposition).	Serdjukova 1951; Babenko 1967; Belozerov 1973a, 1990; Randolph et al. 2002; Randolph 2004, 2008; Dautel, Knülle 2006.
	La engorged. Hibernation of mobile La before the onset of apolysis.	Pre- and post-feeding SD-impact. Opposite LD-impact induces non-diapause development.	Temperate and cold conditions support the state of diapause (together with SD-impact) due to combination of sensitive and diapausing states in engorged larvae.	Retention of photoperiodic and temperature sensitivity ensures the termination of diapause (by impact of LD and increased temperature on engorged larvae). The PDQ is not discovered, but probable.	Larval diapause is similar with photoperiod-dependent quiescence, but is controlled through interaction of LD- and SD-responses.	LD-type response playing the main role in determining the development or diapause before, during and after larval feeding, is affected by additional component of SD-type that modifies LD-response through impact of increased temperature on unfed La (see the text and other remarks).	Loew 1964; Belozerov 1964a,1968; Babenko, Platonova 1965; Babenko 1970; Belozerov, Mikhailova 1966; Belozerov, Ilyin 1974, 1981; Randolph et al. 2002; Randolph 2004, 2008
	Ny engorged. Hibernation of mobile Ny before the onset of apolysis	Control of development is ensured by two-step (SD-LD) photoperiodic reaction.	The covert state of diapause in unfed nymphs is supported by LD-, but eliminated by SD-impact. Overt diapause in engorged nymphs is maintained by SD-response (under low and temperate temperature), which ensures simultaneous SD- or cold-reactivation of engorged diapausing nymphs.	Due to collaboration of two opposite reactions, the covert LD-diapause in unfed nymphs is ceased by SD-impact, while the overt SD-diapause in engorged nymphs is terminated by LD-impact. Photoperiodic sensitivity ends only after initiation of morphogenetic events (not after diapause onset).	PDQ is possible both in unfed, and engorged nymphs after reactivation (with acquiring the developmental potency realized in permissive conditions under impact of LD and higher temperature).	SD-reactivation enables PDQ with recovering ability for LD-response. SD-response attributable to unfed nymphs is intensified by increased temperature (promoting development delays in diapausing nymphs, which are not sensitive to LD-impacts). Both Ny and La are similar in this regard. This modifying effect of increased temperature in unfed La/Ny is characteristic of many tick species.	Loew 1964; Belozerov 1966, 1967, 1968, 1970, 1971, 1972, 1988, 1995; Babenko 1967, 1970; Belozerov et al. 2003; Randolph et al. 2002; Randolph 2004, 2008

Table 1. Continued

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	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 perennial life cycle, hibernation of engorged La and Ny (together with unfed La, Ny and Ad)	**La** and **Nymphs** engorged	Control of development in nymphs is determined by two-step SD-LD reaction as in *I. ricinus* (Inability of eggs and engorged adult females for survival in winter due to absence of developmental diapause).	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.	Babenko, Platonova 1965; Babenko 1967, 1970; Filippova 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 / persucatus*.	The overt diapausing 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 postembrional 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° (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

Table 1. Continued

Dermacentor marginatus Eurasian tick from steppe landscapes. Monovoltine development and hibernation of adult ticks	**Adult females** engorged (overwinter together with unfed adult ticks)	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.	Diapause is maintained by temperate and high temperatures (irrespective of photoperiod due to loss of photosensitivity in feeding and engorged females).	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.	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.	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 *D. reticulatus* (Razumova 1965).	Belozerov 1963, 1964b, 1968, 1988; Belozerov, Kvitko 1965; Belozerov, Lamanova 1967; Razumova 1965
Dermacentor silvarum Asian forest-steppe tick with monovoltine life cycle and hibernation of Ad on hosts	**Adult males** and **females** attachted to host	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.	The delay of engorgement is maintained by low temperature and SD, which produce simultaneously reactivating effect..	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).	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 *D. marginatus*.	Alfeev 1948; Belozerov 1973b; Kolonin et al. 1976
Hyalomma anatolicum Stable-pasture parasite of domestic cattles in Central Asia, Near East and Northern Africa	Engorged **Ny** and **Ad female**, (Eg) (overwinter together with unfed adult ticks)	Development of Ny and oogenesis in females is determined according to norms of LD-reaction: diapause is induced by SD-impact. SD-response in both cases is age-dependent.	Maintenance of diapause is ensured by SD and low temperature producing simultaneously reactivating effect.	Termination of diapause is followed undoubtedly by PDQ (due to early beginning of diapause and long stay of resting engorged ticks in low reactivating temperatures).	In field habitats of Central Asia the onset of diapause in Ad female begans in August, while of nymphs in the middle of September according to their photoperiodic responses.	Modifying effects in unfed La and Ny are not observed.	Berdyev 1974; Mourad, Belozerov 1976; Belozerov, Mourad 1977; Rubina et al. 1982

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.

(especially 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 consideted 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 amblyommine 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 amblyommine 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 plesiotypic 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 subtropics in the Central and West Asia, including North Africa. Diapause of nymphs and females is determined by SD-impact (both before and after feeding) in accordance to the thermostabile LD-reaction, strongly dependent upon the age of SD-ticks (this does not concern LD-influenced ticks). In this regard *H. anatolicum* reveals the deep similarity with some other ixodid ticks, which age reinforces 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-Peňa et al. 2007), might get possible by means of combined diapause/PDQ adaptation. 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 (Pomerantzev 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 ascertained 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 amblyommine 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, Zuchini 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 Koštal (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 2. Behavioral diapause and its termination followed by post-diapause quiescence in some representatives of ixodine and amblyommine ticks (Ixodidae)

Species	Stage of behavioural diapause	Diapause			Quiescence	Remarks	References
		Induction	Maintenance	Termination			
Ixodes ricinus European tick with perennial life cycle. Hibernation of unfed and engorged La, Ny, Ad (and Eggs)	**Unfed La, Ny, Ad**	BD in all life-cycle stages is facultative and induced by SD-impact	By SD- and cold conditions	After reactivating impact by cold and SD	According to Randolph (2004) and Dautel et al. (2008), unfed La overwinter in the state of quiescence	Facultative character of dormancy in unfed ticks and its dependence on day length allow to suggest that they overwinter in the state of SD-dependent consecutive dormancy (quiescence or oligopause).	Babenko 1956; Belozerov 1966, 1967, 1968, 1970, 1976a
Ixodes persulcatus Euroasian tick with perennial life cycle. Hibernation of unfed La, Ny and Ad (together with engorged La and Ny)	**Unfed La, Ny, Ad**	BD in La and Ny is facultative and induced by SD. In Ad it is obligatory	By SD- and cold conditions	After reactivating impact by cold and SD	Quite probable presence of cold-dependent PDQ after obligatory BD in Ad ticks	Stability of obligatory BD in Ad stage is rather low, and its short duration is supplemented undoubtedly by cold-dependent PDQ. Immature ticks are similar with those of *I.ricinus*.	Belozerov 1976a; Filippova 1985
Ixodes scapularis N. American tick with perennial life cycle and hibernation of most stages in unfed and engorged state	**Unfed La, Ny,** (Ad)	BD in La, Ny (and Ad) is facultative and induced by SD	By SD- and cold conditions	After reactivating impact by cold and SD	Quite probable presence of cold-dependent PDQ in Ad ticks	Unfed adults have no BD (Yuval, Spielman 1990), though photoperiod affects their behavior (Goddard 1992).	Yuval, Spielman 1990; Goddard 1992
Haemaphysalis concinna Eurasian forest-steppe tick with perennial life cycle. Hibernation of unfed and engorged ticks (all stages)	**Unfed La, Ny, Ad** (overwinter with engorged La, Ny, Ad in developmental diapause)	In all stages BD is facultative, induced by SD-impact	By SD- and cold conditions.	Termination of diapause is ensured by cold-reactivation and followed probably by PDQ, which is terminated in LD-conditions	PDQ is probable, but not investigated.	Perennial life cycle is characterized by photoperiod/temperature control of behavioral and developmental diapause (induction and termination).	Belozerov 1969, 1974; Zhmaeva 1948; Nosek et al. 1967; Belyaeva, Ryabova 1971
Haemaphysalis longicornis 3-host tick with perennial life cycle in E. Asia and monovoltine development in Australia and New Zealand	**Unfed La, Ny** and **Ad** in northern hemisphere **Unfed Ny** (Ad) in southern hemisphere	Winter BD in unfed La, Ny and Ad (from northern populations) is induced by SD-impact, the same in Ny (and Ad) from southern populations. No adaptive dormancy in engorged ticks.	Impact of SD enables the maintenance of BD in unfed ticks	Impact of LD enables the activation of unfed dormant ticks	The nature of dormancy in unfed ticks needs more thorough study	Besides the dependence of activity and BD upon day length (according to norms of LD-reaction), some traits of development in engorged La, though not adaptive, reveal their dependence on photoperiodical regime of unfed La (according to norms of SD-reaction) due to modifying effect of increased temperature.	Belikova 1969; Sutherst, Moorhouse 1972; Sutherst, Bourne 1991; Belozerov, Luzev 1974; Fujimoto 1995 (see the text and remarks for some other ticks also)

Table 2. Continued

Haemaphysalis parva (= *otophila*) Monovoltine 3-host tick from N. Caucasus	**Unfed Ad**	Summer BD of Ad ticks is induced by LD (similar with winter reproductive diapause)	–	PDQ is not known, but probable.	Eggs, La and Ny are fast-developing summer stages not capable for dormancy	In contrast to LD-induced developmental diapause, the autumn activity of unfed adult ticks is determined by SD photoperiodic impact.	Belozerov 1995c
Dermacentor variabilis 3-host tick from eastern USA with biennial cycle, hibernation of unfed ticks at all stages	**Unfed La, Ny** (Ad)	Facultative BD of unfed La and Ny is induced by SD, while their activity (espedially in Ny) by increased temperature. No dormancy in engorged ticks.	See remarks	See remarks	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.	Smith, Cole 1941; Sonenshine 1972; Burg 2001
Dermacentor andersoni Prairie's tick from western USA, biennial, hibernation of unfed ticks at all stages	**Unfed** (La), **Ny** and **Ad**	Adult ticks have obligatory BD. Traits of diapause induction in La and Ny are not revealed.No dormancy in engorged ticks.	Maintenance of adult diapause and its elimination is ensured only by cold conditions with no photoperiodic impact.	Activation of cold-reactivated adult ticks is enabled by increase of temperature.	Seasonal controlling functions of La and Ny are probable, but not investigated.	In some traits of feeding delays on their hosts, *D. andersoni* adult ticks have similarity with Asian *D. silvarum.*	Wilkinson 1968, 1973
Dermacentor albipictus One-host winter parasite of moose in USA and Canada with monovoltine life cycle	**Unfed La** and **attached Ny**	Summer BD of unfed La determined by LD-impact, and pre-engorgement winter diapause of Ny attached to host	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 pattern may be influenced by photoperiod.	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.	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.	Wright 1968, 1971; Drew, Samuel 1985, 1989; Patrick, Hair 1977

Table 2. Continued

Rhipicephalus appendiculatus Three-host tick from central (with bi-/polyvoltine) and southern Africa (with monovoltine development) and BD of unfed adults	**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
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.

Table 3.
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)

Sequence of events during development of morphogenetic diapause in an insect (according to Koštal 2006)	Pre-diapause	Diapause	Transitional state	Post-diapause quiescence	Active life
	Induction (as a covert event) and preparation (as a first overt event) of diapause	Initiation and maintenance of the arrest as an induced response to endogenous and exogenous impacts.	Termination of diapause as a result of reactivation.	Exogenous arrest enforced by adverse conditions and terminated in permissive conditions.	Active life until the death due to exhausting food reserves.
	Direct development	Endogenous		Exogenous	Direct development
		Developmental arrest			
Sequence of events during development of behavioral diapause in a tick (according to Speybroeck et al. 2006)	Non-diapause direct development	Diapause	Responsive dormant phase	Post-diapause non-dormant phase	Active live
	Active life in permissive conditions	First hidden and non-responsive dormant phase enforced by onset of long day-length and drought, but supplemented by aging decrease of diapause state.	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.	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).	Active life until the death or the repetition of the same patterns of life cycle.

Notes. The method of modeling diapause termination, elaborated by Spreybroeck 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

Genus	Behavioural diapause	Developmental diapause	PDQ after developmental diapause	Nature of associated dormancy
Ixodes ~ 220 species	La +/– Ny +/– Ad +	Egg +/– La +/– Ny +/– Ad +/–	**Egg – 1** **La – 3** **Ny – 3** (+2 ?) Ad –	LD-diapause + PDQ LD- diapause + PDQ SD- diapause + PDQ Diapause ?
Haemaphysalis ~ 150 species	La +/– Ny +/– Ad +	Egg — La +/– Ny +/– Ad +/–	Egg – **La – 1** (+?) **Ny – 1** (+?) Ad	– SD-diapause SD-diapause + PDQ –
Dermacentor ~ 30 species	La +/– Ny +/– Ad +	Egg – La +/– Ny +/– Ad +/–	Egg – La – Ny – **Ad – 2** (+?)	– – – LD-diapause + PDQ
Hyalomma ~ 30 species	La +/– Ny +/– Ad +	Egg + La – Ny +/– Ad +/–	Egg – La – **Ny – 1** (+?) **Ad – 1** (+?)	– – LD-diapause + PDQ LD-diapause + PDQ
Rhipicephalus ~ 54 species (+ *Boophilus* and *Margaropus*)	La +/– Ny +/– Ad +	Egg – La – Ny – Ad +	Egg – La – Ny – Ad –	No developmental diapause at stages of egg, La, Ny ad Ad
Amblyomma ~ 100 species (+ *Bothriocroton*?)	La +/– Ny +/– Ad +/–	Egg +/– La +/– Ny +/– Ad +/–	Egg ? **La – 1** (+?) **Ny – 1** (+?) **Ad – 1** (+?)	– SD-diapause SD-diapause SD-diapause?

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 acarines.

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

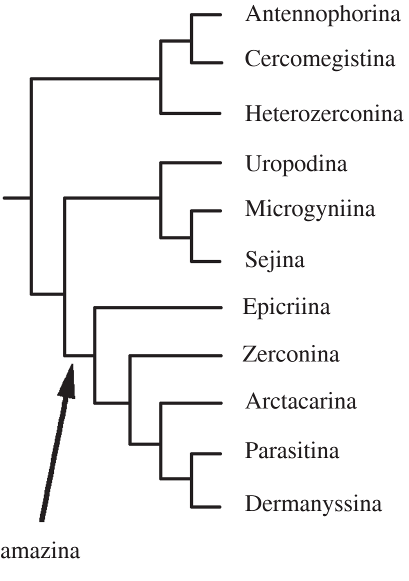

Fig.1. Relationships among infraorders of Mesostigmata (after D.E. Johnston from Norton et al. 1993)

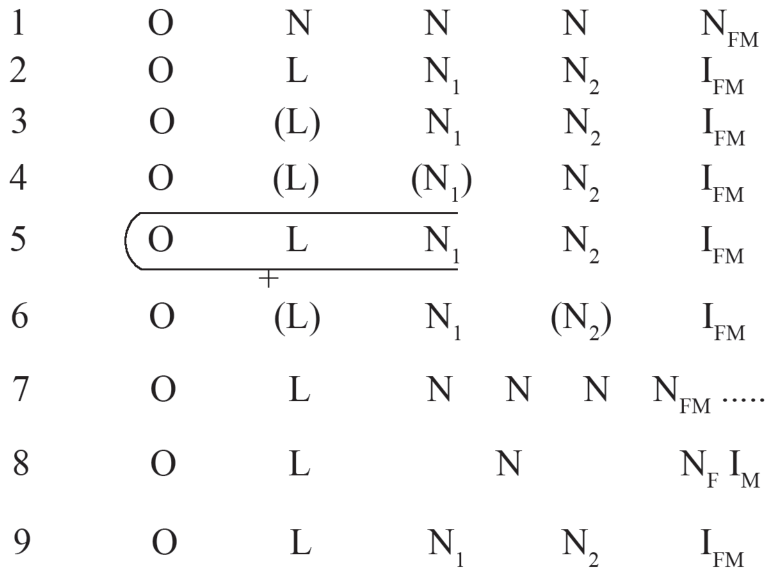

Fig. 2. Evolution of individual development in Parasitiformes.
1 — suggested initial life cycle (a direct development as in most arachnids); 2 — life cycle in most free-living gamasid mites; 3 — some free-living gamasids and facultative blood-sucking mites (Laelaptidae); 4 — representatives of Haemogamasidae and some species of *Hirstionyssus*; 5 — bat mites Spinturnicidae and some species of *Hirstionyssus* with larviparity; 6 — the genus *Ornithonyssus* and some internal parasites from the family Hirstionyssidae; 7 — argasid ticks (Ixodida: Argasidae); 8 — ixodid ticks (Ixodida: Ixodidae); 9 — Uropodida. After Lange (1984, Fig. 74, p. 96)
Notes. O — egg, L — larva, N — nymph (N_1, N_2 — proto- and deutonymph), I — adult. In parentheses — partly or non-feeding nymphs, or lecitotrophic larva.

and four postembryonic stages (La, PN, DN and Ad). Some ontogenetic changes known in Gamasina (embryonization of La and even PN, aphagy of La in most species and of nymphs in some species) 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 other regards to the more uniform suborder Uropodina, the representatives of which are characterized in contrast by K-selected attributes of life history (being biologically similar in this regard to oribatid 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 completion 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 mesostigmatid mites (particularly of gamasids) has concerned morphology and taxonomy (Zakhvatkin 1948, 1952; Bregetova 1956; Karg 1971, 1989; Gilyarov and Bregetova 1977, etc.), as well as problems of ecological and evolutionary parasitology (Nel'zina 1961; Beklemishev 1970; Zemskaya 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 investigations, 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 therefore. According to Table 5, the dormant stage in soil-dwelling gamasid mites with plesiotypic predatory habits (such as parasitids *Androlaelaps,*

Table 5.

Duration (in days) of life cycle stages in some Gamasina (at 18–25°C) with data on their dormant stages

Species	Egg	La	PN	DN	EG–AD	Dormant stage	Habitat	Reference
Arctoseius semiscissus Ascidae	3.3	2.0	1.4	1.2	7.9	Phoretic Ad female	Soil-dwelling predatory mites in mushroom farm, phoretic on sciarid flies	Rudzinska 1998
Androlaelaps sp. *Stratiolaelaps* sp. Laelaptidae	4.9	2.0	8.1	15.2	30.2	Hibernal Ad female 246±156 days	Soil/manure-dwelling predatory mites with long-living adults	Mihm, Chiang 1976
Pergamasus crassipes Parasitidae	1.5	2.0	7.0	11.5	22.0	Ad?	Litter-dwelling predaceous mite	Hartenstein 1962
Parasitellus fucorum Parasitidae	2.8	2.2	4.5	Phoretic resistant DN	12.0 and more	Hibernal DN on adult bee females	Phoretic on bumblebees, reproduction in their nests	Koulianos, Schwarz 1999
Poecilochirus necrophori Parasitidae	1–1.5	2.5–3	3–4	Phoretic resistant DN with obligatory or facultative diapause	8–9 and more	Hibernal DN on adult beetles or their prepupa	Phoretic on *Nicrophorus* beetles with reproduction in their brooding chambers	Belozerov 1957; Schwarz , Koulianos 1998
Macrocheles muscaedomesticae Macrochelidae	6–10 hours	6–11 hours	13–24 hours	17–26 hours	42–71 hours at 27°C	Phoretic Ad female	Phoretic on synanthropic flies and using fly eggs as food	Axtell 1967
Ornithonyssus bacoti Dermanyssidae	1–2	0.5	3–5 up to 120–150	1.0–1.5	From 14–21 up to 90–120 days	Quiescent PN and AD	Temporary ectoparasite of rats with long-living PN and AD	Nel'zina 1951; Bregetova 1956; Belozerov 1958
Allodermanyssus sanguineus Dermanyssidae	4–5	3	4–5	6–10	17–23 and more	Quiescent PN, DN and AD	Temporary ectoparasite of mice	Bregetova 1956
Dermanyssus gallinae Dermanyssidae	2–3	1.0	1.0	1.5–2.0	Capable for long starvation (PN, DN)	Quiescent PN, DN and AD	Temporary ectoparasite of poultry in hen-farms	Zemskaya 1951; Lange 1984
Varroa jacobsoni Varroidae	1	–	2–3	2–3	Before females 7–9, before males 6–7	Diapause is absent. The place of mite survival in winter is bee club.	The major pest of honey bee, as an ectoparasite of immature and adult bees. Phoretic adult female mites during 4–7 days.	Akimov et al. 1993
Amblyseius californicus Phytoseiidae	1.7–3.0	0.6–1.0	1.1–1.6	1.0–1.6	4.4–7.2	Hibernal female diapause	Indigenous mite in Japan feeding on spider mites	Gotoh et al. 2004
Amblyseius potentillae Phytoseiidae	3.0	1.0	3.0	3.0	10.0	Hibernal female diapause	Agent of spider mites control in apple orchards	Van Houten, Veenendaal 1990

Table 5.
Continued

Phytosejulus longipes, *Ph. persimilis* Phytoseiidae	2.2–3.7	0.7–1.0	1.21.8	1.2–2.1	5.3–8.5	Hibernal female diapause	S. African mites introduced in USA for control of spider mites	Badh, McMurtry 1984
Typhlodromus bambusae Phytoseiidae	1.7	1.0	0.8	0.8	4.2–7.5 6.1–7.3	Hibernal female diapause	Predator of spider mites from bamboo in China, Japan	Zhang et al. 1999; Saito 1990
Kampimodromus aberrans Phytoseiidae	2.3	0.9	1.2	2.6	6.9–7.1	Hibernal female diapause	Predator of gall and spider mites infesting different plants	Ozman-Sullivan 2006

Table 6.
Duration (in days) of life cycle stages in some Uropodina (at 18–25°C) and their dormant stages

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

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 (*Dermanyssus gallinae, Allodermanyssus 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, OConnor 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 gamasid 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: Tetranychoidea) and four-legg mites (Acariformes: Eriophyoidea), 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 facultative 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 (Tetranychoidea) 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 *Petrobia 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 seasonal 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 perspectivity 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.

ACKNOWLEDGEMENTS

The study was performed under financial support of RFBR (project 07-04-00361) and of Federal program for supporting the Leading Scientific Schools (project НШ-7130.2006.4). The author is grateful to those who paid the attention to my work, and particularly to Dr. F. Dusbabek (Czech Republic) for commenting the submitted MS and to Dr. H. Klompen (USA) for information on the classification of the Parasitiformes.

REFERENCES

Akimov, I.A., Grobov, O.F., Pileckaya, I.V., Barabanova, V.N., Yastrebtzov, A.V., Gorgol', V.T., et al. 1993. *Pcheliny kleshch Varroa jacobsoni* [Bee mite *Varroa jacobsoni*]. Kiev, 256 pp. [In Russian]

Alfeev, N.I. 1948. [Diapause in ixodid ticks]. *Trudy voenno-med. akademii*, Leningrad, 44: 50–60. [In Russian]

Athias-Binche, F. 1991. Ecology and evolution of phoresy in mites. *In:* F. Dusbabek and V. Bukva (Eds.). Modern Acarology. Academia, Prague, vol. 1, pp. 27–41.

Athias-Binche, F. and Habersaat, U. 1988**.** An ecological study of *Janetiella pyriformis* (Berl. 1920), a phoretic Uropodina from decomposing organic matter. *Mitt. Schweiz. Entomol. Ges.*, 6: 377–390.

Axtell, R.C. 1969. Macrochelidae (Acarina: Mesostigmata) as biological control agents for synanthropic flies. *In:* Proc. 2^{nd} Intern. Congr. Acarology (1967), pp. 401–416.

Babenko, L.V. 1956. [About seasonal events in life of ixodid ticks *Ixodes ricinus* and *I. persulcatus*]. *Med. parasitologiya i parasit. bolezni,* 25: 346–352. [In Russian]

Babenko, L.V. 1967. [Variability in types and duration of development in ticks *Ixodes ricinus* in dependence on the weather of vegetation seasons]. *In:*

Voprosy parasitologii. Kiev, pp. 337–338. [In Russian]

Babenko, L.V. 1970. [Some ecological features of nymphs *Ixodes ricinus*]. *In:* Vtoroe akarologicheskoe soveshchanie (Abstracts.), Kiev. 1970, vol. 1, p. 43–46. [In Russian]

Babenko, L.V. and Gal'chenko, S.S. 1976. [Peculiarities of feeding and development of larvae in *Ixodes kazakstani*]. *Med. parasitologiya i parasit. bolezni,* 45: 331–337 [In Russian]..

Babenko, L.V. and Platonova, V.F. 1965. [On larval diapause of *Ixodes ricinus* and *I. persulcatus*. 1. Experimental data on the impact of photoperiod upon unfed and engorged larvae]. *Med. parasitologiya i parasit. bolezni,* 34: 69–73. [In Russian]

Badh, M.H. and McMurtry, J.A. 1984. Life history and life table parameters for *Phytoseiulus longipes* with comparative studies on *P. persimilis* and *Typhlodromus occidentalis* (Phytoseiidae). *Acarologia*, 25: 111–123.

Balashov, Yu.S. 1959. [Periodization of cycles of development in ixodid ticks]. *Med. parasitologiya i parasit. bolezni*, 28: 469–476. [In Russian]

Balashov, Yu.S. 1962. [Determination of physiological age and the age structure of *Ixodes ricinus* and *Ixodes persulcatus* populations in the Leningrad Region]. *Med. parasitologiya i parasit. bolezni,* 31: 47–55. [In Russian]

Balashov, Yu.S. 1967. *Krovososushchiye kleshchi (Ixodoidea) — perenoschiki bolezney cheloveka i zhivotnykh* [Bloodsucking ixodoid ticks as vectors of human and animal deseases]. Leningrad, 319 pp. [In Russian]

Balashov, Yu.S. 1993. [Significance of continental drift for distribution and evolution of ixodid ticks (Acarina, Ixodidae)]. *Entomol. obozrenie*, 72: 929–936. [In Russian]

Balashov, Yu.S. 1998. *Iksodovye kleshchi — parazity i perenoschiki infektsiy* [Ixodid ticks as parasites and vectors of infections]. St. Petersburg, 287 pp. [In Russian]

Balashov, Yu.S. 2009. *Parazitism kleschey i nasekomych na nazemnych pozvonochnych* [Acari and Insect parasitism on terrestrial vertebrates]. St. Petersburg, 357 pp. [In Russian]

Beklemishev, V.N. 1970. *Biocenologicheskie principy sravnitel'noy parazitologii* [Biocoenologic principles of comparative parasitology]. Moscow, 502 pp. [In Russian]

Belikova, N.P. 1969. Comparative data on feeding activity and duration of morphogenesis in ticks of the genus *Haemaphysalis. Sbornik trudov Vladivostokskogo issled. instituta epidemiologii i microbioogii,* 4: 248–254.

Belozerov, V.N. 1957. [About biology and anatomy of the mite *Poecilochirus necrophori* Vitzt. (Parasitiformes, Parasitidae)]. *Zool. zhurnal,* 36: 1802–1813. [In Russian]

Belozerov, V.N. 1958. [Influence of atmospheric humidity on the mite *Ornithonyssus bacoti* Hirst (Parasitiformes, Liponyssidae)]. *Entomol. obozrenie,* 37: 47–63. [In Russian]

Belozerov, V.N.1963. [Day length as a factor determining the oviposition delay in adult females of *Dermacentor marginatus* Sulz]. *Med. parasitologiya i parasit. bolezni,* 30: 308–313. [In Russian]

Belozerov, V.N. 1964a. [Larval diapause in the tick *Ixodes ricinus* L. and its dependence on exogenous conditions]. *Zool. zhurnal,* 43: 1626–1637. [In Russian]

Belozerov, V.N. 1964b. [Diapause and reactivation in adult females of *Dermacentor marginatus*]. *Vestnik Leningradskogo universiteta* (Ser. 3, biology), 4: 5–11. [In Russian]

Belozerov, V.N. 1966. [Nymphal diapause in the tick *Ixodes ricinus* L. 1. Dependence of behavior of unfed nymphs and of development of engorged nymphs on photoperiodic conditions]. *Med. parasitologiya i parasit. bolezni,* 6: 723–729. [In Russian]

Belozerov, V.N. 1967. [Nymphal diapause in the tick *Ixodes ricinus* L. 2. Different forms of diapause in nymphs and peculiarities of their regulation in ticks *I. ricinus* of Leningrad population]. *Parazitologiya,* 1: 279–287. [In Russian]

Belozerov, V.N. 1968. [Photoperiodic control of seasonal development in ixodid ticks]. *In:* A.S. Danilevsky (Ed.). Fotoperiodicheskie adaptatsii u nasekomykh i kleshchey. Leningrad, p. 100–128. [In Russian]

Belozerov, V.N. 1969. [Photoperiodic reaction of larvae and nymphs of the tick *Haemaphysalis concinna* Koch.]. *Parazitologiya,* 3: 17–21. [In Russian]

Belozerov, V.N. 1970. [Nymphal diapause in the tick *Ixodes ricinus* L. (Acarina, Ixodidae). 3. Photoperiodic reaction of unfed nymphs]. *Parazitologiya,* 4: 139–145. [In Russian]

Belozerov, V.N. 1971. [Nymphal diapause in the tick *Ixodes ricinus* L. (Acarina, Ixodidae). 5. Impact of changes in photoperiodic conditions of unfed nymphs on their development after engorgement]. *Parazitologiya,* 5: 481–487. [In Russian]

Belozerov, V.N. 1972. [An inversion of photoperiodic reaction in the control of development and diapause of nymphs *Ixodes ricinus* L. (Acarina, Ixodidae) and mechanisms of this phenomenon]. *In:* N.I. Goryshin (Ed.). Problemy fotoperiodisma i diapausy u nasekomykh. Leningrad, p. 175–192. [In Russian]

Belozerov, V.N. 1973a. [Egg diapause in *Ixodes ricinus* and its dependence on photoperiodic conditions of unfed adult females]. *Vestnik Leningradskogo universiteta,* 9 (Biol. 2): 33–37. [In Russian]

Belozerov, V.N. 1973b. [Experimental analysis of seasonal adaptations of *Deracentor silvarum* Ol.]. *Parazitologiya,* 7: 14–18. [In Russian]

Belozerov, V.N. 1974c. [Experimental study of seasonal adaptations of *Haemaphysalis concinna* ticks from different sites of the Far East]. *Med. parasitologiya i parasit. bolezni.* 43: 31–38. [In Russian]

Belozerov, V.N. 1976a. [Life cycles and seasonal adaptations in ixodid ticks]. *In*: Doklady 28 yezhegodnykh chteniy pamyati N.A. Kholodkovskogo. Leningrad, pp. 53–101. [In Russian] [In English: NAMRU-3, T1124]

Belozerov, V.N. 1976b. [Seasonal cycle's adaptations in the tick *Rhipicephalus turanicus* B. Pom.]. *In:* Tret'ya vsesoyuznaya konferentsiya po teoreticheskoy i prikladnoy akarologii (Abstracts). Tashkent. pp. 41–42. [In Russian]

Belozerov, V.N. 1977. [Events of oligomerization in transformations of life cycles of ixodid ticks]. *In:* Znachenie polimerizatsii i oligomerizatsii v evolutsii. Leningrad, pp. 25–28. [In Russian]

Belozerov, V.N. 1981. [Ecological rhythms in ixodid ticks and their regulation]. *Parasitol. sbornik,* 30: 22–46. [In Russian]

Belozerov, V.N. 1982. Diapause and biological rhythms in ticks. *In*: F.D. Obenchain and R. Galun (Eds.). Physiology of Ticks. Pergamon Press, Oxford, pp. 469–500.

Belozerov, V.N. 1985a. [Diapause, its place and role in life cycles, mechanisms]. *In:* N.A. Filippova (Ed.). Tayezhny kleshch *Ixodes persulcatus*. Leningrad, pp. 214–219. [In Russian]

Belozerov, V.N. 1985b. [Data on biology of the tick *Rhipicephalus pumilio*]. *In:* Pyataya vsesoyuznaya akarol. konferentsiya (Abstracts). Frunze, p. 30–31. [In Russian]

Belozerov, V.N. 1988. [Photoperiodism and seasonal development of ixodid ticks]. Abstract of the Doctor of Biological Sciences thesis. St. Petersburg State University, 40 pp. [In Russian]

Belozerov, V.N. 1990. [Peculiarities of induction and termination of egg diapause in *Ixodes ricinus*]. *In:* Dostizheniya meditsinskoy entomologii i akarologii (Materialy X kongressa vsesoyuznogo entomol. obshchestva). Leningrad, pp. 72–74. [In Russian]

Belozerov V.N. 1991. Evolution of life cycles in ticks (Ixodidae) due to climate seasonality. *In*: F. Dusbabek and V. Bukva (Eds). Modern Acarology. Prague. Vol. 2, p. 135–139.

Belozerov, V.N. 1995a. [Characteristics of parameters in two-step photoperiodic reaction controlling seasonal development of *Ixodes ricinus* nymphs (Acarina: Ixodidae)]. *Parazitologiya,* 29: 240–249. [In Russian]

Belozerov, V.N. 1995b. [Photoperiodic control of development and diapause in nymphs of the Taiga tick *Ixodes persulcatus* (Ixodidae)]. *Parazitologiya,* 29: 101–104. [In Russian]

Belozerov, V.N. 1995c. Preliminary data on the influence of photoperiod on development of *Haemaphysalis parva* (Acarina, Ixodidae). *Entomol. obozrenie,* 74: 152–154. [In Russian]

Belozerov, V.N. 1998. Role of two-step photoperiodic reaction in the control of development and diapause in the nymphs of *Ixodes persulcatus. Russian J. Zool.,* 2: 414–418.

Belozerov, V.N. 1999. Dormancy in the life cycles of ixodid ticks and their adaptations to predictable and unpredictable environmental changes. *In*: Acarology IX. Vol. 2 (Symposia), USA, Columbus, Ohio, p. 53–56.

Belozerov, V.N. 2006. Seasonal adaptations in the life cycles of the Acari (mites and ticks): comparative and evolutionary aspects. *In*: XII International congress of Acarology (Book of Abstracts). Amsterdam, p. 29.

Belozerov, V.N. 2007. [Distribution of dormant stages in the life cycles of the Acari (Chelicerata: Arachnida) in comparison with mandibulate arthropods (Insects and Crustaceans)]. *Trudy biol. nauchno-issled. instituta St. Peterburgskogo gos. universiteta*, 53: 193–233. [In Russian, Engl. Summary]

Belozerov, V.N. 2008. Diapause and quiescence as two main kinds of dormancy and their significance in life cycles of mites and ticks (Chelicerata: Arachnida: Acari). Part 1. Acariformes. *Acarina,* 16: 79–130.

Belozerov, V.N. 2009. New aspects in investigations of diapause and non-diapausing types of dormancy in insects and other arthropods. *Entomol. Review,* 89: 127–136.

Belozerov, V.N., Bogdanov, V.E. and Kvitko, N.V. 1966. [Seasonal changes in temperature reactions of *Ixodes ricinus* engorged females]. *Vestnik Leningrad. universiteta* (Ser. biology), 3: 37–44. [In Russian]

Belozerov, V.N., Fourie, L.J., Van der Lingen, F.J., and Kok, D.J. 1996. Photoperiodic control of developmental diapause in nymphs of the Karoo paralysis tick *Ixodes (Afrixodes) rubicundus* Neum. (Ixodidae). *In:* Acarology IX (Proc. IX Intern. Congr. Acarol.), USA, 1996, vol. 1, p. 677–680.

Belozerov, V.N., Fourie, L.J., and Kok, D.J. 2003. Photoperiodic control of developmental diapause in nymphs of prostriate ixodid ticks (Acari: Ixodidae). *Exp. Appl. Acarol.,* 28: 163–168.

Belozerov, V.N. and Il'in, Yu.A. 1974. [Combination of long-day and short-day processes in photoperiodic control of development of larvae and nymphs in the tick *Ixodes ricinus*]. *In:* Materialy VII konferentsii vsesoyuznogo entomol. obshchestva. Leningrad, pt. 1: 204–205. [In Russian]

Belozerov, V.N. and Il'in, Yu.A. 1981. [Pecualirities of regulation of larval-nymphal metamorphosis in the tick *Ixodes ricinus* L. (Acarina, Ixodidae) under replacement of photoperiodic regimens]. *Trudy biol. nauchno-issled. instituta Leningradskogo universiteta,* 31: 143–160. [In Russian]

Belozerov, V.N. and Kvitko, N.V. 1965. [Main features of photoperiodic reaction in ticks *Dermacentor marginatus* Sulz. (Ixodidae)]. *Zool. zhurnal,* 44: 363–372. [In Russian]

Belozerov, V.N. and Lamanova, A.I. 1967. [Initiation of winter diapause and the reaction to day length in *Dermacentor marginatus* in Central Kazakhstan]. *Med. parasitologiya i parazit. bolezni*, 36: 464–469. [In Russian]

Belozerov, V.N. and Luzev, V.V. 1974. [Relationship between the behaviour and development of larvae and nymphs of *Haemaphysalis longicornis* Neum. and photoperiodic conditions]. *Parazitologiya,* 8: 515–523. [In Russian]

Belozerov, V.N. and Mikhailova, Z.A. 1966. [Diapause of larvae in the tick *Ixodes ricinus* L. and its dependence on environmental conditions. 2. Interaction of tick maintenance before and after their feeding in processes controlling the diapause of engorged larvae]. *Zool. zhurnal,* 45: 543–550. [In Russian]

Belozerov, V.N. and Mourad, M.G. 1977. [Photoperiodic regulation of nymphal diapause in the tick *Hyalomma anatolicum* Koch]. *Entomol. obozrenie,* 56: 495–504. [In Russian]

Belozerov, V.N. and Naumov, R.L. 2002b. Nymphal diapause and its photoperiodic control in the tick *Ixodes scapularis. Folia parasitol.* (Prague). 49: 314–318.

Belyaeva, N.S. and Ryabova, I.N. 1971. [Life cycles of ixodid ticks in the southern part of Khabarovsk territory]. *In*: Voprosy geografii Dalnego Vostoka. Khabarovsk, pp. 302–326. [In Russian]

Berdyev, A.B. 1973. [Materials on the developmental cycle of *Rhipicephalus turanicus* B. Pom. in natural biotopes of Turkmenia]. *In:* Parasity zhivotnykh v Turkmenii. Ashkhabad, pp. 5–15. [In Russian]

Berdyev, A.B. 1974. [About developmental cycle of *Hyalomma anatolicum excavatum* in Turkmenia]. *Med. parasitologiya i parasit. bolezni*, 43: 38–43. [In Russian]

Berkvens, D.L., Pegram, R.G. and Brandt, J.R.A. 1995. A study of the diapausing behaviour of *Rhipicephalus appendiculatus* and *Rhipicephalus zambeziensis* under quasi-natural conditions in Zambia. *Medical and Veterinary Entomology*, 9: 307–315.

Bregetova, N.G. 1956. *Gamazovye kleshchi (Gamazoidea).* [Gamasid mites]. Moscow-Leningrad, 247 pp. [In Russian]

Brendonck, L. 1996. Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). *Hydrobiologia*, 320: 85–97.

Broufas, G. 2002. Diapause induction and termination in the predatory mite *Euseius finlandicus* in peach orchards in northern Greece. *Exper. Appl. Acarology,* 25: 921–932.

Burg, J.G. 2001. Seasonal activity and spatial distribution of hostseeking adults of the tick *Dermacentor variabilis*. *Medical and Veterinary Entomology,* 15: 413–421.

Danks, H.V. 1987. *Insect dormancy: an Ecological Perspective*. Biol. Survey of Canada, Monograph Series, No. 1, 439 pp.

Danks, H.V. 1991. Life cycle pathways and the analysis of complex life cycles in insects. *Canad. Entomologist,* 123: 23–40.

Danks, H.V. 1999. The diversity and evolution of insect life cycles. *Entom. Science,* 2: 651–660.

Dautel, H. and Knülle, W. 1998. The influence of physiological age of *Argas reflexus* larvae (Acari: Argasidae) and of temperature and photoperiod on induction and duration of diapause. *Oecologia,* 113: 46–52.

Dautel, H. and Knülle, W. 2006. Investigation into the diapause and cold hardiness in *Ixodes ricinus* eggs. In: XII International congress of Acarology (Book of Abstracts). Amsterdam, p. 46–47.

Dautel, H., Dippel, C., Kämmer, D., Werkhausen, A., and Kahl, O. 2008. Winter activity of *Ixodes ricinus* in a Berlin forest. *International Journal of Medical Microbiology*. 298, Suppl. 1: 50–54.

Dogiel, V.A. 1954. *Oligomerizatsiya gomologichnykh organov kak odno iz glavnykh napravleniy evolutsii zhyvotnikh* [Oligomerization of homologous organs as one of the main pathways of animal evolution]. Leningrad, 368 pp. [In Russian]

Doube, B.M. 1975. The biology of the Kangaroo tick, *Ornithodoros (Pavlovskyella) guerneyi* Warburton (Acarina: Argasidae), in the laboratory. *J. Med. Entomol.* 12: 240–243.

Drew, M.L. and Samuel, W.M. 1985. Factors affecting transmission of larval winter ticks, *Dermacentor albipictus* (Paccard), to moose, *Alces alces* L., in Alberta, Canada. *Journal of Wildlife Diseases,* 21: 274–282.

Drew, M.L. and Samuel, W.M. 1989. Instar development and disengagement rate of engorged female winter ticks, *Dermacentor albipictus* (Acari: Ixodidae), following single- and trickle-exposure of moose *(Alces alces). Exper. Appl. Acarology,* 6: 89–196.

Drummond, R.O. 1967. Seasonal activity of ticks (Acarina: Metastigmata) on cattle in Texas. *Ann. Ent. Soc. Amer.,* 60: 439–447.

Emme, A.M. 1953. [Some problems in the theory of insect diapause]. *Uspekhy sovremennoy biologii*, 35: 395–421. [In Russian]

Estrada-Peňa, A., Pegram, R.G., Barré, N., and Venzal J.M. 2007. Using invaded range data to model the climate suitability for *Amblyomma variegatum* (Acari: Ixodidae) in the New World. *Exp. Appl. Acarol*., 41: 203–214.

Evans, G.O. 1992. *Principles of Acarology*. CAB International, UK, 563 pp.

Faasch, H. 1967. Beitrage zur Biologie der einheimischen Uropodiden *Uroobovella marginatra* Koch und *Uropoda orbicularis* Müller, und experimentelle Analyse ihres Phoresieverhalten. *Zool. Jahrb., Syst.,* 94: 521–608.

Filippova, N.A. (Ed.). 1985. *Tayezhny kleshch Ixodes persulcatus Schulze. Morphologiya, sistematika, ekologiya, meditsinskoe znachenie*. Leningrad, 416 p. [In Russian]

Fourie, L.J., Belozerov, V.N. and Needham, G.R. 2001. *Ixodes rubicundus* nymphs are short-day diapause-induced ticks with termolabile sensitivity and desiccation resistance. *Medical and Veterinary Entomology,* 15: 335–341.

Fujimoto, K. 1993. Effect of photoperiod on the attachment and development of immature *Ixodes persulcatus. Japan J. Sanit. Zool.,* 44: 271–277.

Fujimoto, K. 2003. The host-seeking and feeding activities of a new generation of *Amblyomma testudinarium* nymphs (Acari : Ixodidae) in summer observed under experimental conditions. *Med. Entomol. Zoology*, 54: 395–397.

Goddard, J. 1992. Ecological studies of adult *Ixodes scapularis* in central Missisipi: questing activity in relation to time of year, vegetation type and meteorological conditions. *J. Med. Entom*., 29 (3): 501–506.

Gotoh, T., Yamaguchi, K. and Mori, K. 2004. Effect of temperature on life history of the predatory mite *Amblyseius* (*Neoseiulus*) *californicus* (Acari: Phytoseiidae). *Exper. Appl. Acarology*, 32: 15–30.

Guglielmone, A.A. 1994. The seasonal occurrence of *Amblyomma triguttatum triguttatum. Acarologia,* 35: 107–113.

Guglielmone, A.A. and Moorhouse, D.E. 1986. The effect of photoperiod on the development of *Amblyomma triguttatum. J. Med. Entom.*, 23: 274–278.

Gurney, W.S.C., Crowley, P.H. and Nisbet, R.M. 1991. Locking life cycles onto seasons: Circle-map models of population dynamics and local adaptation. *Journ. Mathemat. Biology*, 30: 251–279.

Gurney, W.S.C., Crowley, P.H. and Nisbet, R.M. 1994. Stage-specific quiescence as a mechanism for synchronizing life cycles to seasons. *Theoretical population biology*, 46: 319–343.

Gilyarov, M.S. and Bregetova, N.G. (Eds.). 1977. *Opredelitel' kleshchey, obitayushchikh v potchve. Mesostigmata* [Identification Keys of soil-dwelling mites Mesostigmata]. Leningrad, 718 pp. [In Russian]

Harris, J.A. 1973. Structure and dynamics of a cave population of the Guano mite, *Uroobovella coprophila* (Womersley). *Australian Journal of Zoology,* 21: 239–275.

Hartenstein, R. 1962. Life histories of *Pergamasus crassipes* and *Amblygamasus septentrionalis* (Parasitidae). *Ann. Ent. Soc. Amer.*, 55: 196–202.

Helle, W. and Sabelis, M.W. (Eds.). 1985. *Spider mites. Their biology, Natural Enemies and Control.* Amsterdam. Elsevier. Vol. 1B, 458 p.

Hodek, I. 1996. Diapause development, diapause termination and the end of diapause. *Europ. Journal of Entomology*, 93: 475–487.

Hodek, I. 2002. Controversial aspects of diapause development. *Europ. Journ. of Entomology,* 99: 163–173.

Hoogstraal, H. 1956. *African Ixodoidea. I. Ticks of Sudan*. Wash., 1101 pp.

Houck, M.A. and OConnor, B.M. 1991. Ecological and evolutionary significance of phoresy in the Astigmata. *Annual Review of Entomology,* 36: 611–636.

Karg, W. 1971. Acari (Acarina), Milben. Unterordung Parasitiformes (Anactinochaeta). Die freilebenden Gamasina (Gamasides), Raubmilben. *In:* Die Tierwelt Deutschlands. Teil 59. VEB G. Fischer Verlag, Jena. 475 s.

Karg, W. 1989. Acari (Acarina), Milben. Unterordung Parasitiformes (Anactinochaeta). Uropodina Kramer, Schildkrötenmilben. *In:* Die Tierwelt Deutschlands. Teil 67. VEB G. Fischer Verlag, Jena. 203 s.

Klompen, H., Lekveishvili, M. and Black, W.C. 2007. Phylogeny of parasitiform mites (Acari) based on rRNA. *Molecular Phylogenetics and Evolution,* 43: 936–951.

Kolonin, G.V., Pikunov, D.G., Basylnikov, V.I. et al. 1976. [Hibernation of ixodid ticks on wild ungulate animals of the Maritime territory]. *Zool. zhurnal,* 55: 1253–1255. [In Russian]

Koštal, V. 2006. Eco-physiological phases of insect diapause. *Journal of Insect Physiology,* 52: 113–127.

Koulianos, S. and Schwarz, H.H. 1999. Reproduction, development and diet of *Parasitellus fucorum* (Mesostigmata, Parasitidae), a mite associated with bumblebees (Hymenoptera, Apidae). *Journ. Zool*., 248: 267–269.

Krasinskaya, A.L. 1961. [Morpho-biological pecualiarities of the post-embbryonic development of uropodid mites in the Leningrad Region]. *Parazitol. sbornik,* 20: 108–147. [In Russian]

Labruna, M.B., Amaku, A., Metzner, J.A., Pinter, A., and Ferreira, F. 2003. Larval Behavioral Diapause Regulates Life Cycle of *Amblyomma cajennense* (Acari: Ixodidae) in Southeast Brazil. *J. Med. Entomol*. 40: 170–178.

Lange, A.B. 1984. [Subtype Chelicerata]. *In*: M.S. Gilyarov (Ed.). Zhizn' zhivotnykh. Moscow. Vol. 3: 8–108. [In Russian]

Lehtinen, P.T. 1991. Phylogeny and zoogeography of the Holothyrida. *In*: F. Dusbabek and V. Bukva (Eds.). Modern Acarology, vol. 2. SPB Academic, Prague, pp. 101–113.

Lindquist, E.E. 1984. Current theories on the evolution of major groups of Acari and on their relationship with other groups of Arachnida, with consequent implications for their classification. *In*: D.A. Griffiths and C.E. Bowman (Eds.). Acarology VI, vol. 1. Ellis Horwood, pp. 28–36.

Lindsay, L.R., Barker, I.K., Surgeoner, G.A. et al. 1995. Survival and development of *Ixodes scapularis* under various climate conditions in Ontario. *Journ.Med. Entomol.,* 32: 143–152.

Liu, J.Z., Liu, Z.N., Zhang, Y. et al. 2005. Biology of *Dermacentor silvarum* (Acari: Ixodidae) under laboratory conditions. *Exper. Appl. Acarology*, 36: 131–138.

Loew, J. 1964. Über den Einfluss der Photoperiode auf die Metamorphose von *Ixodes ricinus. Angew. Parasitol.*, 5: 3–13.

Lord, C.C. 1995. Seasonal activity of nymphal *Ixodes scapularis* in different habitats of New Jersey. *Journ. Med. Entomol.,* 32: 66–70.

MacDonald, I.L. and Zuchini, W. 1997. *Hidden Markov and other models for discrete-valued time series*. Chapman and Hall, London.

Madder, M., Speybroeck, N., Brandt, J., Tirrry, L., Hodek, I., and Berkvens, D. 2002. Geographic variation in diapause response of adult *Rhipicephalus appendiculatus* ticks. *Exper. Appl. Acarol.,* 27: 209–221.

Madder, M., Speybroeck, N., Brandt, J., and Berkvens, D. 1999. Diapause induction in adults of three *Rhipicephalus appendiculatus* stocks. *Exp. Appl. Acarogy,* 23: 961–968.

Mihm, J.A. and Chiang, H.C**.** 1976. Laboratory studies of the life cycle and reproduction of some soil- and manure-inhabiting predatory mites (Laelaptidae). *Pedobiologia*, 16: 353–363.

Mourad, M.G. and Belozerov, V.N. 1976. [Photoperiodical control of adult diapause in ticks *Hyalomma anatolicum*]. *In:* Tretiya vsesoyuznaya konferentsiya po teoreticheskoy i prikladnoy akarologii (Abstracts). Tashkent*,* p. 73–74. [In Russian]

Müller, H.J. 1970. Formen der Dormanz bei Insekten. *Nova Acta Leopoldina,* N.F., 35: 7–27.

Müller, H.J. 1992. *Dormanz bei Arthropoden.* G. Fischer Verlag, Jena. 289 s.

Murrell, A., Dobson, S.J., Walter, D.E., Campbell, N.J.H., Shao, R., and Barker, S.C. 2005. Relationships among the three major lineages of the Acari (Arthropoda : Arachnida) inferred from small subunit rRNA: paraphyly of the parasitiformes with respect to the opilioacariformes and relative rates of nucleotide substitution. *Invertebrate. Syst*., 19, 383–389.

Nawar, M.S., Shereef, G.M. and Ahmed, M.A. 1993**.** Effect of food on development, reproduction and survival of *Chiropturopoda bakeri* (Acarina: Uropodidae). *Exp. Appl. Acarol.,* 17: 277–281.

Nel'zina, E.N. 1951. *Krysiny kleshch* [The rat mite]. Moscow, 100 pp. [In Russian]

Nel'zina, E.N.and Danilova, G.M. 1960. [*Rhipicephalus schulzei* as inhabitant of the little suslik burrows (*Citellus pygmaeus* Pall.)]. *Med. parasitologiya i parasit. bolezni,* 29: 291–300. [In Russian]

Norton, R.A., Kethley, J.B., Johnston, D.E., and OConnor, B.M. 1993. Phylogenetic perspectives on genetic systems and reproductive modes of mites. *In*: D.L. Wrensch and M.A. Ebbert (Eds.). Evolution and Diversity of Sex Ratio in Insects and Mites. Chapman and Hall, New York, pp. 8–99.

Norval, R.A.I. 1977a. Ecology of the tick *Amblyomma hebraeum* in the eastern province of South Africa. 1. Distribution and seasonal activity. *J. Parasitol.*, 63: 734–739.

Norval, R.A.I. 1977b. Ecology of the tick *Amblyomma hebraeum* in the eastern province of South Africa. 2. Survival and development. *J. Parasitol*., 63: 740–747.

Nosek, J., Lichard, M., Sztankay, M. 1967. The ecology of ticks in the Tribec and Hronsky Inovec mountains. *Bull. Org. Mond. Sante*, 36 (Suppl. 1): 49–59.

Ogden, N.H., Lindsay, L.R., Beauchamp, G, Charron, D., Maarouf, A., O'Callaghan, C.J., Waltner-Toews, D., and Barker, I.K. 2004. Investigation of relationships between temperature and developmental rates of tick *Ixodes scapularis* (Acari: Ixodidae) in the laboratory and field. *J. Med. Entomol.,* 41: 622–633.

Oliveira, P.R., Borges, L.M.F., Leite, R.C., and Freitas, C.M.V. 2003. Seasonal dynamics of the Cayenne tick, *Amblyomma cajennense*, on horses in Brazil. *Medical and Veterinary Entomology,* 17: 412–416.

Overmeer, W.P.J. 1985. Diapause. *In*: W. Helle and M.W. Sabelis (Eds.). Spider Mites. Their Biology, Natural Enemies and Control. Vol. 1B, Elsevier, Amsterdam, pp.95–102.

Ozman-Sullivan, S.K. 2006. Life history of *Kampimodromus aberrans* as predator of *Phytoptus avellanae* (Acari: Phytoseiidae, Phytoptidae). *Exper. Appl. Acarology,* 38:15–23.

Patrick, C.D. and Hair, J.A. 1975. Ecological observations on *Dermacentor albipictus* in eastern Oklahoma. *J. Med. Entomol.*, 12: 393–394.

Pegram, R.G., Mwaze, E.T., Zivkovic, D. and Jongejan, F. 1988. Morphognetic diapause in *Amblyomma variegatum* (Acari: Ixodidae). *Medical and Veterinary Parasitology,* 2: 301–307.

Pomerantzev, B.I. 1948. [Main directions of the evolution in Ixodoidea]. *Parasitol. sbornik,* 10: 5–19. [In Russian]

Pomerantzev, B.I. 1950. *Iksodovye kleshchi* [Ixodid ticks (Ixodidae)]. Fauna of the USSR, Paukoobraznyye 4 (2). Leningrad, 224 pp. [In Russian]

Putman, W.L. 1962. Life-history and behaviour of the predacious mite *Typhlodromus caudiglans* (Phytoseiidae) in Ontario, with notes on the prey of related species. *Can. Entomol.*, 94: 163–177.

Radinovsky, S., 1965. The biology and ecology of granary mites of the Pacific Northwest. Life history and development of *Leiodinychus krameri* (Uropodidae). *Ann. Ent. Soc. Amer.,* 58: 259–267.

Radovsky, F.J. 1994. The evolution of parasitism and the distribution of some Dermanyssoid mites (Mesostigmata) on vertebrate hosts. *In*: M.A. Houck (Ed.). Mites: Ecological and evolutionary analyses of life-history patterns. Chapman & Hall, p. 186–217.

Randolph, S E. 1993. Climate, satellite imagery and the seasonal abundance of the tick *Rhipicephalus appendiculatus* in southern Africa: a new perspective. *Medical and Veterinary Entomology*, 7: 243–58

Randolph, S.E**.** 1997. Abiotic and biotic determinants of the seasonal dynamics of the tick *Rhipicephalus appendiculatus* in South Africa. *Medical and Veterinary Entomology*, 11: 25–37.

Randolph, S.E. 2004. Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology*, 129: 37–65.

Randolph, S.E. and Rodgers, D.J. 1997. A generic population model for the African tick *Rhipicephalus appendiculatus. Parasitology,* 115: 265–279.

Randolph, S.E., Green, R.M., Hoodless, A.N., and Peace, M.F. 2002. An empirical quantitative framework for the seasonal population dynamics of the tick Ixodes ricinus. *Intern. Journal for Parasitology,* 32: 979–989.

Razumova, I.V. 1965. [Seasonal course of diapause appearance in *Dermacentor pictus* and factors of its stimulation]. *Med. parasitologiya i parasit. bolezni*, 1965, 34: 46–52. [In Russian]

Rechav, Y. 1981. Ecological factors affecting the seasonal activity of the brown ear tick *Rhipicephalus appendiculatus*. *In:* G.B. Whitehead and J.D. Gibson (Eds). Tick Biology and Control, South Africa, Grahamstown University, pp. 187–191.

Rubina, M., Hadani, A. and Ziv, M. 1982. The life cycle of the tick *Hyalomma anatolicum excavatum* maintained under field conditions in Israel. *Rev. Elev. Med. Vet. Pays Trop*., 35: 255–264.

Rudzinska, M. 1998. Life history of the phoretic predatory mite *Arctoseius semiscissus* (Acari: Ascidae) on a diet of sciarid fly eggs. *Exper. Appl. Acarology*, 22: 643–648.

Saito Y, 1990. Life-history and feeding habit of *Typhlodromus bambusae,* a specific predator of *Schizotetranychus celarius*. *Exp. Appl. Acarology,* 10: 45–51.

Sapozhnikova, F.D. 1964. [Photoperiodic response of the mite *Typhlodromus (Amblyseius) similis* (Acarina: Phytoseiidae)]. *Zool. zhurnal,* 43: 1140–1144. [In Russian]

Saulich, A.Kh. and Musolin, D.L. 2007. [Yearth seasons: diversity of seasonal adaptations and ecological mechanisms controlling seasonal development of true bugs (Heteroptera) in the temperate climate]. *Trudy biol. nauchno-issled. instituta St. Peterburgskogo gos. universiteta*, 53: 25–106. [In Russian, Engl. Summary]

Schwarz, H.H. and Koulianos, S. 1998. When to leave the brood chamber? Routes of dispersal in mites associated with burying beetles. *Exper. Appl. Acarology*, 22: 621–631.

Serdyukova, G.V. 1951. [Hibernation of *Ixodes ricinus* eggs in conditions of Karelian peninsula]. *Doklady AN SSSR*, 81: 1171–1173. [In Russian]

Short, N.J. and Norval, R.A.I. 1981. Regulation of seasonal occurrence in the tick *Rhipicephalus appendiculatus* Neum. *Tropical Animal Health and Production,* 13: 19–26.

Smith, C.N. and Cole, M. 1941. Effect of length of day on the activity and hibernation of the American dog tick *Dermacentor variabilis*. *Ann. Ent. Soc. Amer.*, 34: 426–431.

Sonenshine, D.E. 1988. Diapause in tick vectors of desease. *In*: The Arboviruses: epidemiology and ecology, vol.1, p. 219–243.

Sonenshine, D.E. 1991. *Biology of Ticks.* Oxford. Vol. 1, 472 pp; 1993, Vol. 2, 488 pp.

Speybroeck, N., Madder, M., Van den Bossche, P. Mtambo, J., Berkvens, N., Chaka, G., Mulumba, M., Brandt, J., Tirry, L., and Berkvens D. 2002. Distribution and phenology of ixodid ticks in southern Zambia. *Medical and Veterinary Entomology,* 16: 430–441.

Speybroeck, N., Lindsey, P.J., Billiouw, M., Madder, M., Lindsey, J. K., and Berkvens, D.L. 2006**.** Modeling diapause termination of *Rhipicephalus appendiculatus* using statistical tools to detect sudden behavioral changes and time dependencies. *Environ. Ecol. Stat.,* 13: 69–87.

Sutherst, R.W. and Bourne, A.S. 1991. Development, survival, fecundity and behavior of *Haemaphysalis longicornis* at two locations in Southeast Queensland. *Intern. J. Parasitol*., 21: 661–672.

Sutherst, R.W. and Moorhouse, D.E. 1972. The seasonal incidence of ixodid ticks on cattle in Southeastern Queensland. *Austral. J. Agr. Res*., 23: 195–204.

Tauber, M.J., Tauber, C.A. and Masaki, S. 1986. *Seasonal Adaptations of Insects.* Oxford Univ. Press, 411 pp.

Ushatinskaya, R.S. 1976. Insect dormancy and its classification. *Zool. Jahrbücher, Abt. Systematik*, 103: 76–97.

Vail, S., Smith, G. and Lord, C. 1994. Population biology of *lxodes scapularis,* the vector of Lyme Disease in the Eastern and North Central United States. *Parasitic and Infectious Diseases,* 19: 263–277.

Van Houten, Y.M., and Veenendaal, R.L. 1990. Effects of photoperiod, temperature, food and relative humidity on the induction of diapause in the predatory mite *Amblyseius potentillae. Exp. Appl. Acarol.,* 10: 111–128.

Veerman, A. 1985. Diapause**.** *In*: W. Helle and M.W. Sabelis (Eds). Spider Mites. Their Biology, Natural Enemies and Control. Amsterdam, Vol. 1A, pp. 279–316.

Veerman, A. 1992. Diapause in phytoseiid mites: a review. *Exper. Appl. Acarology,* 14: 1–60.

Wainstein, B.A. 1977. [Family Phytoseiidae (Gamasina)]. *In*: M.S. Gilyarov and N.G. Bregetova (Eds.). Opredelitel' kleshchey, obitayushchikh v potchve. Mesostigmata. Leningrad, pp. 226–243. [In Russian]

Walker, J.B., Keirans, J.E. and Horak, I.G. 2000. *The Genus Rhipicephalus (Acari, Ixodidae). A guide to the brown ticks of the world.* Cambridge Univ. Press, 635 pp.

Walter, D.E. and Proctor, H.C. 1999. *Mites. Ecology, Evolution and Behaviour.* UNSW Press, CABI Publishing, 322 pp.

Weigmann, G. 1996. Zonation and phenology of Uropodina (Uropodidae) in marine littoral saltmarches. *In*: Acarology IX (Proceedings), vol. 1, Prague, Academia, p. 603–605.

Wilkinson, P.R. 1968. Phenology, behaviour and host-relations of *Dermacentor andersoni* in outdoor "rodentaria" and in nature. *Canad. J. Zool.*, 46: 677–589.

Wilkinson, P.R. 1973. Termination of diapause in laboratory-reared *Dermacentor andersoni* adults. *Proc. 3rd Intern. Congr. Acarology*. Praha, pp. 803–806.

Wright, J.E. 1969. Photoperiodic induction of diapause in larvae of the winter tick, *Dermacentor albipictus. Ann. Entomol. Soc. Am.*, 62: 285–287.

Wright, J. E. 1971. Relationship of seasonal activity of *Dermacentor albipictus* (Acarina: Ixodidae) to photoperiod: a laboratory study. *Ann. Entomol. Soc. Am.,* 64: 1456–1458.

Yuval, B. and Spielman, A. 1990. Duration and regulation of the developmental cycle of *Ixodes dammini. Journ. Med. Entomol.,* 27: 196–201.

Zakhvatkin, A.A. 1948. [Systematics of the genus *Laelaps* (Acarina, Parasitiformes) and problems of its epidemiological significance]. *Parazitol. sbornik,* Leningrad, 10: 51–76. [In Russian]

Zakhvatkin, A.A. 1952. [Division of Acarina in orders and their places in the system of the Chelicerata]. *Parazit. sbornik*, Leningrad, 14: 5–46. [In Russian]

Zaslavsky, V.A. 1972. [Two-step photoperiodic reactions as the basis for elaboration of a model of photoperiodic control of development in arthropods]. *Entomol. obozrenie,* 52: 217–239. [In Russian]

Zaslavsky, V.A. 1974. [The principles of photoperiodic control of arthropod development]. *Zhurnal obshchey biologii,* 35: 717–736. [In Russian]

Zaslavsky, V.A. 1984. *Photoperiodicheskiy i temperaturny control razvitiya nasekomych* [Photoperiodic and temperature control of insect development]. Leningrad, 180 pp. [In Russian] [In English: Springer, 1987]

Zein-Eldin, E.A. 1956. Studies on the legume mite, *Petrobia apicalis. Journal of Economical Entomology*, 49: 291–296.

Zemskaya, A.A. 1951. [Biology and development of the poultry mite *Dermanyssus gallinae* due to its epidemiologic importance]. *Zool. zhurnal,* 30: 51–63. [In Russian]

Zemskaya, A.A. 1973. *Parazyticheskye gamazovye kleshchy i ikh meditsinskoye znachenie* [Parasitic gamasid mites and their medical importance]. Moscow, 167 pp. [In Russian]

Zhang, Y.X., Zhang, Z.Q., Liu, Q.Y., and Lin, J.Z. 1999. Biology of *Typhlodromus bambusae* (Acari: Phytoseiidae), a predator of *Schizotetranychus nanjingensis* (Acari: Tetranychidae) injurious to bamboo in Fujian, China. *Systematic and Applied Acarology,* 4: 57–62.

Zhmaeva, Z.M. 1948. [The tick *Haemaphysalis concinna* in Primor'e]. *In:* Voprosy kraevoy, obshchey i exper. parazitologii. Moscow, pp. 46–55. [In Russian]