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

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ABSTRACT: A review of available data on diapause and quiescence as two main kinds of dormancy in life histories of the acariform mites (Arachnida: Acari), particularly of Oribatida, Astigmata and Prostigmata, and on the role of both dormant states in life cycles of these mites due to their adaptations to predictable (seasonal) and unpredictable (irregular) environmental changes. The survival during periods of adverse conditions is enabled in the acariform mites by both kinds of dormancy controlled either endogenously (diapause), or exogenously (quiescence), and also in both ways. However, the role of dormancy in the control of life-cycle seasonality, well known for diapause, is doubtful for the common form of quiescence, arisen as a direct response to unfavorable environmental changes at any life-cycle stage, and called as "the stage-independent quiescence". However another form, ascertained in insects as "the post-diapause quiescence", and characteristic of many acariform mites also, is of great significance for seasonal time-adjustment in both these groups of terrestrial arthropods. Similar function is characteristic probably of "the stage-specific quiescence" ascertained theoretically for insects. Representatives of the Acari reveal a high diversity of the life-cycle seasonal control systems (from plesiotypic types with numerous diapause-capable ontogenetic stages up to apotypic types with single or limited number of such stages, also enabling the reliable life-cycle seasonality). An adaptation to environmental unpredictability in mites with plesiotypic systems is based on overlapping flexible life cycles (with capability of some stages for quiescence also), while in mites with apotypic systems — on special resting stage (often with phoretic dispersal). A combination of diapause and post-diapause quiescence known in many extant prostigmatid mites is suggested as an initial ancestral state of dormancy in adaptations of acariform mites (particularly of Oribatida) to adverse environmental changes. Such a hypothesis gives reasonable solution of controversial interpretations concerning the nature of dormancy in extant oribatid mites during their hibernation.

KEY WORDS: Acariform mites, life history, life-cycle control, dormant stages, diapause, quiescence, post-diapause quiescence

INTRODUCTION

The alternation of active and dormant stages is an especially conspicuous trait in life histories of invertebrate animals (in particular of insects, crustaceans, arachnids and other arthropods) that determines duration, phenology, flexibility and other peculiarities of their life cycles. Such alternation of activity and dormancy in life cycles of arthropods reflects deep adaptations to both regular and irregular environmental changes in their habitats. For all animal and plant inhabitants of the Earth with its regular and predictable (seasonal, daily), and unpredictable (occasional, irregular) changes of environment, the ability for dormancy is of great vital importance. Naturally, this phenomenon (with all its diversity in destinations, mechanisms and manifestations) has attracted much attention from biologists of different profile, dealing with different invertebrates, in particular with terrestrial and aquatic arthropods.

Concerning the Acari (mites and ticks), some aspects of this question, particularly the number and distribution of dormant stages in their life cycles, and possible evolutionary changes in their ontogenetic systems connected with adaptation to climate seasonality, were considered in two my previous papers (Belozerov 2007, 2008b), as well as in a review on the ontogenetic phenomenon of calyptostasy, characteristic of the prostigmatid parasitengone mites and related in some degree to seasonal adaptations (Belozerov 2008a). In the present paper I continue this study, paying attention to the diversity of dormant states in the Acari, in particular to the presence and properties of two main kinds of dormancy (diapause and quiescence) in their life cycles, and to relationships (ecophysiological and evolutionary) between these opposite types of dormant state. As before, I try to retain a comparative and partly taxonomic approach to the problem during the description and analysis of data concerning dormancy in mites and ticks. The first part of this review is devoted to representatives of the acariform mites (Oribatida, Astigmata and Prostigmata), as they are considered in the system used by Evans (1992) and Kethley (1982). Some comments due to the contemporary taxonomy of Acariformes (Mironov and Bochkov, in press) are given in footnotes.

GENERAL CHARACTERISTICS OF DORMANCY IN ARTHROPODS

The ability to survive in a dormant state is a widespread feature among invertebrates, as is shown in the comprehensive review of Cáceres (1997). It is characteristic (either in inducing and enforcing the dormancy at regular ontogenetic instars, or in producing the specialized resting stages, or both) of most groups of invertebrates from the protists and sponges through the hemichordates. The highest capability for survival in dormant state is found in the rotifers, nematodes and

tardigrades, but our best insights into the nature and regularities of dormancy relate to the arthropods (particularly insects and crustaceans).

It is essential that dormant stages in arthropods enable not only their survival during unfavorable harsh seasons, but also the conformity of their life cycles with environmental changes, in particular the synchronization of active development and reproduction with favorable seasons (Lees 1955; Danilevsky 1961; Saunders 1982, 2002; Zaslavsky 1984; Tauber et al. 1986; Danks 1987; Saulich 1999; Saulich and Volkovich 2004 — for insects; Elgmork 1980; Alekseev 1990; Dahms 1995; Alekseev and Starobogatov 1996; Brendonck 1996; Fryer 1996; Hairston and Cáceres 1996; Cáceres 1997; Alekseev et al. 2007 — for crustaceans). The same concerns the representatives of chelicerate arthropods, in particular the acarines (Belozerov 1982, 2007; Veerman 1985, 1992; Walter and Proctor 1999; Wohltmann 2001) and spiders (Schaefer 1987), as well as other invertebrates. From an ecological standpoint, dormant stages are much more common among invertebrates from terrestrial and fresh-water habitats than in taxa with exclusively or mainly marine representatives (for the crustaceans see Alekseev and Starobogatov 1996; Hairston and Cáceres 1996). Among parasitic arthropods, dormant stages are characteristic only of temporary parasites, and are almost absent in permanent parasites.

Two basic types of dormancy differ in their fundamental ecophysiological properties (Shelford 1929), as recognized now by all students of this phenomenon in insects (Emme 1953; Lees 1955; Danilevsky 1961; Müller 1970, 1992; Ushatinskaya 1973, 1976; Tauber et al. 1986; Danks 1987; Saunders 2002; Saulich and Volkovich 2004; Vinogradova 2007; etc.) and crustaceans (Alekseev 1990; Alekseev and Starobogatov 1996; Brendonck 1996; Cáceres 1997; Alekseev et al. 2007; etc.). *Quiescence* is an arrest of development or activity arisen under direct impact of either adverse environmental conditions, or deficit of vitally essential factors, that is due to some exogenous constraints, and recovered after cessation of their action. By contrast, *diapause* is an anticipated arrest of development or activity arisen according to internal program, either genetically fixed, or induced through effect of token factors signalling in time an approach of unfavorable conditions, and eliminated by special mechanism of reactivation. Due to their main traits, quiescence was considered by Müller (1970) as a consecutive

dormancy, while diapause as a prospective dormancy (Ushatinskaya 1973, 1976; Saulich 1999). Whenever quiescence has a seasonal basis, it is called non-diapause dormancy (Tauber et al. 1986; Siepel 1994). It is possible also to call quiescence an enforced dormancy, while diapause is an induced dormancy (Gurney et al. 1994).

Diapause is the more diverse of the two. Classified according to destination it may be either a *hibernation* (winter diapause), or an *aestivation* (summer diapause); according to the approached ontogenetic instar it may be an *egg (embryonic), larval, nymphal or adult (imaginal, reproductive)* diapause; while according to the program it is *obligatory* or *facultative.* According to ecological and physiological mechanisms of its incidence and termination diapause was classified by Müller (1970) into three types of dormancy: *parapause* (an obligatory hereditary arrest of development or activity arising in every generation at a species-specific instar), *oligopause* (an arrest of development or activity with control of its induction, maintenance and termination, similar for all these periods), and *eudiapause* (also a facultative arrest of development or activity with different controlling mechanisms of induction and termination, *e.g.* through photoperiod and chilling respectively). In general, this subdivision of diapausing arrests is recognized until now (Saunders 2002), though there have been modifications both by Müller (1992) himself, and by other entomologists (Mansingh 1971; Thiele 1973; Ushatinskaya 1973; 1976; etc.). There is a meaning, however, that elaborated systems hardly are viable (Danks 1987; Koštal 2006).

The majority of insects enter diapause at a single species-specific stage in their life cycle. However some of them are capable of generating dormancy in different (two or more), but also species-specific instars. There are known cases in which diapause is combined with quiescence in different instars and stages of life cycle, or at the same instar, *e.g.* in species with summer diapause followed by the autumn-winter quiescence after diapause termination (Katsoyannos et al. 2005). Such a combination is more common, undoubtedly, in insects with winter diapause followed by winter quiescence (Koštal 2006).

While not as diverse as diapause, the state of quiescence varies somewhat with regard to its destination and mechanisms. According to destination it can be either hibernating, or aestivating, while in respect to the generating factors (cold,

drought, lack of oxygen etc.) it may be considered as a case similar to some forms of anabiosis (cryptobiosis), *e.g.* cryobiosis, anhydrobiosis, anoxybiosis etc. (see Schmidt 1955; Keilin 1959; Ushatinskaya 1990; Clegg 2001), though with not as deep an inhibition of metabolism (Alekseev et al. 2007). It is well known that quiescence is possible, as a rule, at any instar (or stage), and this type of dormancy has been termed "stage-independent quiescence" (Gurney et al. 1981). However, special "stage-specific quiescence" is capable of synchronizing particular cases of seasonal development (instead of diapause) at some specific stage of the life cycle (Gurney et al. 1984).

Unfortunately, information on peculiarities of quiescence is rather limited. Nevertheless there are some important data giving a possibility for fresh view and new interpretation of relations between diapause and quiescence. These data are from analytical reviews by Hodek (1996, 2002) and Koštal (2006) evidencing that quiescence may have a very close relationship with diapause, being its terminal phase (**the post-diapause quiescence**) that ensures the maintenance of a dormant state (with covert potentiality for development after the end of diapause) and enables the continuation of development after adequate environmental changes. More extensive consideration of this form of quiescence, its properties and significance will be given below.

The number, position and character of dormant stages (diapause or/and quiescence), as well as their relationships during ontogenesis, are of great importance for phenology and duration of life cycles in insects and other arthropods. Their development, according to the length of generations, can be multivoltine (= polyvoltine, with some generations per year), univoltine (= monovoltine, with one generation per year), semivoltine (= biennial, with one generation per two years) and many-years-long (= perennial, with one generation per three and more years). In special analysis of ecological mechanisms controlling diapause, Saulich (1999) has shown that all known cases of multivoltine development of insects are controlled only by facultative diapause, while mechanisms of univoltine development are very diverse, being provided not only with obligatory diapause, but also with facultative diapause and also with combination of some different types of dormancy. More prolonged developmental cycles were not considered by her (Saulich 1999), however it is possible to suggest (taking into attention the sea-

sonal control of life cycles in ixodid ticks — see Belozerov 1982, 1988), that biennial and perennial life cycles, involving some instars with one-year duration, are comparable by their regulation with univoltine development, inasmuch as they are also controlled by different mechanisms that can combine a number of various dormant stages.

DORMANCY IN THE ACARI

From an analysis of dormant stages distribution in mites and ticks, given in my previous reviews (Belozerov 2007, 2008b), the main peculiarities of life cycles in Acari (their duration, voltinism, phenology, flexibility etc.) depend on the function of a special, species-specific **System of Seasonal Control (SSC)**, the organizing role in which is enabled by dormant stages of diapausing character. Quiescence was not a focus of these reviews, though its possibility in the acariform mites was suggested there (Belozerov 2007). Plesiotypic traits of seasonal life cycles in the Acari are characterized by complex SSC with numerous dormant stages enabling the control of perennial, semivoltine and monovoltine development, while apotypic traits are expressed in the presence of reduced SSC with limited number of dormant stages for control of mono- and polyvoltine development. Thus, the evolution of seasonal adaptations in the Acari was considered to occur through transformation of ancestral polymeric SSC (with numerous dormant stages) into oligomeric and monomeric systems (with reduced number of diapausing stages).

Though quiescence and diapause seem to be quite distinct, they can be difficult to distinguish in practice for the majority of arthropods due to the lack of adequate ecological and physiological investigations. This concerns not only chelicerate arthropods, such as acarines and other arachnids, but even their relatives, mandibulate arthropods (*i.e.* insects and crustaceans), which are investigated much better, though with nonequal attention in regard to diapause (the main subject of investigations in insects) and quiescence (studied in crustaceans somewhat more than in insects). No wonder, therefore, that the evaluation given by L. Brendonck (1996) for crustaceans, that "the extent to which dormancy … is controlled endogenously (diapause) or exogenously (quiescence) is not always clear", fits for chelicerates to a much higher degree. For Acari, one could almost substitute the phrase "is always unclear".

Therefore, it is important to continue the comparative and evolutionary study of dormancy in

the Acari, particularly in regard to distribution of diapause and quiescence among phylogenetically different taxa, and the association of these two dormant states with different ontogenetic instars of their life cycles. This first of two reviews deals with the acariform mites — Oribatida, Astigmata and Prostigmata. In regard to all these groups, and particularly the latter polyphyletic order (Prostigmata), I follow in general the classifications used by Evans (1992) and Kethley (1982). Updated information on the taxonomy and phylogeny of acariform mites can be found in Mironov and Bochkov (in press) and my footnotes.

ORIBATIDA

Oribatid mites (**Oribatida = Cryptostigmata**) represent a basal taxon of ordinal (Evans 1992) or subordinal level (Norton 1994) that includes more than 9000 species. Among major groups of Acari, this taxon is peculiar in expressing the full set of conservative plesiotypic traits related to life history, life cycles, and other biological features, due to its historical connection with the soil environment (Lange 1984; Norton 1994). They retain the ancestral acariform life cycle including the egg and six postembryonic instars — prelarva (PLa), larva (La), protonymph (PN), deutonymph (DN), tritonymph (TN), and adult (Ad)[*]. An important plesiotypic trait, common to all oribatids, is their dispersal during the adult instar. Most oribatid mites from temperate forest soils (as an ancient and relatively plesiotypic, if not original, habitat — as noted by Norton 1994) possess rather low developmental rates and fecundity. The generation time of these mites usually is one or two years, though besides such typical cases of monovoltine and semivoltine development many oribatid mites reveal either more rapid (bivoltine and polyvoltine), or more slow (perennial) life cycles. The life-history attributes of most oribatids seem typical of organisms considered to be "K-selected", though species with more rapid development demonstrate rather "r-selected" properties (according to "r/K" system of life strategies — see MacArthur and Wilson 1967, Pianka 1970), while especially slow-developing mites with perennial life cycles may be considered as possessing the "A"-attributes (Convey 1994; Peck et al. 2006), according to the "r-K-A" triangle system of life histories developed by Southwood (1977) and Greenslade (1983). In regard to the last group it is necessary to say that

terrestrial life-history strategies in extreme environments fit the features of adversity ("A-selection") characterized by long life cycles, slow overall growth rates, low reproductive output, low dispersal ability and high investments in survival adaptations.

The prolonged development is characteristic especially of more derived oribatid mites (*e.g.* 4.2 years as in *Ceratozetes kananaskis* — Mitchell 1977a), while evolutionary specialized mites, as a rule, have generations of much less duration (in some cases one month and shorter as in *Oppiella nova* — Woodring and Cook 1962) (see also Lebrun 1971; Weigmann 1975; Mitchell 1977b; Luxton 1981; Grishina 1991).

Thus, the interspecific diversity of developmental rates in oribatid mites reveals some dependence on their phylogenetic and taxonomic position. However, it is more important ecologically, that most oribatid mites are characterized by intraspecific variability, flexibility and plasticity of their development due to variable and extended duration of their instars according to environmental and seasonal conditions, which results in overlapping generations, though they are nevertheless efficiently synchronized through the presence of some or many dormancy-capable, hibernating or aestivating instars within their life cycles. Though this is a typical property of most oribatid mites from temperate habitats, it is especially characteristic of slow-developing oribatids living in hard climatic conditions with extreme seasonality revealed in short cool summer and long winter, as the terrestrial mite *Alaskozetes antarcticus* from maritime Antarctic (Convey 1994, 1996; Block and Convey 1995; Peck et al. 2006), the littoral Arctic mite *Ameronothrus lineatus* (Søvik and Leinaas 2003; Søvik et al. 2003; Søvik 2004), the mountain North Norwegian *A. lapponicus* (Tilrem 1994) and the alpine Austrian mite *Oromurcia sudetica* (Schatz 1985). Each instar in these mites is capable of hibernation and takes the whole year for its development. Their life cycles may be completed therefore during 5–6 years only (Table 1). It is very important that the flexibility and variability in total cycle length, as well as their overlapping, allows *A. antarcticus* (similar to other polar arthropods — see Danks 1999a, 2006) to survive environmental unpredictability of irregular repeated changes of harsh and mild conditions, that might be fatal for less flexible species (Convey 1994). Unfortunately information concerning peculiarities of life cycles in tropical or even sub-

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[*] These abbreviations (Ad, Eg, PLa, La, PN, DN and TN) will be used throughout this paper.

Table 1. Different types of dormancy (quiescence/diapause) in dormant stages of the oribatid mites.

Mite species	Main traits	Dormant stages	Type of dormancy		Remarks	References
			Quiescence	Diapause		
1. *Alaskozetes antarcticus*	Maritime Antarctic oviparous mite with **perennial** life cycles (5–6 years or more).	**Eg, La, PN, DN, TN, Ad**	Pre-hatch, pre-moult and pre-reproduction quiescence in winter.	–	Oviposition, hatch and moulting synchronized after hibernation by increase of temperature in early summer. There are pre-diapause traits before hibernation.	Convey 1994, 1996; Block, Convey 1995
2. *Ameronothrus lineatus*	Holarctic littoral ovoviviparous mite with **perennial** cycle (5–6 years or more) (Spitsbergen) or **monovoltine** flexible life cycle (North Germany).	Spitsbergen: **L, PN, DN, TN** and **Ad**	**DN, TN, Ad** The pre-moult and pre-reproduction quiescence in winter.	–	Larviposition and moulting synchronized after hibernation by increase of temperature in early summer.	Søvik, Leinaas 2003; Søvik, Leinaas, Ims, Solhoy 2003; Søvik 2004
		N. Germany: PN, DN, TN and **Ad**	Quiescence of PN and DN (?)	Winter diapause of DN, **TN, Ad** after migration	Presence of autumn pre-diapause migration of DN, TN and Ad into hibernating places.	Bücking et al. 1998
3. *Madheinia wilsoni*	Continental Antarctic larviparous mite with **perennial** cycle (3 years or more).	**PN, DN, TN, Ad**	The pre-moult, pre-reproduct. Quiescences in winter.	–	Moulting and reproduction synchronized after hibernation by increase of temperature in early summer.	Marshall, Convey 1999
4. *Ameronothrus marinus*	European littoral ovoviviparous mite with **monovoltine** flexible life cycle.	In N. Germany DN, **TN, Ad**	DN ?	**Winter diapause of TN** and **Ad**	Presence of autumn pre-diapause migration of TN and Ad into hibernating places.	Bücking et al. 1998
		In S. Britain **TN** (mainly)	–	**Winter diapause of TN**	–	Pugh, King 1986
5. *Ameronothrus maculatus*	Supralittoral mite from N. Germany with **monovoltine** rigid life cycle.	DN, TN, Ad	**DN**, Ad ?	**Winter diapause of TN**	Rigid mechanism of diapause in TN with pre-diapause migration to hibernating places.	Bücking et al. 1998
6. *Ameronothrus lapponicus*	Lichen-dwelling mite from mountains of North Norway with **perennial life cycle (4–6 years)**.	**L, PN, DN, TN** and **Ad**	?	?	–	Tilrem 1994 (cited from Bucking et al. 1998)
7. *Achipetria holomonensis*	Soil-dwelling mite from Greece (with **semivoltine** cycle).	**L, PN, DN, TN** and **Ad**	Inactivity of all stages at low temperatures in winter.	?	Restoration of development by temperature increase above 10°C.	Stamou 1989
8. *Achipetria coleoptrata*	European forest soil-dwelling mite with **semivoltine** cycle.	L, PN, **DN, Ad**	?	?	–	Luxton 1981
9. *Damaeus clavipes*	European forest soil-dwelling mite with **semivoltine** cycle.	**DN, TN, Ad**	?	?	–	Luxton 1981

Species	Characterization	Stages		Diapause	Comments	Reference
10. *Damaeus boreus*	European forest soil-dwelling mite with mono/**semivoltine** flexible cycles.	**Eg, L, PN, DN, TN** and **Ad**	?	?	—	Sitnikova 1959
11–13. *Eohypochthonius magnus, Archoplophora villosa, Quadroppia quadricarinata*	Temperate forest soil-dwelling mites from Japan with **semivoltine** cycles.	**Eg, L, PN, DN** and **Ad**	?	?	TN is non-hibernating instar.	Kaneko 1989
14. *Phthiracarus japonicus*	Inhabitant of pine needles in soil of alpine pine shrubs of Central Japan.	**L, PN, DN, TN** and **Ad**	?	?	The whole life cycle in rather cold soil of alpine zone is 4 years (or more). Duration of each stage (together with winter dormancy) is not less than one year.	Soma 1990
15. *Adoristes ovatus*	Soil-dwelling colonizer of needles of *Abies alba* (and *Picea abies*) fallen in the soil (semivolt/ biennial development).	**TN, Ad**	?	?	Egg-laying in June-July by overwintered females. The first year is completed by hibernating TN, which need the summer to transform into Ad in autumn. In Norway (Hågwar) the cycle is completed in two years.	Gourbiere et al. 1985; Lions, Gourbiere 1989; Hågwar 1998
16. *Chamobates cuspidatus*	European forest soil-dwelling mite with **monovoltine** cycles.	**DN, TN, Ad**	?	Reproductive winter diapause of adult females?	Cold reactivation of females for oviposition (Woodring, Cook 1962).	Luxton 1981
17. *Platynothrus peltifer*	Soil/litter-dwelling mite with **long life cycle** distributed in Holarctic.	In Europe: **PN, DN, TN, Ad**	?	Reproductive winter diapause of adult females	Suggested role of photoperiod for induction of adult diapause (Harding 1973). Synchronized season of oviposition (spring) and larval hatching (summer).	Block 1965; Harding 1973; Weigmann 1975; Schenker 1985
		In Siberia: **L, PN, Ad**	?	Reproductive winter diapause of adult females?	Synchronized season of oviposition (spring) and larval hatching (late summer).	Grishina 1997
18. *Steganacarus magnus*	Litter-dwelling mite from S. England with **mono-** and **semivoltine** cycles.	**PN, DN, TN, Ad**	?	Reproductive winter diapause of adult females?	Presence of oviposition delay of 3–6 months.	Webb 1977; Luxton 1981
19. *Tectocepheus velatus*	East US forest soil-dwelling mite with **semivoltine** cycle.	**PN, DN, Ad**	?	Reproductive winter diapause of adult females?	Synchronized season of egg-laying (after hibernation) and larval hatching (June-July).	Reeves (1969)
20. *Oribella* sp.	East US forest soil-dwelling mite with **semivoltine** cycle.	**PN, DN, Ad**	?	Reproductive winter diapause of adult females?	The same	Reeves 1969

21. *Pergalumna altera*	East US forest soil-dwelling mite with **monovoltine** cycle.	**Ad** (not DN and TN as in Reeves paper)	?	Reproductive winter diapause of adult females?	Regular succession of juvenal stages in summer-autumn after synchronized egg-laying in early summer.	Reeves 1969
22. *Oppiella nova*	Forest soil-dwelling mite from Eastern US with **bivoltine** life cycle.	**TN, Ad**	?	Reproductive winter diapause of adult females?	Regular succession of juvenal stages from two summer generations after synchronized egg-laying in early summer.	Reeves 1969
23. *Oppia subpectinata*	Forest soil-dwelling mite from Eastern US with **bivoltine** life cycle.	**Ad**	?	Reproductive winter diapause of adult females?	The same	Reeves 1969
24. *Scutovertex minutus*	European mite inhabiting moss-covered or on roofs of buildings. Very resistant to drought. Voltinism and generation time are unknown.	**TN, Ad**	Both adults and immatures enter immobile comatose **quiescent state under extreme dry conditions**. The reverse process occurs two hours after remoistening.	–	The quiescent state lasts at least 10 days and is generally characterized by an empty gut, guanine deposition and, in adults, by the resorption of spermatids or oocytes and eggs.	Smrž 2002
25. Undescribed ameronothrid mite from Eastern USA, similar ecologically with some African ameronothrids.	This inhabitant of small ephemeral pools in deserts of the Colorado plateau (USA) has similar case of dormancy enforced by drying of pools and terminated by watering. Life cycle is unknown.	**Ad, immatures**	In periods of drying pools these mites survive in state of quiescent, being burrowed in sediment during long period, but rapidly revive after moistening.	–	The quiescent state lasts from some days up to two years.	Norton et al. 1996

Note. Column "Dormant stages": More probable dormant stages — in bold print, less probable — in normal print.
Column "Type of dormancy": Stages of definite corresponding type of dormancy — in bold, while of probable type — in normal print.
In Tables 2–5 the notes of the same content.

tropical oribatid mites is absent or extremely scarce.

As seen in Table 1, including data on 25 different oribatid mites with life histories studied more or less thoroughly in field conditions, about half (11 species) have semivoltine (sometimes biennial) life cycles with 2–6 (mean 3.8) dormancy-capable overwintering instars, and a similar number of species (9) have rapid development (mono- and bivoltine) with 1–3 (mean 2.0) dormant instars, while only 5 polar species have perennial cycles with 4–6 (mean 5.0) dormant instars. Thus, some important traits of life histories in oribatid mites, such as duration of generations, voltinism of development, and flexibility of their life cycles, definitely depend on and are determined by the number of dormancy-capable, overwintering stages that compose together the organized System of Seasonal Control (SSC) consisting of single, some or many dormant stages (Belozerov 2007, 2008b).

These and some other characteristics of oribatid life histories (particularly the phenology) depend also on the localization of dormant stages along the chain of ontogenetic instars. It is accepted as a common rule that such stages participating in the seasonal control of life cycles in Insects, Acari and other arthropods are species-specific (Danilevsky 1961; Luxton 1981; Tauber et al. 1986; Danks 1987; Alekseev and Starobogatov; 1996; Belozerov 2007, 2008b; etc.), though with some exceptions related usually to their geographic variability. Such exceptions are known in oribatid mites also (Table 1). One is the holarctic *Ameronothrus lineatus*, which has five dormant instars and perennial life cycle in its polar populations, but only a couple of dormant instars (some adults, but mainly tritonymphs) and monovoltine life cycle in the temperate European population (see Søvik 2004; Bucking et al. 1998). Another is the European monovoltine mite *Ameronothrus marinus*, overwintering in North Germany in three instars (DN, TN, Ad), but in South Britain only as a single TN-instar (Bucking et al. 1998; Pugh and King 1986). A significant example of such geographic variability is the holarctic soil-dwelling mite *Platynothrus peltifer* with all-round common semivoltine cycles, but with different sets of overwintering instars in temperate Europe (PN, DN, TN, Ad) and continental Siberia (L, PN, Ad) (Block 1965; Grishina 1997). However, the latter case may be complicated by the existence of cryptic species in different areas (Heethoff et al. 2007).

Though some corrections may be necessary after further studies in regard to the sets of instars capable of dormancy and hibernation in the mentioned species (Table 1), and the addition of others, I believe that the above conclusion on the relationship between the number of dormant stages, and the duration and flexibility of life cycles will hold.

The exact nature of overwintering dormancy in oribatid mites (quiescence or diapause) is rarely indicated in literature and its identification is hampered by the deficit of adequate ecophysiological information. In most cases oribatologists use for this purpose, as a rule, the indefinite terms "inactive", "dormant" or "resting", avoiding strict designations. The real exceptions concern Norton (1994) who considers winter dormancy in oribatid mites as a cold-induced quiescence and manifestation of metabolic constraints at low temperatures, as well as. Convey (1996) and Søvik (2004), who studied the biology of polar oribatids with perennial life cycles (the Antarctic mite *A. antarcticus* and the littoral Arctic mite *A. lineatus* respectively), and concluded that the dormant state of numerous hibernating instars in these mites represents a quiescence enforced and terminated by the direct effect of temperature. In accordance to their opinion, there is little evidence of true diapause mediated by environmental cues in these mites due to disadvantages resulting from possible incorrect cueing of entry into or exit from diapause under these harsh and often unpredictable conditions (Convey 1996; Danks 1999a; Peck et al. 2006). For the oribatid *A. antarcticus* the term "non-diapause dormancy" was used by Young and Block (1980), and this term has found currency in cases where quiescence has a seasonal basis (Tauber et al. 1986; Danks 1987; Siepel 1994).

Nevertheless in studies of polar oribatids, some data give evidence of a diapausing nature to the overwintering state in nymphs and adults of these littoral oribatids. First is the presence of a resting pre-ecdysial (pre-moult) phase[*] in *A. antarcticus* mites that prepare for hibernation at the end of summer before the onset of cold, and is accompanied by active clearing the gut, as shown by Convey (1996). Second, the autumn migrations of

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[*] Unfortunately the real ontogenetic and physiological traits of this "pre-moult phase" are not described and not explained in the mentioned papers (Convey 1996, etc.), and I suggest that the onset of this resting state precedes the apolysis, representing the first step of moulting events, and mites overwinter therefore with no traits of morphogenetic processes.

deutonymphs and tritonymphs of *A. lineatus* to hibernating places takes place before the onset of the dormant state (the same is true in other intertidal ameronothrids, *A. marinus* and *A. maculatus,* with their "rigid diapause" according to Bucking et al. 1998). These peculiarities have allowed me (Belozerov 2007, 2008b) to use the term "diapause" for the mentioned cases of dormancy in polar oribatids with perennial life cycles, and consider this "resting pre-moult phase" as an expression of real diapause preceding the onset of apolysis (but not of ecdysis itself). Short remarks on the presence of diapause in life cycles of soil-dwelling oribatid mites, though with no special explanation and support, were given also by Grishina (1991) and some other authors.

Unfortunately, the available data (Table 1) and the above considerations of species from extreme habitats give no definite answer to the question of the real nature of dormant states in overwintering instars. Its solution needs, of course, ecophysiological data permitting the identification of quiescence (as direct response to adverse conditions) and diapause (as a programmed response to token factors signalling the approach of adverse conditions). However, such data for overwintering instars in oribatid mites are absent, or very fragmentary, sometimes conjectural or contradictory, as illustrated in Table 1, particularly by the opposite opinions of Søvik (2004) and Bucking et al. (1996) concerning the nature of dormancy in *Ameronothrus lineatus*.

A more definite and clear situation probably exists in dormancies arising in oribatid mites as a response not to low temperature, but to low humidity. The real quiescent state of such dormancy is known in nymphs and adults of the European mite *Scutovertex minutus* (inhabitants of moss on roofs of buildings) which reveal the onset of a comatose dormant state as a rapid response to drought with an immediate exit from it after moistering (Smrž 2002). The similar case of dormancy enforced by drying of small ephemeral pools in desert habitats of the Colorado plateau (USA) and swiftly terminated by pool watering is presented by an ameronothrid oribatid mite (Norton et al. 1997).

As a conclusion to this part of the paper, I should like to remind two opinions on the character of life histories of oribatid mites in extreme polar conditions. Their life histories are considered by many oribatologists (Norton 1994; Convey 1996; Behan-Pelletier 1999) as an extreme version of the typical ancestral oribatid life history that has

been preadapted to Arctic and Antarctic conditions (without special polar adaptations). However, no less possible, as was suggested by Søvik (2004), that the success of oribatid mites in polar habitats is attributable to a combination of both derived ancestral preadaptations and special derivative adaptations. The solution of this "polar" problem is quite impossible without establishing the real nature of dormancy (quiescence, diapause or their combination) in typical versions of oribatid life histories, which is still unknown. Naturally, there is a great need in further ecophysiological investigations of dormant stages in life cycles of oribatid mites from climatically different habitats, which is a difficult, but interesting and necessary task.

ASTIGMATA

The situation, quite different from the above considered Oribatida, is observed in the related, but derivative taxon **Astigmata**, a large, monophyletic order with some 75 families and 850 genera of mites, whose ancestral ecology and ontogeny involve exploitation of ephemeral temporary habitat patches and the use of phoresy on insect or vertebrate carriers to ensure dispersal for colonizing new adequate habitats (OConnor 1982). Due to some important apomorphies (mainly of morphologic and biochemical character), Astigmata are accepted as a subgroup of Oribatida (Norton 1994, 1998; Sakata and Norton 2001; Maraun et al. 2004) evolved within the oribatid mites as a paedomorphic lineage (Zachvatkin 1953; OConnor 1984). According to Norton (1998), the derivation of Astigmata has occurred within Desmonomata, one of the middle-derivative groups of Oribatida (Fig. 1), particularly within the super-
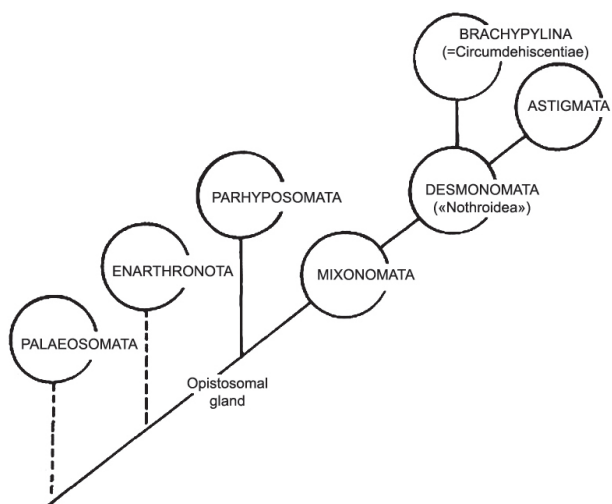

Fig. 1. Schematic relationships of major oribatid mites groups and the Astigmata (after Norton 1994).

family Malaconothroidea, confirmed later by Sakata and Norton (2001). The possibility of close relations of Astigmata and Oribatida is supported by Mironov and Bochkov (in press) in their comprehensive analysis of macrophylogeny in acariform mites. However, some other authors see no connections between Astigmata and Oribatida (Grandjean 1937; Woas 2002). For instance, the results of recent molecular investigations (Domes et al. 2007) placed Astigmata outside Oribatida, as a sister-group of the endeostigmatid mites (particularly Alicorhagiidae).

The Astigmata represent an outstanding example evidencing that life-history evolution in Acari may play a principal role in their radiation, particularly through changes of their dispersal style and instar involved. An important life-history difference that oribatid mites disperse as adults, while astigmatid mites disperse only as immatures (usually phoretic deutonymphs) is considered a key to the radiation of the Astigmata (Norton 1994).

The Astigmata includes two big groups of mites (namely the free-living Acaridia and the parasitic/symbiotic Psoroptidia) differing in many biological and ecological properties, but similar in some essential traits in their life-history strategies. They all are mostly characterized by small size, rapid development and rather high reproduction potential. In contrast to Oribatida, where K-attributes are typical, the Astigmata in general belongs to "r"-selected lineage of life-history strategies, irrespective of "r/K" (MacArthur and Wilson 1967; Pianka 1970), or "r-K-A" their models (Southwood 1977; Greenslade 1983).

The systems controlling life cycles in Astigmata (in contrast to Oribatida) have apotypic traits of reduction (oligomerization), usually with single (Acaridia) or no dormant instars (Psoroptidia). In Acaridia the function of dormancy, often combined with the function of dispersal through phoresy, belongs usually only to the heteromorphic deutonymph (hypopus) that can be facultative or obligatory. The presence of facultative DN between PN and TN, or its failure, is determined at previous instars (La and PN) by an interaction of environmental and genetic factors (Knülle 1999, 2003) that evidences the diapausing traits of its dormant state. These resistant heteromorphic DNs, capable for survival and dispersal, are typical for the major part of Acaridia exploiting ephemeral habitats (Athias-Binche 1991; Houck and OConnor 1991; Houck 1994).

Really, 21 of 25 species of these mites presented in Table 2 possess deutonymphal hypopodes (either phoretic, or sedentary) with diapausing properties and in some cases with real traits of post-diapause quiescence (Fig. 2). Such species are different taxonomically, being representatives of the whole set of families. Only in four species the function of dormancy seems belong to the TN (instead of DN, which may be lost or retain phoretic function only). Probably in these cases, particularly in marine hemisarcoptid *Hyadesia fusca* (Bucking 1999; Bucking et al. 1998) the resting TN is characterized by the state of quiescence (Table 2), and only in the acarid *Naiadacarus arboricola* (from tree-holes in North America) does the TN have the traits of winter diapause, while the DN enables a summer dispersal by phoresy synchronized with eclosion of dipterous carriers (Fashing 1977, 1994).

Thus, terrestrial temperate species of Acaridia are characterized by the presence of a single immature dormant instar adapted for survival and dispersal (mainly as heteromorphic non-feeding DN with vestigial mouthparts and some morphologic adaptations for phoresy). The rapid polyvoltine development of these mites may be broken through formation of a resting hypopus and restored after its transformation into an active TN followed by Ad. The regularities and mechanisms controlling the onset and maintenance of dormant state in hypopodes were studied by many authors, but especially deep insight into these mechanisms has been taken by W. Knülle and coworkers from the FU, Berlin (Knülle 1987, 1991a,b, 1995, 2003; Corente and Knülle 2003; etc.) in a series of investigations on the glycyphagid *Lepydoglyphus destructor*, and perfectly presented by Danks (1994, 1999b) in his scheme of different developmental pathways of this mite (Fig. 2) in diapausing (with long or short diapause at DN instar) and non-diapausing direction (with direct transformation of PN into TN without DN), as well as with the obvious presence of post-diapause quiescence in this acaridian mite. Nevertheless, the mechanisms of termination of hypopus stage and its transformation into the TN instar require further thorough investigations.

Dormant hypopodes of Acaridia serve usually as tools for survival in conditions of unpredictability in their ephemeral habitats, though in species associated with insects, the hypopodes reveal seasonal adaptations synchronizing the hibernation and dispersal of both associates (Table 2). An es-
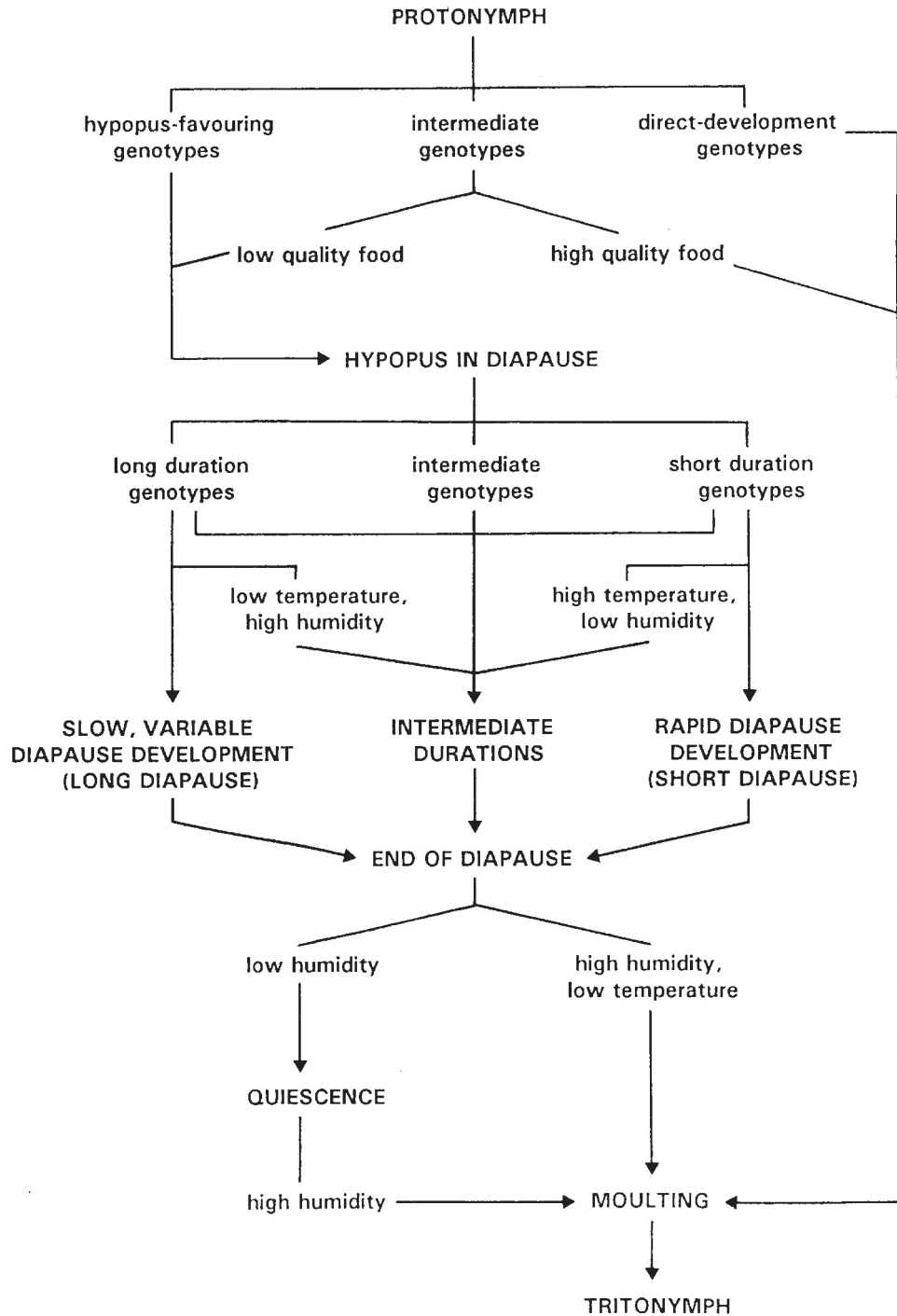
PROTONYMPH

hypopus-favouring genotypes — intermediate genotypes — direct-development genotypes

low quality food — high quality food

→ HYPOPUS IN DIAPAUSE

long duration genotypes — intermediate genotypes — short duration genotypes

low temperature, high humidity — high temperature, low humidity

SLOW, VARIABLE DIAPAUSE DEVELOPMENT (LONG DIAPAUSE) — **INTERMEDIATE DURATIONS** — **RAPID DIAPAUSE DEVELOPMENT (SHORT DIAPAUSE)**

END OF DIAPAUSE

low humidity — high humidity, low temperature

QUIESCENCE

high humidity ⟶ MOULTING

TRITONYMPH

Fig. 2. Life-cycle pathways in *Lepidoglyphus desrtuctor* (Astigmata: Glyciphagidae) (after Danks 1999, according data by Knülle 1991).

pecially original example is represented by the mentioned acarid *Naiadacarus* that inhabits water-filled tree-holes and hibernates there as TN (in the state of seasonal diapause) with other stages (in the state of quiescence), while its DN serves as a phoretic tool for summer dispersal on dipterous insects (Fashing 1977, 1994). Some traits of adaptation for hibernation are known in the TN of saprophagous *Tyrophagus*, aggregating in autumn within hay patches (Sorokin 1946). Similar divergence in stages adapted for predictable and unpredictable environmental changes is quite probable in other families of Acaridia, though the key role in them (Norton 1994) belongs to the phoretic DN (hypopus). Dormancy of seasonal character is characteristic here for species which associate with insects possessing obvious seasonal life cycles. First place belongs, of course, to the family

Table 2. Different types of dormancy (quiescence/diapause) in dormant stages of astigmatid mites.

Mite species	Main traits	Dormant stages	Type of dormancy		Remarks	References
			Quiescence	Diapause		
ACARIDIA						
1. *Histiostoma heinemanni* 2. *H. laboratorium* (Histiostomatidae)	Polyvoltine mites from decaying vegetation (1), from *Drosophila* cultures (2) etc. with generation = 4–8 day.	**DN (=Hypopus)**	–	**DN**	Dispersal is realized, as in most Acaridia, by resistant hypopodes (heteromorphic DN).	Perron 1954; Hill, Deahl 1978
3. *Hornosianoetus mallotae* (Histiostomatidae)	Filtering (monovoltine?) mite from water-filled tree-holes in N. America	**DN (=Hypopus)**	–	**DN**	Phoretic hypopodes are formed during summer season (May–June) for dispersal on insects and partly for hibernation.	Fashing 1994
4. *Tyrophagus putrescentiae* 5. *Tyrophagus similis* (both Acaridae) 6. *Glycyphagus domesticus* 7. *Glycyphagus privatus* * 8. *Glycyphagus ornatus** 9. *Lepydoglyphus destructor* 10. *Gohieria fusca* (all five Glycyphagidae)	Polyvoltine mites (from soil, litter, nests, stored products) with generation = 10–15 days. Usually have one morph of facultative hypopus. Species noted by * have dimorphic hypopodes (phoretic and sedentary).	**DN (=Hypopus)**	–	**DN**	Sedentary hypopodes are more resistant than phoretic hypopodes, but both are adapted for unpredictable environmental changes. TN of *L.destructor* have post-diapause quiescence (Danks 1999).	Boulanova 1937; Barker 1967, 1968; Hart, Fain 1988; Knülle 1991, 2003; Kasuga, Amano 2003
11. *Ctenocolletacarus* sp. (Acaridae)	Monovoltine mite with symbiotic and phoretic contacts to Stenotritid bees *Ctenocolletes* in Australia.	**DN (=Hypopus)**	–	Hibernating diapause of **DN** in bee cells together with diapausing bee prepupa	The transformation of PN to DN is initiated by defecations of metamorphized bee larvae. Hibernated phoretic hypopodes are dispersed in spring by eclosed adult bees.	Houston 1987
12. *Kennethiella trisetosa* (Winterschmidtiidae)	Monovoltine mite associated with solitary wasp *Ancistrocerus antilope*.	**DN (=Hypopus)**	–	Hibernating diapause of **DN**	Phoresy of hypopodes on wasps and further development (until formation of next DN phoretic) on larval/pupal wasp stages.	Cowan 1984
13. *Ensliniella kostylevi* (Winterschmidtiidae) and other Ensliniellinae mites associated with solitary vespids	Bivoltine mite associated with larval and pupal *Allodynerus rossi* in nests of this solitary vespid. Both generations have DN, but summer DN are phoretic, while autumn DN overwinter on host prepupa or pupa.	**DN (=Hyppous)**	–	Hibernating diapause of DN from autumn generation	Appearance of summer phoretic DN is synchronized with discharge of tree sap attracting adult wasps used by mites for phoresy.	Klompen, Lukoschus, OConnor 1987; Houck, OConnor 1991
14. *Calvolia fraxini* (Winterschmidtiidae)	Inhabitant of galleries of scolytid *Leperisinus fraxini*, with bivoltine development (summer generation without DN, autumn generation. with hibernating hypopodes).	**DN (=Hyppous)** of autumn generation	–	Hibernating diapause of **DN** of second, autumn generation	Diapause of phoretic DN (hypopodes) from August to May.	Kielczewski, Seniczak 1972

Species (Family)	Description		Quiescence	Diapause / Overwintering	Remarks	References
15. *Kurosaia jiju* (Winterschmidtiidae)	Mite from Japan, phoretic as DN on *Anterhynchium* into the wasp cell when the wasp is laying eggs.	DN (=Hypopus)	—	Overwintering phoretic DN	DN molted to TN in host cell, where TN and Ad feed on hemolymph of wasp prey and host larvae, whereas La and PN scavenge debris and feces. Mite eggs hatch on prepupal host and reach PN on host pupae. DN appear before host eclosion, and attach to overwintering adult hosts.	Okabe, Makino 2003
16. *Sancassania* (=*Caloglyphus*) *berlesei* (Acaridae)	Saprophagous polyvoltine mite with generation = 6–8 days and facultative resistant hypopus.	DN (=Hypopus)	—	Diapause of facultative DN	—	Timms et al. 1981
17. *Chaetodactylus krombeini* (Chaetodactylidae) 18. *Horstia virginica* (Acaridae)	Polyvoltine mites in cells of solitary bees.	DN (=Hypopus)	—	DN ?	—	Krombein 1967
19. *Hemisarcoptes cooremani* 20. *H. coccophagus* (Hemisarcoptidae)	Mites feeding on diaspidid scale insects and phoretic as facultative hypopodes on *Chilocorus* beetles.	DN (=Hypopus)	—	?	Termination of DN instar occurs after its phoresy on beetles.	Houck, OConnor 1991; Ji et al. 1996
21. *Carpoglyphus lactis* (Carpoglyphidae) 22. *Tyrophagus longior* (Acaridae)	Polyvoltine nidicoles and domestic mites from stored food reserves etc. (generation time in *Carpoglyphus* is 29–66 days). They have TN or PN as dormant stages (instead of the lost DN).	TN	TN ?	—	In *C. lactis* TN is a dominant stage during depression period of mite culture (simultaneously with single hypopodes). TN in *T. longior* dominates in autumn hays.	Sorokin 1946; Zyromska-Rudzka 1964; Wharton 1976
23. *Naiadacarus arboricola* (Acaridae)	Saprophagous larviparous mite from water-filled tree-holes in N. America with hibernation of all instars (with exception of phoretic DN). Dominant hibernating stage is diapausing TN synchronizing overlapping life cycles.	(L) PN,TN, (Ad)	Winter quiescence of L, PN and Ad	Winter diapause of TN, while DN ia a facultative seasonal phoretic hypopus occuring in May-June for dispersal on flies.	The accumulation of TN as main hibernating instar begins from middle summer, while synchronized spring moult into adults occurs after winter reactivation. Phoretic DN appear in summer for dispersal.	Fashing 1977, 1994
24. *Hyadesia fusca* (Hemisarcoptidae)	European littoral mite with two overlapping summer generations (in N. Germany). Generations = 46–73 days. Hypopus is absent.	(L, PN), TN, Ad	The cold quiescence of TN and Ad	—	—	Bucking et al. 1998; Bucking 1999
25. *Czenspinskia lordi* (=*Calvolia transversostriata*) (Winterschmidtiidae)	—	TN	—	Obligate winter diapause of TN	Development of tritonymphs stops in August until next spring (even at lab. conditions).	Dosse, Schneider 1957

PSOROPTIDIA					
1. *Sarcoptes scabiei* (Sarcoptidae) 2. *Psoroptes* sp. (Psoroptidae)	Polyvoltine parasites in mammalian skin (Ss), and on skin surface (Ps), with generation of 10–12 days.	–	–	Due to infestation through direct host contact, there are no dormant stages in mites.	Dubinin 1954; Meleney 1985; Arlian et al. 1989
3. *Chorioptes bovis* (Psoroptidae)	Polyvoltine parasite on surface of mammalian skin (generation of 21–28 days).	–	–	The same	Dubinin 1954; Meleney 1985
4. *Otodectes cynotis* and other species of this genus (Psoroptidae)	Permanent ear parasites of cats with polyvoltine development and short survival off-host for TN and Ad (about 6–7 days).	–	–	The same	Sweatman 1958; Otranto et al. 2004
5. *Proctophyllodes corvorum* 6. *Analgopsis corvinum*	Feather mites of jackdaws with reproduction during nesting period of hosts (VII–IX). Monovoltine mites with hibernating nymphs.	PN, TN	?	?	Zekhnov 1946
7–8. *Pterolichus obtusus* and *P. solutocurtus*	Feather mites of hens.	TN, Eg	–	TN, Eg (?)	Dubinin 1951
9. *Bdellorhynchus polymorphus*	Feather mite of ducks.	TN, Eg	–	TN, Eg (?)	Dubinin 1951
10. *Pterodectes bilobata*	Feather mite of skylarks.	Eg	–	Eg (?)	Dubinin 1951
11. *Monojoubertia microphylla*	The chaffinch *Fringilla coelebs* reveals summer increase of this feather mite population (with domination of immature instars) and accumulation of females for spring and autumn migration.	Ad ?	Ad ?	?	Mironov 2000
12–15. *Dermatophagoides pteronyssinus, D. evansi, D. farinae, D. microceras* (Pyroglyphidae)	Polyvoltine nidicoles and domestic mites from food reserves, house dust etc. With generation of 18–26 days. Important allergenic mites.	PN, TN	(PN), TN	–	Wharton 1976; Dubinina, Pletnev 1977; Mumcuoglu, Lutsky 1990
16. *Suidasia medanensis* (=*pontifica*) (Suidasiidae)	Tropical domestic allergenic mite with generation = 13 days and adult life 50 days. DN is absent.	TN ?	Better survival of TN than other instars	–	Mercado et al. 2001

In spring and autumn migration the mite population is represented mainly by females, while immature instars reveal predomination during summer nesting of *F. coelebs*. During migrations the diapause in mites was not observed.

There is no DN (Hypopus) in life cycle of this pyroglyphid mites.

There is no DN (Hypopus) in life cycle of this mite (as well as in Pyroglyphidae).

Winterschmidtiidae, where the main function of phoretic hypopodes with diapausing dormancy includes synchronizing seasonal development of these mites and their carriers (Table 2). Good examples of this synchronization by means of phoretic hypopodes are represented by polyvoltine *Kurosaia jiju* associated with the wasp *Anterhynchium* in Japan, by two bivoltine mites, *Calvolia fraxini* (associated with scolytid beetles) and *Ensliniella kostylevi* (associsated with solitary vespids), both of which produce phoretic hypopodes only in their autumn generation, and monovoltine *Kennethiella trisetosa*, also associated by development and dispersal with solitary vespids (Table 2).

The Psoroptidia, as permanent parasites and symbionts (paraphages) of vertebrate animals (birds and mammals), differ from their free-living relatives (Acaridia) by the obligate absence of deutonymphal instar in their nymphal phase (they retain only PN and TN). This enables more rapid and non-interrupted development, especially due to favorable microclimate within their habitats (on or inside the skin or plumage of hosts). From parasitological data on mammalian psoroptids (Dubinin1954; Meleney1985; etc) it is known that these mites, as a rule, do not need special resistant stages for long off-host survival (because the infestation of hosts occurs through their direct contact) and demonstrate therefore no programmed seasonality in their life histories. The same infestation modus concerns the avian psoroptids, though they reveal some traits of seasonality in their micropopulations, due to regular and manifold seasonal events of their hosts (migrations, nesting, moulting etc.), and the ability of some instars in feather mites (teleonymphs, adults, and eggs) for seasonal hibernating arrest (Dubinin 1951). Quite possibly, such a difference between avian and mammalian psoroptids is connected with the origin of Psoroptidia as parasites of birds, with a secondary radiation onto mammals with a dominance of host-parasite relations (OConnor 1994).

For feather mites representing the huge complex Analgesoidea (Dubinin 1951) with its three main superfamilies — Analgoidea, Pterolichoidea, and Freyanoidea (Proctor 2003), it has been shown that in those species of mites associated with migratory and non-migratory birds that nest in temperate zones of the Northern hemisphere, reproduction of mites and their active development occur during spring-summer season, while the hibernating "reserve" is formed in autumn by two dormant stages — TN and eggs (Dubinin 1951). Such dormant stages, considered by Dubinin (1951) as diapausing, are typical, for instance, for *Trouessartia corvina* (a parasite of corvine and passerine birds) and *Bdellorhynchus polymorphus* (duck's parasite), as well as for *Pterolichus obtusus* and *P. solutocurtus* (hen's parasites) (Dubinin 1951; Dubinin and Vasilev 1958); while *Proctophyllodes corvorum* and *Analgopsis corvinum* (parasites of jackdaws) have PN and TN as dormant instars (Zekhnov 1946). All these mentioned hosts belong to the group of non-migratory birds living in temperate areas with summer and winter seasons. But some feather mites of migratory passerine birds (for instance *Pterodectes bilobata* from skylarks) overwinter only as eggs (Dubinin 1951). Comparison of migratory and non-migratory birds in their "summer" and "winter" areas is doubtless necessary for solving the questions of seasonal dynamics and changes of instar structure in populations of feather mites, as well as of their dormant instars.

The study of *Monojoubertia microphylla* conducted by Mironov (2000) has shown the regularity of seasonal dynamics in micropopulations of this feather mite on its migratory passerine host, the chaffinch *Fringilla coelebs*. During the summer nesting season in the European part of Russia, micropopulations of this mite, represented mainly by immature instars, increase both on old birds and on nestlings which are initially infested by the TN and Ad through the contact with parents; but after some decrease during the moulting of birds, the mite population increases again to be dominated by females of mites for the autumn migration, and this prevalence retained in birds recovering their nesting places during spring migration. Though all adult and immature mites on birds during both their migrations were active, as noted by Mironov (2000), and "diapause in them was not observed", such a conclusion is only suggestive (as well as the above mentioned notes of Dubinin about diapausing state of hibernating TN and eggs in other feather mites), and needs special reinvestigation.

In spite of real seasonal changes in population structure of feather mites (Zekhnov 1946; Dubinin 1951; Dubinin and Vasilev 1958; Mironov 2000; etc), it is impossible to give a clear answer about the modus of overwintering in these mites. Quite possibly, in psoroptid mites with their life style as permanent mammalian and avian parasites, the main role in their life histories belongs to symbi-

otic adaptations determining their permanent contacts and relationships with host organisms (as a milieu of the first order), but not to ecophysiological adaptations determining their relations with external environment (as a milieu of the second order). This makes seasonal adaptations to be of low necessity. The abundance and location of vane-dwelling feather mites depend mainly on the host behavioural and physiological state, particularly on activity of uropygial glands (Blanco and Frias 2001; Proctor 2003). Similar opinions were impressed already by OConnor (1984): "As mites adapt to a completely parasitic existence in a relatively stable "host" environment, the selective pressures which originally favored life-history traits such as fast generation time and good dispersal ability become somewhat reversed and coevolutionary processes begin to dominate".

As we have seen, immature instars (DN or TN) possessing in **Acaridia** the functions of survival (through dormancy expressed in the form of diapause and apparently of post-diapause quiescence) and dispersal (through phoresy) enable, as a rule, adaptations to environmental non-predictability of their ephemeral habitats (though in mites associated with insects the mentioned functions enable the adaptation to seasonal peculiarities of their insect associates). By contrast, **Psoroptidia**, due to domination of parasitic or mutualistic adaptations, are characterized by the loss of ability for dormancy and dispersal in some instars of their life cycles (as well as by the obligate absence of the DN), though in feather mites the ability for dormancy in some instars (not as diapause, but sooner as quiescence determined by host-parasite relationships) may be retained.

PROSTIGMATA (= Trombidiformes)[*]

Representatives of the order **Prostigmata** by their morphological, biological and ecological diversity, as well known, overcome all others acariform mites. This huge and diverse taxon (with many unsolved systematic problems) includes more than 14000 species related to some 6–8 subordinal groups of different size and importance. The available data on life cycles and dormant stages in prostigmatid mites (due to their diversity in regard to life histories) are presented in Tables 3–5 in accordance to the taxonomic systems used by Evans (1992) and Kethley (1982). The Table with respective data on the parasitengone mites is available in my paper on calyptostasy (Belozerov 2008a).

The most derived traits are peculiar for the suborder **Endeostigmata** represented usually by small hygrobiotic mites from humid habitats (forest soil/litter, moss etc), though others in this group are xerophiles from deserts habitats. Some of them retained the ancestral acariform type of development with two free-living active larvae and three free-living active nymphs (as *Speleorchestes),* though majority retain the single active larva, that follows the embryonalized prelarva, while some others (*Neonanorchestes*) demonstrate a modified metamorphosis with alternating calyptostasy, that is more characteristic of another suborder of prostigmatid mites, namely Parasitengona (Wohlmann 2001; Belozerov 2008a). According to the latest molecular studies (Domes et al. 2007) the astigmatid mites may be considered as a sister-group of the endeostigmatid mites (fam. Alicorhagiidae), and get its origin therefore not from apotypic oribatids, but from plesiotypic endeostigmatid mites.

We have more data on the life history for the suborder **Eupodina** including different terrestrial predaceous and phyto/myceto/saprophagous mites from superfamilies Eupodoidea (with families Eupodidae, Penthaleidae, Rhagidiidae), Tydeoidea (Tydeidae, Ereynetidae[**]), Bdelloidea (Bdellidae, Cunaxidae), and the bdelloid-like marine mites (predatory and phytophagous) from the superfamily Halacaroidea (Table 3).

Especially full information among Eupodina concerns the herbivorous penthaleid mites, *Halotydeus destructor* ("redlegged earth mite") and some cryptic species of "blue oat mites" of the genus *Penthaleus,* important pests of plant cultures and grasses in Australia and S. Africa[***], where they have polyvoltine development in winter from April up to November (with 2–3 active generations lasting 6–8 weeks each) and resistant egg diapause for survival during dry summer season (December-April). Depending on the mite species,

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[*]Prostigmata and Trombidiformes in contemporary understanding [see Mironov and Bochkov (in press)] are not synonyms, but subdominant (in taxonomic meaning) groups in ranks of the infraorder and suborder, respectively. In regard to Endeostigmata, it is necessary to know, that this group had complex structure and its subgroups are transferred now into the suborders Trombidiformes and Sacoptiformes.

[**]Some representatives of the family Ereynetidae adapt to endoparasitic habits (on vertebrates) with transformation of normal development to complex calyptostasy (André and Fain 1991).

[***]*Penthaleus* mites with the same life history of winter plant pests are known also from the southern parts of the U.S.A. (Bauernfeind 2005).

Table 3. Different types of dormancy (quiescence/diapause) in dormant stages of prostigmatid mites.

Mite species	Main traits	Dormant stages	Type of dormancy		Remarks	References
			Quiescence	Diapause		
ORDER PROSTIGMATA: SUBORDER ENDEOSTIGMATA						
1. *Nanorchestes amphibiosus* (Nanorchestidae)	Supralittoral mite from North Germany with bivoltine development and overlapping generations, as well as with hibernation of all instars (similar to halacarid mite *Isobactrus unicutatus*).	**Eg L, DN, Ad** (probably calyptostasic instars – PN and TN also)	**Eg L, DN, Ad** (?)	?	?	Bucking et al. 1998
2. *Neonanorchestes* sp. (Nanorchestidae)	Sandsoil-dwelling (phyto- and fungivorous) mites.	**The same?**	?	?	Cycle: **Eg-La-(PN)-DN-(TN)-Ad.** In brackets — calyptostases.	Kethley 1991
SUBORDER EUPODINA						
EUPODOIDEA						
3. *Halotydeus destructor* (Penthaleidae)	Redlegged earth mite is an important plant-pest from S. Australia with winter development (2–3 generations of 6–8 weeks each) and summer dormancy (aestivating eggs produced by females of the pre-summer generation) terminated by impact of high temperature followed by watering.	**Eg**	–	**Eg** (aestivating resist. diapause terminated by 2-month hot treatment and changed into post-diapause quiescence.	Cycle: **Eg-La-PN-DN-TN-Ad** (phytophagous). Summer dormancy of aestivating eggs is ensured by diapause, followed by post-diapause quiescence.	Wallace 1970 a,b; James, O'Malley 1993; Ridsdill-Smith 1997; Ridsdill-Smith, Annelis 1997; Umina, Hoffmann 2003; Umina, Weeks 2004; Ridsdill-Smith et al. 2005
4. *Penthaleus* spp. (*P. major, P. falcatus* etc.) (Penthaleidae)	Winter oat mites from S. Australia and USA giving 2–3 winter generations and summer dormancy (aestivating eggs that are laid by females of all winter generations).	**Eg**	–	**Eg** (aestivating resist. diapause terminated by hot treatment and changed into post-diapause quiescence.	The same	James, O'Malley 1993; Umina, Hoffmann 2003; Umina, Weeks 2004; Umina, Hoffmann, Weeks 2004; Bauernfeind 2005
5. *Rhagidia gelida* (Rhagidiidae)	Relict periglacial predatory mite with monovoltine development and hibernating eggs.	**Eg**	–	**Eg**	Hibernating eggs, spring-summer immature stages and summer-autumn adult mites.	Zacharda 2004
BDELLOIDEA						
Bdellidae Cunaxidae	Mites with plesiotypic traits (slow monovoltine development, low reproduction).	?	?	?	Cycle as in Penthaleidae: **Eg, La, NI, NII, NIII** and **Ad.** All postembr. instars are predaceous.	Alberti 1973, 1974

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Species (family)	Life cycle characterization	Eg / aestivation	Post-diapause quiescence	Summer Egg diapause / winter diapause	Remarks	References
6. *Bdellodes lapidaria* (Bdellidae)	Australian mite with winter development and egg diapause during the summer. Needs watering of eggs and low temperature to hatch after the completion of diapause development.	**Eg** aestivation	Post-diapause quiescence is terminated by watering and cool temperature	Summer **Egg** diapause followed by quiescence	Similarity of phenology and its control with penthaleid *Halotydeus* (see Wallace 1970).	Wallace 1971
TYDEOIDEA						
7. *Homeopronematus anconai* (Tydeidae)	Polyvoltine mite (about 10 generations during April-October); with generation time = 21 days at 24°C. Reproductive winter diapause in mated, nongravid females induced by short-day photoperiod. Food — fungi, pollen etc.	**Ad**	–	**Ad** Reproductive facultative diapause of mated females	Cycle: **Eg-La-PN-DN-TN-Ad** (fungi- and phytophagous). Photoperiodic adult diapause.	Knop, Hoy 1983
8. *Parapronematus acaciae* (Tydeidae)	Acacia-inhabiting fungiforous mite from Florida (USA), having polyvolt. development with generation time of 15–18 days at 25°C.	?	?	?	The same (but diapause is unknown).	McCoy et al. 1969
HALACAROIDEA						
9. *Metarhombognathus armatrus*. Similar monovolt. cycles with rigid diapausing control in DN, typical also for *Halacarellus basteri*, *H. balticus*, *Rhombognathus pascens*, *R. notons*, *R. seahami*	Holarctic mite (with two nymphal instars) from eulittoral in Weser estuaria (Germany). Monovoltine development with aestivation diapause of DN (in V–XII), cold reactivation, and long hibernating quiescence of Ad ovipositing in winter.	**DN, Ad**	**Ad** (quiescent winter arrest followed by oviposition in December–January)	**DN** summer-autumn diapause terminated by cold in late autumn)	Synchronization of life cycles in *M. armatrus* occurs by means of diapause in DN, characterized by increased resistance to dryness and by necessity in cooling for reactivation (and transformation into Ad). Duration of instars at 20°: L–9, PN–14, DN–96±32, Ad –407±148 days.	Sokolow 1952; Makkaveeva 1956 (for *H. basteri*); Straarup 1968; Bartsch 1972; Pugh, King 1986; Siemer 1996, 1999; Bucking et al. 1998 (for *M. armatrus*)
10. *Isobactrus uniscutatus*. Similar development in *I. ungulatus* and *Rhombognathides spinipes*	Mono/bivoltine littoral mite (with three nymphal instars) from England and Germany with overlapping generations and year-round presence of all instars.	L, PN, **DN, TN, Ad**, EG	**DN, TN, Ad**	–	Halacaridae comprise some groups with 1, 2 and 3 nymphal instars, from three (*Isobactrus*) to one (*Copidognathus*).	Bartsch 1972; Pugh, King 1986; Bucking et al. 1998
SUBORDER ANYSTINA						
11. *Anystis baccarum* (Anystidae)	Common predatory mite in apple orchards, vineyards etc. with 2–3 generations. Females of all generations migrate down to the soil for oviposition. Eggs laid by females of spring generation are non-diapause, while eggs laid by females of summer-autumn generations have facultative, photoperiod-determined winter diapause.	**Eg**	–	Facultative **Eg** diapause in mites of the autumn generations	Study with *Anystis* mites fed on *Rhopalosiphum insertum* (apple-grass aphid) used as a food. In contrast to *A. baccarum* (with only egg diapause) some other anystid mites have more rich set of dormant stages in most instars (see Olomski 1955 in Wohltmann 2001).	Lange et al. 1974; Golovach 1989; Cuthbertson, Murchie 2004

the production of diapausing eggs occurs either during the whole winter (by females of all winter generations in *Penthaleus* spp., that lay diapausing eggs on the ground and plants), or at the end of winter only (by females of the last, pre-summer generation of *H. destructor*, whose diapausing eggs are retained in dead female bodies, while females from its previous generations lay non-diapause eggs on the ground and plants, similar to diapausing eggs of *Penthaleus* spp.). The egg diapause in *H. destructor* is facultative and photoperiod-dependent, while in *Penthaleus* spp. it is obligatory, but in both cases termination of diapause is enabled by reactivating impact of high summer temperatures during 1–2 months, though the realization of development in potentially reactivated eggs becomes possible only after they are affected by moistering and temperature decrease. Such peculiarities of life cycles in penthaleid mites and of their control by means of aestivating diapause of eggs are thoroughly enlighten in publications of Australian acarologists (Wallace 1970 a,b; James and O'Malley 1993; Ridsdill-Smith 1997; Ridsdill-Smith and Annellis 1997; Umina and Hoffmann 2003; Umina et al. 2004; Ridsdill-Smith et al. 2005; etc). The egg diapause in penthaleid mites considered usually as the single dormant stage controlling their life cycles, is combined really with a separate stage of quiescence (as the post-diapause phase — see Hodek 1996 and Koštal 2006) retained under hot and dry summer conditions, but terminated by the opposite factors (raining and cooling). That is, as it follows from primary studies of Wallace (1970a,b), the seasonal synchronization of life cycle in penthaleid mites is ensured by combination of both kinds of dormancy at the egg stage — by real diapause and by post-diapause quiescence.

The available data of other terrestrial Eupodina (though very limited) concern dormant stages in rhagidiid mites (the monovoltine *Rhagidia gelida*), life history traits of which are common with the considered penthaleids, as far as the dormant stage in them is represented by diapausing eggs also (Zacharda 2004). The tydeoid and bdelloid mites retain the common (basic) acariform ontogenesis and predatory habits of their soil-dwelling ancestors (André and Fain 2000), but usually reveal polyvoltine development. Some representatives of bdelloid mites (*Bdellodes lapidaria* from Australia) by their life-history traits are very close to penthaleid mites due to winter development and summer egg diapause with post-diapause quies-

cence (Wallace 1971). However the tydeoid mites are rather different in this regard. One of them, namely *Homeopronematus anconai* (fam. Tydeidae), is a myceto/pollen feeder and partly predator in vineyards (USA), where it has approximately ten generations during summer, and the reproductive facultative diapause induced in mated, non-gravid females by decreased autumn photoperiod (Knop and Hoy 1983). It is possible to conclude, therefore, that in most terrestrial Eupodina with polyvoltine development, the system of life-cycle control and seasonal synchronization is based on the single regulatory dormancy-capable instar, either with diapause (as in females of tydeid mites), or with combination of diapause and quiescence (as in eggs of penthaleid and bdellid mites).

Quite different peculiarities of life history are characteristic of specialized group of prostigmatic eupodine mites adapted as predators and algophags for life in variable marine habitats. According to Bartsch (2004) the superfamily Halacaroidea comprises more than 1000 species. They are oviparous mites with one larval and one to three nymphal instars before the final moult to the adult. There are known two types of seasonal life cycles in halacarids, noted by the early students of halacarid biology (Lohman 1893) and supported by recent acarologists. The majority of species from temperate North Atlantic waters (*Metarhombognathus armatus, Rhombognathus pascens, R. seahami, Halacarellus balticus*) have monovoltine development (Straarup 1968; Bartsch 1972; Pugh and King 1986; Bucking et al. 1998) with rapid seasonal succession of La and PN, and aestivational arrest of DN during 2–4 month, followed by transformation into hibernating Ad. Such monovoltine development is determined mainly by the presence of rigid seasonal arrest in DN instar, considered as aestival diapause by Bucking et al. (1998); but as parapause by Siemer (1999). The same phenology is known for monovoltine predatory mite *H. basteri* both in the northern Barents See (Sokolow 1952) and in the southern Black See (Makkaveeva 1956), that is undoubtedly may be explained by mechanisms of life-cycle control, similar with the above mentioned halacarids, though special attention to ascertain aestivational diapause in DN was not paid here. Another type of development is known in some species of *Isobactrus* (*I. ungulatus, I. uniscutatus, I. setosus*) and in *Rhombognathides spinipes* with mono- and bivoltine development, overlapping generations and slowly expressed seasonality due to the year-round

occurrence practically of all instars (Bartsch 1972; Pugh and King 1986; Bucking et al. 1998), which probably are capable for quiescence.

The regularities and peculiarities of monovoltine halacarid development are especially well studied in European populations of the holarctic eulittoral algophagous *Metarhombognathus armatus* (Bucking et al. 1998, Siemer 1999) with rapid development of larvae in February-May and protonymphs in March-June (with duration of 9 and 14 days respectively), followed by aestivational arrest of DN in May-December and their transformation (after cold reactivation) into adults, which represent a real hibernating stage with capability for oviposition in winter. Undoubtedly, the last two instars — DN in the state of summer-autumn diapause (with post-diapause quiescence) and adult females in the state of winter quiescence — are both responsible for maintaining the phenological regularity of monovoltine life cycle. It is quite probable, however, that very long survival of adult females in this mite (1–2 years according to Siemer 1999) may result the possibility of two overlapping generations (monovoltine as basic, and semivoltine as additional), the synchronization of which is enabled by both dormant instars (diapausing DN with post-diapause quiescence, and quiescent Ad) in autumn and winter.

The suborder **Parasitengona** represents an especially interesting group in Prostigmata. It consists also (similarly to the above considered Eupodina with its marine Halacaroidea and other terrestrial superfamilies) of two ecologically different complexes — terrestrial Trombidia and aquatic (fresh-water) Hydrachnidia, including about 2000–3000 and 4000–5000 nominated species respectively (Kethley 1982; Welbourn 1991). They have common origin from terrestrial predatory mites, the typical acariform ontogenesis of which has been modified into special metamorphosis with alternating calyptostasy, characterized by an alternation of active feeding stages (parasitic La and predaceous DN and Ad) and non-feeding calyptostases (PLa, PN and TN), and retained in almost all extant parasitengone mites. Special characteristic of them concerns the differences in feeding habits of larvae (parasites of vertebrate animals in case of trombiculid chiggers from a part of Trombidia, and of different invertebrates in case of Hydrachnidia and most Trombidia), while deutonymphs and adult mites always are predators of small arthropods and their eggs.

Parasitengone mites display usually the uni- and semivoltine life cycles completed in one or two years respectively. Some many species are characterized also by uni-semivoltine development, when some individuals complete their development within one year, while others need two years. Such life cycles of plesiotypic character may be considered as characteristic of the stem species of Parasitengona along with two other correlated traits expressed in the nymphal calyptostasy and larval parasitism (Wohltmann 2001; Wohltmann et al. 2001). Multivoltine development with some generations per year is apotypic and not common in Parasitengona from temperate climate, especially in terrestrial Trombidia, though tropical and subtropical trombiculid mites may give up to 3–5 generations per year (Sasa 1961).

The high degree of life cycle synchronization found in most species of parasitengone mites is explained usually by their need in simultaneous appearance of parasitic larvae and their hosts (Wohltmann 2001). Such an explanation fits quite well the situation with these mites, the larvae of which use insects and other mobile arthropods not only for many-days parasitism, but also for efficient dispersal. But, unfortunately, this approach does not consider the more general aspect of evolving the synchronized life cycles in parasitengone mites as an adaptation to climate seasonality itself, that determines also the seasonal events in their hosts (see also Siepel 1994). Though the role of synchronization of life cycles in parasitengone mites with hosts is more evident, the available data give manifold confirmation for important role of adaptations to climate seasonality and their regulatory functions for this synchronization, that is ensured, according to Wohltmann (2001), mainly by diapause of obligatory character at particular developmental stage, such as the egg (*Echinothrombium rhodinum, Johnstoniana rapax*), the adult female (*Trombidium brevimanum, Eutrombidium trigonum*) or the calyptostasic protonymph (*Leptus ignotus*; *L. fernandezi*). These data are presented with more details in numerous papers of A. Wohltmann (1995, 1996, 1997, 1998, 1999) with colleagues (Wendt et al. 1992, 1994; Wohltmann et al. 1994, 1996, 2001; etc.), in his review on the evolution of life histories in parasitengone mites (Wohltmann 2001), and in my review on their calyptostasic stages (Belozerov 2008a).

As it follows from these reviews, the obligatory diapause in mites with uni-semivoltine development is usually supplemented by other dormant

stages (with properties of quiescence or diapause) in variable ontogenetic position. It is of no doubts that such combinations are peculiar not only for mites with complex uni-semivoltine life cycles (majority of Microtrombidiidae, Trombidiidae, Johnstonianidae, and Trombiculidae), but may occur in mites with typically univoltine development (most Erythraeidae and some Johnstonianidae), that is illustrated by the univoltine erythraeids *Leptus fernandezi* with diapausing protonymphal calyptostase and facultative hibernation of eggs (Wohltmann 1995, 2001), by *L. trimaculatus* with diapausing adults and hibernating protonymphal calyptostases also (Wendt et al. 1992), and by johnstonianid *Johnstoniana eximia* (= *J. tuberculata*) with diapausing eggs and hibernating adult females (Wohltmann et al. 1994).

Naturally, that in Trombidia with semivoltine life cycles, every postlarval instars (sometimes even larvae) in the state of quiescence have the capacity to survive winter, while active (non-dormant) instars in strictly univoltine species are not able to overwinter (Wohltmann, pers. comm.). According to another information from Wohltmann, the capacity to survive winter in quiescence is present sometimes even in eggs. Such affirmations evidence the obligatory need of parasitengone, as of all other mites, in possessing dormant state of any kind for efficient hibernation at definite instars.

The simple treatment of data from my paper on calyptostasy (Belozerov 2008a) have shown that Microtrombidiidae with uni-semivoltine cycles have 2–4 dormant instars (majority have two, one of which is adult female), Trombidiidae have 2–3 (usually two, one of which is female also), and Johnstonianidae have three (one of which is egg stage). In contrast, mites with strongly monovoltine cycles (practically all Erythraeidae[*]) have as a rule the single diapausing instar (of variable ontogenetic location, but usually eggs or calyptostasic PN). Namely these two dormant stages of erythraeids can be found during the most part of the year, in contrast to active La, DN and Ad with their limited occurrence along the year (Southcott 1961).

Unfortunately chiggers (the family Trombiculidae), being the most important group among terrestrial Trombidia (as vectors and agents of human diseases) are investigated quite insufficiently in regard to their seasonal adaptations. It is of no wonder, therefore, to read in the last comprehensive review on trombiculid mites (Shatrov and Kudryashova 2006) that "the seasonal pattern of trombiculid mite development and stages at which they overwinter (hibernate) are still unclear". I can add that especially unclear in them are relations of hibernating dormant instars to diapause and quiescence. Nevertheless, it is known that some chiggers with uni-semivoltine development (*e.g. Neotrombicula autumnalis* and *Hirsutiella zachvatkini* in Europe) have the plesiotypic capability for overwintering of most instars (Ad, Eg, La, nymphs) (Daniel 1961; Shatrov 2000; etc.), while univoltine chiggers *Leptotrombidium akamushi* and *L. pallidum* from Japan have more limited number of instars capable for hibernation (Ad+DN and Ad+La+TN, respectively) (Takahashi et al. 1993, 1995).

Similar situation with the sets of dormant stages is characteristic of the life cycles in Hydrachnidia, as shown by specialists in this group (Böttger 1977; Proctor and Harvey 1998; De Sabatino et al. 2001; Smith et al. 2001; etc) and shortly summarized in my reviews (Belozerov 2007, 2008a) on life cycles of parasitengone mites. The diversity of dormant stages in Hydrachnidia is about the same as in their terrestrial relatives, inasmuch as in both groups for seasonal dormancy are able not only mobile Ad and DN, but also immobile eggs and calyptostases (PN and TN), and even larvae (not only unfed and engorged, but also attached to their hosts for feeding). The presence of numerous dormant stages ensures not only the better seasonal synchronization of life cycles, but also increases their flexibility and therefore the more efficient adaptation of parasitengone mite populations to unpredictable environmental changes.

The suborder **Anystina** is represented by eight families of soil/litter-dwelling, middle-sized predaceous mites, plant-inhabiting representatives of which reveal their connections with soil through oviposition. It is considered as a sister taxon of Parasitengona (Wohltmann 2001), but ontogenetically the Anystina are characterized by two active nymphal instars. One of its species, the so called 'whirli-gig' mite, *Anystis baccarum*, is very common and efficient predator of small arthropod pests in apple orchards, vineyards etc. According to data from Russia (Lange et al. 1974; Golovach 1989) and Ireland (Cuthbertson and Murchie

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[*]The family Erythraeidae is considered now as a separate taxon (Erythraeina) that is equivalent for Trombidiina and Hydracarina inside the Parasitengona (Mironov and Bochkov, in press).

2004), *A. baccarum* has two-three generations developed on plants and the same number of corresponding egg-layings into soil with non-diapause eggs in first generation, and diapausing hibernating eggs in next generation(s). Naturally, the egg diapause in this bi/polyvoltine mite is facultative, and probably is determined by photoperiod. Some ontogenetic peculiarities (two-nymphal postlarval development) and the reduced character of life-cycle control (with the only diapausing egg stage) evidence for rather apotypic evolutionary trait of this species, though other representatives of this group are known to be more plesiotypic, as far as the control of their life cycles is quite diverse, being supported not only by diapause (obligatory or facultative), but also by dormancy of consecutive type, *i.e.* quiescence (Olomski 1995 — cited from Wohltmann 2001).

The next subordinal taxon, **Eleutherengona** (= Raphignathina), consists of four superfamilies, two of which (Raphignathoidea and Cheyletoidea) are represented mainly by predaceous mites with rather derived traits, and also by deeply specialized parasites of vertebrate animals[*], while two others (Tetranychoidea and Eriophyoidea) comprise highly specialized phytophagous mites (Table 4), some of which are important agricultural pests making serious injury for diverse plants (Jeppson et al. 1975).

One of the raphignathoid mites from the family Stygmaeidae, arboreal acarophagous *Zetzellia mali* (studied in apple orchards of southern Canada) has polyvoltine development broken by hibernal diapause of adult females and restored next spring after cold reactivation of overwintered females (White and Laing 1977). Quite possible that tropical stygmaeid mite *Agistemus floridanus,* an important predator of *Tenuipalpus heveae* in Brazil, may have the seasonal dormancy in adult females also, as far as its prey *T. heveae* possess the capability for reproductive diapause (Poutier et al. 2000).

Very few we know about dormant events in cheyletoid mites, especially in common predaceous representatives of the family Cheyletidae (possibly due to their low efficiency as controlling agents), though some cases of phoresy of cheyletid females on beetles are known, that allows to compare this trait of them with dormancy and other properties of phoretic DN in astigmatid mites.

Special place among Cheyletoidea take representatives of seven separate families, comprising big number of mites adapted to diverse form of parasitism on vertebrate animals. As was noted by Kethley (1982), each of these families is characterized by rather morphologic uniformity through great reduction, and by close restriction of these permanent parasites to a definite class of hosts. The families of Demodicidae, Myobiidae and Psorergatidae are parasites of mammals, while the families of Syringophilidae and Harpyrhinchidae are parasites of birds. The last two families (Ophioptidae and Cloacaridae) represent ectoparasites of snakes and turtles respectively. Being the specialized permanent parasites of mentioned vertebrate animals, these parasitic cheyletoids are quite comparable with psoroptid representatives of astigmatid mites (especially with parasites of mammals) in regard to the reduction of seasonal adaptations (in general) and to the failure of special dormant stages (in particular) due to dominance of parasitic adaptations.

Much more we know about the life history traits in the specialized and agriculturally important, phytophagous eleutherengone mites from two superfamilies — **Tetranychoidea** (with plesiotypic features in morphology and ontogenesis, but with apotypic traits in systems of their seasonal control), and **Eriophyoidea** (with great apotypic reductions in their morphology and ontogenesis, but, in contrast, with more derived, plesiotypic and variable systems controlling the seasonal life cycles).

The superfamily Tetranychoidea contains 5 families, three of which are monogeneric and biologically not investigated, while two other families — Tetranychidae (spider mites) and Tenuipalpidae (false spider mites) are obligate plant feeders and agricultural pests of great economic importance. The first family (Tetranychidae) contains approximately 40 genera and over 600 species, inhabiting higher flowering plants and trees (subfam. Tetranychinae) or grasses and low-growing plants (subfam. Bryobiinae). They are medium-sized oviparous mites with rapid polyvoltine development (5–7 and more generations in the season with the average generation time of two weeks — Sabelis, 1991), that is stopped either by egg (embryonic) diapause (in eight genera — *Bryobia, Petrobia, Schizonobia, Aplonobia, Eurytetranychus, Schizotetranychus, Panonychus* and *Oligonychus*), or by reproductive diapause of adult females

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[*]More information on predaceous and parasitic representatives of cheyletid mites is given in a book by Akimov and Gorgol' (1990).

Table 4. Different types of dormancy (quiescence/diapause) in dormant stages of Eleutherengona.

Mite species	Main traits	Dormant stages	Type of dormancy		Remarks	References
			Quiescence	Diapause		
PROSTIGMATA: ELEUTHERENGONA						
RAPHIGNATHAE						**Kethley 1982**
RAPHIGNATHOIDEA (contains 9 families of primarily predaceous mites; some species of Stigmaeidae are phytophagous)						
1. *Zetzellia mali* (Stigmaeidae)	Species of *Zetzellia, Agistemus, Mediolata* are arboreal predators of phytophagous mites and insects in orchards of many countries.	**Ad**	–	**Ad** (winter reproductive diapause)	The acarophagous mite *Z. mali* from Canada was studied under laboratory conditions. Mean generation time is 21 days. Diapause in overwintered females is terminated after cold reactivation.	**White, Laing 1977**
2–4. *Agistemus floridanus, A. cypriu, A. industani* (Stigmaeidae)	*A. floridanus* is predator of *Tenuipalpus heveae* in Brazil. Longevity of females = 25–35 days.	?	–	**Ad** ?	Cycle: **Eg, La, PN, DN, Ad.** All three species of *Agistemus* fed spider mite eggs and plant pollen. Generation times of them is 30–38 days.	**Ferla, Moraes 2003; Goldarazena et al. 2004**
CHEYLETOIDEA (contains 8 families of predaceous and parasitic mites)						
5. *Cheyletus malaccensis* (Cheyletidae)	This predaceous cheyletid is taken from the culture of grain mite *Aleuroglyphus ovatus*.	?	?	?	Cycle: **Eg, L, PN, DN, Ad.** Development from Eg to female lasts at 25°C 20–23 days, to male (without DN) 15–17 days.	**Saleh et al. 1986**
6. *Cheletogenes ornatus* (Cheyletidae)	This predaceous cheyletid mite from Egypt cultured on tetranychid eggs and immatures. No data on its seasonality.	?	?	?	Development time of female (with two nymphs) is 37–43 days, of male (with one nymph) 30–36 days at 25°C. Longevity of female 70–95 days.	**Zacher et al. 1981**
7. *Paracheyletia bakeri* (Cheyletidae)	Low efficient agent for control of spider mites with life cycle of 2 month.	?	?	?	Development time of Eg and L (6–6.5 days each), PN and DN (5–6 days each) at 75°F.	**Kanavel, Selhime 1967**
8. *Acaropsis docta* (Cheyletidae)	Culturing in India on eggs of *Trogoderma*.	?	?	?	Generation lasts 14.4 days at 35°C. Survival of Ad is 10–13 days. Predaceous.	**Kapil, Bhanot 1972**
9. *Cheyletus eruditus* (Cheyletidae)						**Boczek 1959**

TETRANYCHOIDEA		Ad / Egg				Kethley 1982
10. *Tetranychus urticae* (Tetranychidae)	Cosmopolitan plant pest with polyvoltine development and reproductive diapause of adult females.	Ad	—	Hibernating or aestivating **female diapause** determined by photoperiods.	Photoperiod is connected both with induction and maintenance of diapause. During diapause it serves to retain the state of diapause until the arrival of low temperatures. Diapause development is ended at the beginning of winter, but mites retain dormant state till spring (by means of post-diapause quiescence).	**Bondarenko 1950; Geispitz, Orlovskaja 1971; Glinyanaya 1972; Veerman 1985; Kroon, Veeendaal 1998; Grbic et al. 2007**
11. *Tetranychus kanzawai* (Tetranychidae)	Common polyphagous spider mite from Japan and S. Asia.	Ad	—	Hibernating **female diapause.**	Great similarity in mechanisms controlling winter diapause with *Tetranychus urticae.*	Ushida 1980; Veerman 1985
12. *Eotetranychus tiliarium* (Tetranychidae)	Lime tree inhabitant with polyvoltine development and winter diapause of females.	Ad	—	Hibernating **female diapause.**	Mass migration of females in autumn down to the trunk for their places of hibernation (before pigmentation changes, specific for diapausing specimen).	Veerman 1985
13. *Bryobia cristata* (Tetranychidae)	Usually develops on grasses with diapause in eggs laid in May-June.	Egg	—	Summer and winter diapausing **eggs.**	In Central Europe this mite laid aestivating and hibernating eggs hatching simultaneously in spring. Active development in summer. The hibernation of eggs, larvae and adults is possible in Iceland, but in Switzerland it has year-round development with a few of diapausing eggs laid in summer.	Gabele 1959; Veerman 1985; Hallas, Gudleifsson 2004
14. *Bryobia praetiosa* (Tetranychidae)	On grass and herbaceous plants. In Switzerland this clover mite has two generations, separated by aestival and hibernal diapauses of eggs.	Egg		Aestivating and hibernating diapausing **eggs.**	Hatching of winter eggs in Canada begins in early spring. Aestivated eggs begin to hatch in September with hatching peak before the cool period.	Veerman 1985
15. *Bryobia rubrioculus* (Tetranychidae)	The brown mite infesting fruit trees. In Switzerland it is polyvoltine species.	Egg		Hibernating diapausing **eggs.**	Hatching of winter eggs occurs in Canada 2–3 weeks earlier than of *Panonychus ulmi.*	Veerman 1985
16. *Bryobia ribis* (Tetranychidae)	This monovoltine species infest berry bushes in Switzerland.	Egg		Hibernating diapausing **eggs.**	Egg diapause completes in January.	Veerman 1985
17. *Petrobia harti* (Tetranychidae)	Cosmopolitan mite living on leaves of *Oxalis* and other plants. Active polyvoltine development in cool season, with egg diapause in summer.	Egg (aestivation)	—	**Egg diapause** of facultative summer character.	Diapausing eggs are laid by females under long-day photo-periods. Arrest of late embryos is maintained by low humidity, and terminated after eggs were hydrated. Diapause is finished in 2 month (with no chilling).	Koveos, Tzanakakis 1991

Species (Family)	Description	Stage		Diapause type	Details	Reference
18. *Panonychus ulmi* (Tetranychidae)	Cosmopolitan arboreal mite with polyvoltine development (4 generations in Sweden, 6–8 in USA). Red diapause eggs are laid from September to November.	**Egg**		Hibernating diapausing **eggs**	Diapause is photoperiodically determined and reqieres very long chilling (150–200 days and more) to be completed. The diapause termination is followed by post-diapause cold quiescence.	**Lees 1950; Miller 1950; Veerman 1985**
19. *Panonychus akitanus* (Tetranychidae)	Hibernation of this mite in Hokkaido normally takes place at egg stage, though winter population from Sapporo consists of eggs and "winter-habit" females.	**Egg, Ad**	—	Hibernating **Egg** diapause. **Ad** (?)	Egg diapause is induced by short-day photoperiod in females, and terminated by 40-day cold exposure (as well as by 50-day exposure of "winter-habit" females from Sapporo).	**Gotoh 1986**
20. *Oligonychus ununguis* (Tetranychidae)	The conifer mite distributed from Finland to Japan.	**Egg**	—	Hibernating **Egg** diapause	Diapause of winter eggs completes from January and reaches max in February/March with 50% hatch in April/May.	**Loyttyniemi 1970; Shinkaji 1975**
21. *Cenopalpus irani* (Tenuipalpidae)	An apple pest in Iran with polyvoltine development and overwintering females.	**Adult females**	—	**Hibernating reproductive diapause**	Overwintering females begin activity at the end of April and give three generations per year. Development from egg to egg at 32°C =26 (female) and 19 (male) days.	**Rashki et al. 2004**
22. *Cenopalpus pulcher* (Tenuipalpidae)	Flat scarlet mite is pest of pear/apple. In Europe has one generation, in Iran, Iraq and Egypt three generations per year.	**Adult females**	—	**Hibernating reproductive diapause**	—	**NPAG data 2000**
23. *Cenopalpus bakeri* (Tenuipalpidae)	Apple tree pests in Turkey with two generations and hibernation of females.	**Adult females**	—	**Hibernating reproductive diapause**	—	**Düzgünes 1969**
24. *Tenuipalpus heveae* (Tenuipalpidae)	Duration of generation 44.5 days.	**Adult females**	—	**Hibernating reproductive diapause**	—	**Poutier et al. 2000**
25. *Brevipalpus californicus* (Tenuipalpidae)	Important citrus pest with polyvoltine development and hibernating adult females.	**Adult females**	—	**Hibernating reproductive diapause**	11 generations (in Egypt) with duration of 17 days each in summer up to 47 days in late autumn.	**Attiah et al. 1973**
26. *Brevipalpus phoenicis* (Tenuipalpidae)	Life cycle is completed in 20 and 30 days (at 21°C and 27°C respectively).	**Adult females**	—	**Hibernating reproductive diapause**	—	**Lakshman 1978**
27–30. *Brevipalpus californicus, B. obovatus, B. phoenicis, B. lewisi* (Tenuipalpidae)	Longevity of each species is two to three times more than in various tetranychid mites.	**Adult females**	—	**Hibernating reproductive diapause**	—	**Childers et al. 2003**

ERIOPHYOIDEA						
31. *Aceria chondrillae* (Eriophyidae)	S. European polyvoltine gall mite with only one form of females. Hibernation in leaf rosettes of *Chondrilla juncea* without reproduction and gall formation.	**Ad? N?**	—	**Ad? N?**	—	**Caresche, Wapshere 1974**
32. *Aceria malherbae* (Eriophyidae)	Gall mite from *Convolvulus arvensis*. Overwinters as an adult or nymph below ground on rhizome buds.	**Ad + N2**	—	Ad + N2	—	**Internet**
33. *Phytoptus avellanae* (Phytoptidae)	Common pest of filbert (hazelnut) with 2 types of life cycles (simple in gall mites and modified complex in vagrants).	**Nq2, N3 and Ad**	—	In gall form **N2**, in vagrants **Ad** + Tegonotus-like **N3**.	Gall form with a single nymphal type. and simle life cycle. In spring its nymphs migrate from old buds to healthy buds, where occurs development.	**Ozman, Toros 1997; Ozman 2000**
34. *Cecidophyopsis vermiformis* (Eriophyidae)	Also pest of filbert (hazelnut) with modified complex cycle. Inhabits buds, where develops and hibernates.	**N2 and Ad**	—	**N2 and Ad**	Inhabits the same buds, as gall form of *Phytoptus avellanae*. Reproduction continues during winter.	**Ozman, Toros 1997**
35. *Rhincaphytoptus negundivagrans* (Diptilomiopidae)	The leaf vagrant on ornamental box elder *Acer negunde* in Turkey with polyvoltine summer development (3–4 generations) and overwintering deutogynes (in bark crevices).	**Deutogynes**	—	Deutogynes	Similar complex cycles with deuteroginy have also *Rhincaphytoptus ulmi* vagrans from elms *Ulmus* and two species of *Vasates* from maples *Acer* spp. (Jeppson et al. 1975).	**Ozman 2001**
36. *Aceria cladophthirus* (Eriophyidae)	Gall mite from *Solanum dulcamara* wiuth simple polyvoltine development.	**No**	—	No	Without alternating females specialised for hibernation;	**Westphal et al. 1990**
37. *Floracarus perrepae* (?)	The important pest of climbing fern, *Lygodium microphyllum*, having non-interrapted development with producing leaf roll galls.	**No**	—	No	A potential biological control agent of climbing fern by means of premature fern defoliation of this aggressive weed in Australia.	**Ozman, Goolsby 2005**
38. *Aculus schlechtendli* (Phytoptidae)	Vagrant mite, very common polyvoltine pest of apples with deuterogeny.	**Deutogynes**	—	Deutogynes		**Jeppson et al. 1975; Kozlowski, Boczek 1989; Oldfield, Manson 1996**
39. *Epitrimerus pyri* (Phytoptidae)	Vagrant mite, very common polyvoltine pest of pears with deuterogeny.	**Deutogynes**	—	Deutogynes	—	**Jeppson et al. 1975; Oldfield, Manson 1996**

Species	Description				Notes	Reference
40. *Eriophyes laevis* (Eriophyidae)	Bivoltine alder leaf gall mite with hibernating deutogynes from second generation.	Deutogynes	—	Deutogynes	—	**Shevchenko 1957**
41. *Eriophyes leionotus* (Eriophyidae)	Leaf-eryneum birch mite with aestivo-hibernating deutogynes.	Deutogynes	—	Deutogynes	—	**Sokolov 1986**
42. *Cisaberoptus kenyae* (?)	Vagrant mite infesting mango leaves in many tropical countries.	—	—	**Non-dormant deutogynes** serving for dispersal	—	**Hassan, Keifer 1978**
43. *Nalepella haarlovi* (Phytoptidae)	Vagrant coniferous mite from *Picea* needles with polyvoltine development and diapausing eggs.	**Hibernating eggs**	—	**Diapausing eggs**	*N.haarlovi*, infests needles of *Picea abies* and gives 4–8 generations, overwinter only as diapausing eggs laid by females from two last generations. The cold reactivation of diapause eggs occurs by January and followed afterwards possibly with cold quiescence.	**Löyttyniemi 1971**
44. *Trisetacus bagdasariani* (Phytoptidae)	Gall fir mite from *Abies sibirica* with biennial development and hibernating nymphs of second generation.	**Nymphs 2**	—	**Nymphs 2**	—	**Bagnjuk 1984**
45. *Trisetacus kirghizorum* (Phytoptidae)	Gall mite with biennial development in "berries" of mountain *Juniperus* is peculiar by every-year change of summer and winter generations.	**Deutogynes and protogynes plus eggs**	**Protogynes plus eggs ?**	**Deutogynes**	—	**Shevchenko, De-Millo 1968**
46. *Trisetacus piceae* (Phytoptidae)	Gall mite with biennial development in buds of *Picea* characterized by every-year alternation of protogyne and deutogyne generation which are capable to hibernate together with eggs and immature instars also.	**Deutogynes, protogynes plus eggs and nymphs**	**Protogynes plus eggs and nymphs ?**	**Deutogynes**	—	**Bagnjuk 1976**
47. *Abacarus hystrix* (Phytoptidae)	Common grass-inhabiting mite, known as vector of virus diseases.	**Protogynes**	**Hibernating protogynes**	—	—	**Sukhareva, Sapozhnikova 1975; Sukhareva 1992**
48. *Phytocoptes deschampsiae* (Phytoptidae)	Common grass-inhabiting mite.	**All stages of simple life cycle**	**All stages of life cycle may hibernate**	—	—	**Sukhareva, Sapozhnikova 1975; Sukhareva 1992**

(in mites from four other genera — *Tetranychus, Eotetranychus, Platytetranychus* and *Neotetranychus*, plus one species of the genus *Oligonychus*, namely *O. pratensis*). The egg diapause is considered as a derived ancestral trait, while the adult diapause as a secondary apotypic feature (Gutierrez and Helle 1988). Quite possible that this trait concerns some other acariform mites. Both types of diapause in spider mites are facultative, and have a lot of common with insects in their photoperiodic control (Veerman 1985, 2001). The role of photoperiod in diapause induction was discovered simultaneously in *Panonychus ulmi* with egg diapause (Lees 1950; Miller 1950), and in *Tetranychus urticae* with adult diapause (Bondarenko 1950). The latter species, owing to easy cultivation, rapid development and accuracy of photoperiodic responses, is one of the main models (together with some insects) in the study of mechanisms of seasonal photoperiodism in arthropods (Veerman 1985, 2001). Due to the noted and other advantages, *T. urticae* is suggested also as the perspective genetic model for studies in developmental biology (Grbic et al. 2007).

The diapause in spider mites has been considered (mainly on the basis of studies of its induction) as the main, if not the single instrument that determines peculiarities of their seasonal development. However, some available data on termination of diapause make to suggest, that restoration of active development after diapausing state involve also processes of quiescence in the same manner, as in penthaleid prostigmatid mites (see p. 97). I mean the data concerning the aestivating egg diapause in *Petrobia apicalis* (Zein-Eldin 1956) and *P. harti* (Koveos and Tzanakakis 1991) requiring high temperature and relatively dry atmosphere for maintenance of resting state, but rather low temperature and high humidity to break it and to evoke embryonic development. Being very expressive in cases with aestivating diapause, the role of quiescence as synchronizing agent is less obvious in cases with hibernating diapause, as far as the resting state is maintained here (simultaneously with events resulting the developmental potentiality) by low temperatures and is broken during post-diapause quiescence by an increase of temperature. The interface of these events enabling firstly to reach the covert potentiality for development (at the end of diapause), and to realize it afterwards during post-diapause quiescence (Hodek 1996; Koštal 2006) is of great adaptive significance for "coarse" and "fine" time-adjust-

ment of hatch in overwintered eggs of spider mites (Veerman 1985). The same conclusion concerns, of course, the synchronization of reproduction in overwintered adult females of spider mites, and of moult in overwintered immatures of some other mites.

There are known some cases when tetranychid mites reveal unusual peculiarities in their hibernating stages. For instance, the monovoltine *Bryobia cristata* in subarctic conditions of Iceland can overwinter not only by diapausing eggs, but also at larval and immature instars in unknown dormant state (Hallas and Gudleifsson 2004). The possibility of hibernation in spider mites at some instars, though with low survival (as in *Tetranychus takafujii* infesting *Solanum nigrum* in Central Japan), can be explained suggestively by their introduction from tropical or subtropical areas (Ohashi et al. 2003). Another, more interesting example is represented by *Panonychus akitanus* that hibernate in Hockaido (Japan) both by diapausing eggs and adult "winter-habit" females, and such a population with two different dormant stages may represent a transient evolutionary state from egg to adult diapause, or vice versa (Gotoh 1986). In spite of those supplementary notes, the typical trait for spider mites (Tetranychidae) is represented by diapause in eggs (as of primary kind) or adult females (as of secondary kind).

The second family (Tenuipalpidae) contains 15 genera and 290 nominated species distributed mainly in tropical and subtropical regions. These small-sized mites with many traits of morphological and ontogenetic reduction are important pests of commercial orchards, vineyards, tea plantations and grass pastures. They are oviparous and have rapid polyvoltine development that is stopped only at the stage of adult females with reproductive diapause. The mentioned apotypic specialized traits in morphology and ontogeny coincide here with the same apotypic features of their dormant instar. False spider mites develop slower than tetranychids (see Table 5), their generation time is about 20–40 days at 20–30°C. Species of the genus *Cenopalpus* give annually from one (in Europe) to two (in Turkey) and three generations (in Iran, Iraq and Egypt). Hibernating females are in the state of diapause, which is unfortunately not studied in details.

The last eleutherengone superfamily **Eriophyoidea** (the so called four-legged mites) contains three families (Eriophyidae, Phytoptidae and Diptilomiopidae, comprising more than 50 genera

Table 5. Different types of dormancy (quiescence/diapause) in dormant stages of heterostigmatid mites.

Mite species	Main traits	Dormant stages	Type of dormancy		Remarks	References
			Quiescence	Diapause		
ORDER PROSTIGMATA, SUBORDER HETEROSTIGMATA						
TARSONEMOIDEA						
1–3. *Tarsonemus ips, T. krantzi, T. fusarii* (Tarsonemidae)	Phoretic females of these micetophagous mites on the pine beetle *Dendroctonus frontalis*, which larvae need fungus *Ophiostoma minus*, the best food for all three mites.	**Ad female**	?	?	Cycle: **Eg-La-Ad.** In 40 days (developmental time of beetle generation) increase of *Tarsonemus* population is 170–380. Generation time in all mites is 18–19 days. Female lives 28 days. Fungivorous.	Lombardero et al. 2000
4. *Polyphagotarsonemus latus* (Tarsonemidae)	Tropical and subtropical plant pest with polyvoltine development. The generation lasts 1 week under 25°C. Annually may give 20–30 generations.	?	?	?	Cycle: **Eg-La-Ad.** Pharate females (often termed "pupae" or "quiescent nymphs"). Short-lived males and females (about 1 week). Phytophagous.	Gerson 1992
5–6. *Daidalotarsonemus hewitti, D. vandefriei* (Tarsonemidae)	Two species of mites (algo-lichenophagous) from Elm bark with strong seasonality of adult and larval abundance correlated with bark epiphytic algae dynamics.	?	?	?	*D. hewitti* adult peaces in autumn (Aug-Oct) and in spring (March-May), but of *D. vandefriei* — in winter (max January). Algophagous.	Doberski 1986
7. *Tarsonemus granaries* (Tarsonemidae)	Mycophagous mite. Generation is 10 days, life of females 17 days.	?	?	?	There are no seasonal changes in mite abundance, in spite of strong changes of temperature in granaries. Fungivorous.	White, Sinha 1982
8. *Acarapis woodi* (Tarsonemidae)	The honey bee tracheal mite, is an internal parasite of adult bees. It has one generation per host in short-lived summer bees, but multiple generations of mites in each bee in winter.	**Ad** Mite female as a short-lived agent of infestation of new bees	?	**?**	Mites live in tracheal tubes of adult honey bees and only move outside the host as **females** to infest other bees. Parasitic.	Baker, Wharton 1952; Internet 2007
9. *Podapolipus diander* (Podapolipidae)	Ectoparasite of locusts in North Africa with alternation of larval and adult females. Infestation of hosts (by means of larval mite females) during host's copulation.	**Larval female** as an agent of infestation of adult locusts during host copulation	—	—	The family Podapolipidae comprises parasites of different arthropods and characterized by the highest level of ontogenetic and morphological reduction..	Volkonsky 1940 (cited from Baker, Wharton 1952)
10. *Locustacarus trachealis* (Podapolipidae)	Mite parasitic within tracheal tubes and air sacs of locusts and grasshoppers. Eggs are laid by physogastric females also there.	**La** as an agent of infestation	—	—	The same	Baker, Wharton 1952

PYGMEPHOROIDEA

Taxon	Biology	Dispersal stage			Cycle	References
1. *Brennandania lambi* (Pygmephoridae)	Monophagous pest in mushroom farms, with polyvoltine development (generation time is 10 days at 27°C); phoretic as adult females on some flies. Food — *Agaricus bisporus* mycelium.	**Ad female** phoretomorph	?	**Ad**	Cycle: **Eg-La-Ad** (phoretic and physogastric females). Detachment of phoretic mites and their reproduction is determined by the presence of mycelium *Agaricus* in the soil. Fungivorous.	Clift, Larsson 1987; Gao Zou 2001
2. *Pediculaster flechtmann* (Pygmephoridae) Also *Pediculaster mesembrinae* (Pygmephoridae)	Polyphagous fungiforous mites using different wild moulds as a food. Rapid development with generation time = 5 days at 21–25°C.	**Ad female** phoretomorph	?	**Ad**	Cycle: **Eg-La-Ad**. Two types of females — phoretic (dispersal on Diptera) and non-phoretic. Fungivorous.	Cross, Kaliszewski 1988
3. *Dolichocybe perniciosa* (Pygmephoridae)	New pest in mushroom farms. Its food is mycelium of wild moulds and *Agaricus*.	?	?	?	Cycle shortened to **Eg-Ad**. No data on phoretic dispersal. Fungivorous.	Gao, Zou 2001
4. *Luciaphorus auriculariae* (Pygmephoridae)	Olygophagous pest of farming mushroom *Auricularia polytricha*.	?	?	?	Cycle shortened to **Eg-Ad**. Eggs develop directly into adults within physogastric female, where mating occurs. Fungivorous.	Zou et al. 1993
5. *Parapygmephorus costaricanus* (Pygmephoridae)	Polyvoltine mite (Costa-Rica), associated with polyvoltine bees *Agapostemon nasutus*.	?	?	?	Saprophagous/fungivorous mite feeding in bee nests on faeces of bee larvae.	Rack, Eickwort 1979
6–7. *Pyemotes tritici, P. ventricosus* (Pyemotidae)	Polyvoltine ectoparasitoid of *Sitotroga* moth and other grain pests. Mite females are agents of human hay (grain) itch.	**Ad** Dispersing non-phoretic unfed females	?	?	Direct development of adult mites (female and male) inside the physogastric female.	Baker, Wharton 1952; Bruce, LeCato 1979
8. *Pyemotes herfsi* (Pyemotidae)	*P. herfsi*, parasite of larval midges that induce leaf galls of pin oaks. Polyvoltine mite with physogastric females developed in April-November and dispersed as unfed females in August-December.	**Ad** (gravid females in fallen galls and unfed females of different generations	?	?	Cycle: direct development of adult mites (female and male) inside the physogastric female. Parasitoids.	Keith, Kalisch, Broce 2005
9. *Scutacarus acarorum* (Scutacaridae)	Phoretic females occur on hibernating females of bumblebees *Bombus* and *Psithyrus*.	**Ad** (phoretic females)	—	**Ad** (diapausing phoretic females)	Fungivorous. Easy cultured on mycelium of *Histoplasma capsulatum*. Reproduction by physogastric females.	Schousboe 1986

and 2000 species of obligatory phytophagous mites with high host-specifity[*]. Morphological and ontogenetic peculiarities of eriophyoid mites (extremely small-sized vermiform body, retaining only two pairs of legs, the reduced postembryonic development with only two immature instars considered as larva and nymph, or nymphs I and II) are uniform in all these mites, having monophyletic origin and possessing very tight co-evolutionary connections with their host-plants. But in contrast, they have a large diversity in their life cycles (poly-, bi-, mono- and semivoltine development), and in their systems of seasonal control (with many, some and single dormant stages) enabling diverse versions of life cycles (Table 5). Thus, Eriophyoidea reveal quite contrasting situation, as was told above, concerning the relationships between apotypic morphological and ontogenetic traits (from one side), and rather plesiotypic traits in diversity of their life histories, especially of seasonal peculiarities of life cycles (from another side).

Such diversity is revealed firstly in the presence of two categories of these mites (according to places of their feeding, reproduction and development). They live either in buds, galls, erineums and other plant deformations giving them a shelter and food source (namely "the gall mites"), or inhabit rather open surface of leaves and other vegetative and generative plant organs (the so called "vagrants"). Diptilomiopid mites are principally surface vagrants, while eriophyids and phytoptids relate to gall mites usually (Kethley 1982). Representatives of both these categories may have life cycles of different complexity — either **simple cycles** (with one type of adult females that reproduce throughout the year under favorable conditions), or more common **complex cycles** (usually with two types of adult females — summer reproductive protogynes and dormant deutogynes with diapausing arrest of reproduction). Simple cycles are characteristic, for instance, of the gall mite *Aceria cladophthirus* from *Solanum dulcamara* (Westphal et al. 1990) and subtropical *Floracarus perrepae* with non-interrupted polyvoltine development on its native host, the climbing fern *Lygodium microphyllum*; with formation of leaf roll

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[*]The used taxonomic approach corresponds to Kethley (1982). More recent taxonomy of Eriophyoidea is presented in the Catalog of Amrine and Stasny (1994). The full information about these mites is given in the comprehensive manual "Eriophyoid Mites — Their Biology, Natural Enemies and Control" (1996) under the editorship of Lindquist, Sabelis and. Bruin, published by Elsevier Science.

galls and premature defoliation of this Australian aggressive weed (Ozman and Goolsby 2005).

The presence of two types of females (deuterogeny) is typical for the majority of these mites from deciduous plants in temperate areas with obvious seasonality, but occurs in species from evergreen and tropical plants also (Table 4). In general, the heteromorphic deutogyne females serve for hibernation and aestivation in the state of diapause, but are capable for dispersal also. Deutogynes of tropical vagrant *Cisaberoptus kenyae* from mango leaves have no dormancy, and serve for dispersal only.

It is of interest that no true deutogyne females were discovered in grass-inhabiting eriophyoid mites that overwinter either at the stage of protogyne females (*Abacarus hystrix*), or at every stages of their life cycle (*Phytocoptes deschampsiae*) (Sukhareva and Sapozhnikova 1975; Sukhareva 1992). It is possible that in the last case (but may be in both cases) the hibernation is realized through the state of quiescence, as far as populations of grass-inhabiting eriophyoid mites are affected by temporary and unpredictable environmental factors quite more, than arboreal eriophyids (Skoracka and Kuczyński 2003).

Eriophyoid mites reveal a large diversity in regard to their systems of seasonal control that may involve many overwintering stages, as in the gall/bud-living coniferous mites *Trisetacus kirghizorum* (Shevchenko and De-Millo 1968) and *T. piceae* (Bagnjuk 1976), or the only overwintering eggs in the vagrant coniferous mite *Nalepella haarlovi* (Löyttyniemi 1971), as well as the only deutogyne females in vagrants *Aculus schlechtendali* and *Epitrimerus vitis* (Kozlowski and Boczek 1989; Manson and Oldfield 1996) from apple-trees and grapes, and in the alder gall mite *Eriophyes laevis* (Shevchenko 1957). It is known now, that in some eriophyoid mites the arrest of development at the stage of adult females (mainly deutogynes, but protogynes in some cases also) is induced by photoperiod (Sapozhnikova 1982), while its termination is enabled usually by long chilling in winter, as in many other species with diapausing dormancy (Jeppson et al. 1975). For instance, the cold reactivation of diapause in overwintering eggs of *N. haarlovi* is completed by January (Löyttyniemi 1971), being followed afterwards undoubtedly with the cold-maintained post-diapause quiescence.

Deutogyne females are the main dormant stages in eriophyoid mites. Nevertheless, in some

species the same role is characteristic of nymphal instar specialized for hibernation and resumption of spring development after overwintering, either together with adult females as in *Aceria malherbae*, inducing gall formation in the field bindweed *Convolvulus arvensis*, and in the vagrant form of the filbert pest *Phytoptus avellanae* (Ozman and Toros 1997; Ozman 2000), or among other hibernating stages as in the coniferous bud mite *Trisetacus piceae* (Bagnjuk 1976), or even alone as in the gall fir mite *Trisetacus bagdasariani* (Bagnjuk 1984) and in the gall form of the filbert mite *P. avellanae* (Ozman and Toros 1997; Ozman 2000).

Some more data on seasonality of development and on dormant stages in eriophyoid mites are given in the book of Jeppson, Keifer and Baker (1975), and in recent review by Manson and Oldfield (1996). Nevertheless, it is worth to illustrate the eriophyoid life-cycle diversity by some additional examples.

The typical complex life cycles (with reproductive summer protogynes and hibernating dormant deutogynes) are characteristic of some diptilomiopid vagrant mites *Rhincaphytoptus* and *Vasates* from different deciduous *Acer* trees (Ozman 2001) and *Calepitrimerus vitis* from vineyards (Pérez-Moreno and Moraza-Zorrillab 1998.). More complicated cycles with 2-year duration and hibernation of some (or all) ontogenetic instars are peculiar for mites of the genus *Trisetacus*, inhabitants of galls and buds in coniferous trees. The biennial development of *T. kirghisorum* in "berries" of *Juniperus semiglobosus* is characterized by the every-year change of summer and winter generations with hibernation of both deutogyne and protogyne females, as well as of eggs (Shevchenko and De-Millo 1968), while the development of *T. piceae* in host buds occurs with annual change of generations with protogyne adults and deutogyne adults, which are capable to hibernate together with eggs and immature instars also (Bagnjuk 1976). From my meaning, plesiotypic life-history traits of gall-producing coniferous eriophyoid mites (*Trisetacus*) revealed in the presence of numerous dormant stages, that enable hibernation and seasonal control of biennial life cycles, coincide quite well with their archaic plesiomorphic traits. In contrast, arboreal vagrant mites (*Aculus, Epitrimerus, Nalepella* etc.) with rapid polyvoltine development and limited number of dormant stages (adult deutogyne females or overwintering eggs)

have apparently secondary, derivative characters (Belozerov 2007).

The special case of life cycles is presented by the mentioned *P. avellanae* (Krantz 1979; Ozman and Toros 1997; Ozman 2000). Differing from other phytoptids, this filbert (hazelnut) mite has two different types of life cycles (simple cycle in the gall form and specific complex cycle in the vagrant form). In both vagrant and bud forms of this species the overwintering instars are represented by nymphs, which hibernate in buds. In gall form the hibernated nymphs migrate in spring from old buds to new healthy buds, where they reveal the temporary, month-long dormancy before moulting to adults, and further development of stationary polyvoltine population begins only afterwards inside the infested bud. The same temporary dormancy after spring migration of hibernated nymphs is characteristic of vagrant form also. Its complex life cycle is characterized by two versions (with two and three nymphal stages, the third of which is heteromorphic Tegonotus-like nymph), that is unknown in any eriophyid mites. Hibernating instars are presented here by Tegonotus-like nymphs and adult mites with their spring migration from old big buds onto open places for summer polyvoltine development (vegetative and generative parts of the plant, and new small buds also). Polyvoltine development ends in September with accumulation of Tegonotus-like nymphs, migrating together with adults to winter places (as in summer to new places for feeding).

Unfortunately, the presented data on life histories of Eriophyoidea give few materials for determination of definite kinds of dormancy in them. Nevertheless, it is quite probable, that the control of seasonal life cycles in most four-legged mites is enabled by hibernating and aestivating diapauses in adult females (as a rule by deutogynes, although sometimes by protogynes), in nymphs and in eggs. The hibernation and aestivation in the state of quiescence may be quite possible (particularly in grass-inhabiting mites), but needs special ecophysiological investigations. Such investigations are of great importance also for clearing the presence of post-diapause quiescence in processes of developmental arrest termination, known in many acariform mites. There is a great field yet for thorough study of seasonal cycles and their control mechanisms in eriophyoid mites.

The more specialized traits concerning the morphology, ontogeny and life history are characteristic of the suborder **Heterostigmata** with its

numerous representatives demonstrating the trends to parasitism and reduction (Kethley 1982). According to Wainstein (1978), this taxon (considered by him as the cohort Tarsonemina) displays the strongly limited group, differing from other trombidiform mites, and comprising subgroups of big similarity. Heterostigs, as they were called by Kethley (1982), comprise 5 superfamilies, two of which (Tarsocheyloidea and Heterocheyloidea) include the derived and slow studied mites with three immature stages (La, PN and DN), while three others (Pygmephoroidea, Pyemotoidea and Tarsonemoidea) represent more specialized taxa that demonstrate apotypic traits of increasing morphological and ontogenetic reduction (their life cycles may be condensed to a larval stage or even to its loss, when adults give birth directly to adults), combined with close phoretic or parasitic associations with insects. The developmental rate is very high and may overcome even that of astigmatid mites.

Pygmephoroidea comprise 3 families, two if which — Pygmephoridae (300 nominated species) and Scutacaridae (400 nominated species) — have diverse associations with insects, mammals, their nests and litter. The females, often physogastric, are either oviparous or larviparous. Life cycles are with no nymphal stage. Pyemotoidea consists of 4 families, three of which are associated with beetles, while the representatives of Pyemotidae are predators or parasitoids of immature instars in very different insects. The life cycles of pyemotids are highly modified. For instance, all development of *Pyemotes tritici* takes place within a gravid physogastric female with approximately 200 progeny, and males (sons) just after birth mate with their sisters. Life cycle lasts 4–7 days at 25°C. Representatives of Pygmephoroidea and Pyemotoidea due to their morphological similarity and low level of taxonomic study sometimes refer to the combined group (*e.g.* to Pygmephoroidea in Table 5). The last superfamily Tarsonemoidea (with two families) has no nymphal stages in life cycles also. The family Podapolipidae is represented by parasites of insects and other arthropods, while Tarsonemidae are extremely diverse in their food relations (fungi-, herbi- and entomophagous mites, symbionts and parasites of insects). One of the most important pests among tarsonemoid mites is the honey bee tracheal mite, *Acarapis woodi*, a cosmopolitan endoparasite of *Apis mellifera*. There is possible only one generation of this parasite per host in short-lived summer bees, but mul-

tiple generations may develop in each bee in winter. The function of dormancy is unknown, and distant dispersal is absent in these mites. As adult females they move outside the host only for a short time to infest other bees, usually young workers.

Some other examples of Heterostigmata are given in Table 5. The dormant stages are known mainly in pygmephoroid mites associated with insects through phoresy and parasitism. For instance, the fungivorous oligophagous mite *Brennandania lambi,* an important polyvoltine pest in mushroom farms, has its dispersal by phoretic adult females on sciarid and phorid flies. The related fungivorous mites, *Pediculaster flechtmanni* and *P. mesembrinae*, feeding on wild moulds, have two forms of adult females for dispersal (phoretic and non-phoretic). Adult females serve as non-phoretic dispersing agents in different pyemotid mites, parasitic on stored-product insect pests (*Pyemotes tritici, P. ventricosus*) and on midges producing leaf galls (*Pyemotes herfsi*). Phoretic females of fungiphorous scutacarid mite, *Scutacarus acarorum*, serve as dormant overwintering phoretics on hibernating bumblbee females. There is a real similarity in life-history traits of some heterostigmatid and astigmatid mites, especially associated with insects as phoretics and parasites/paraphags. Diapausing state of phoretic stages in heterostigmatid mites is quite similar, probably, to such states in hypopodes of astigmatid mites.

DISCUSSION AND CONCLUSION
General distribution of diapause and quiescence in acariform mites

The main seasonal peculiarities of life cycles in the Acari, as already noted, depend on the function of special, species-specific System of Seasonal Control (SSC), which affects the duration, voltinism, phenology, flexibility and other life-cycle traits. The organizing role in these systems is enabled by dormant stages of diapausing character (Belozerov 2006, 2007, 2008b). The number and distribution of such stages are determined by evolutionary transformation of the named systems — from ancestral polymeric SSC (with numerous diapausing stages) into oligomeric and monomeric SSC (with reduced number of these stages). The presence of another kind of dormancy in acariform mites (quiescence) is apparent, but its participation in these control systems would seem improbable according to the common belief of insect ecologists, but the presented data suggest an opposite opinion.

From materials presented above, survival during unfavorable conditions is doubtless enabled in acariform mites by both kinds of dormancy, controlled either endogenously, (diapause), exogenously (quiescence), or in both ways. However, such opposite kinds of dormancy in these mites are hardly similar functionally as adaptations for time-adjustment of their life cycles to predictable environmental changes. While the real necessity for quiescence occurs under conditions of non-predictability, it is rather ambiguous for diapause in the same situation. Diapause in mites is of decisive importance for life-cycle synchronization with environmental seasonality (as in most other arthropods), but the same role of quiescence needs special comparative analytical consideration. All available data concerning quiescence and diapause in acariform mites, considered in this review, are presented for this purpose in Tables 1–5 and summarized in Table 6.

Among **Oribatida,** according to general opinion (Norton 1994), all soil-dwelling oribatid mites from temperate climate conditions (with uni-semi-voltine life cycles and other "K"-attributes of life-history strategies) are quiescent during hibernation. The same idea about the ability of temperate oribatid mites to overwinter in the state of quiescence (similarly with Collembola and other soil-dwelling microarthropods) was expressed by Siepel (1994). Quiescence is assigned also as the only dormant state for hibernation (with no traits of diapause) in those oribatid species that live under conditions of extreme polar seasonality and possess perennial life cycles and "A"-attributes of life-history (Convey 1996; Søvik 2004), as well as many polar insects (Danks 1999a, 2004; Peck et al. 2006). But this is not the only conclusion for polar oribatid mites, since before hibernation they exhibit some diapausing traits (see above: p. 86–87). Their life histories look and are considered as extreme versions of the typical ancestral oribatid life history that has been preadapted to Arctic and Antarctic conditions without special polar adaptations (Norton 1994; Convey 1996; Behan-Pelletier 1999). Unfortunately, the problem of identifying real nature of dormancy (quiescence, diapause or their combination) in typical versions of oribatid life histories has no definite solution (due to the lack of sufficient information for temperate soil-dwelling mites, as well as to some doubts and contradictions). However, according to Reeves (1969) and some other acarologists, almost all oribatid species with "K"- and "r"-attributes seem to hibernate in the state of diapause under conditions of temperate seasonality (Table 1). In contrast to the cold-dependent hibernating dormancy, the nature of which in oribatid mites is still unclear, the presence of typical drought-dependent quiescence in these mites is quite definite, being discovered in case of summer rest (with temporary comatose state) in the European species *Scutovertex minutus* (Smrž 2002), and in one ameronothrid mite in the western USA from ephemeral pools after their drying (Norton et al. 1996). A similar form of quiescence as a response to humidity deficit is known also in some erythraeid mites (Prostigmata: Parasitengona:) with eggs and calyptostasic instars (PLa and PN), capable to survive the drought during a month-long period in the state of dryness-dependent quiescence (Wohltmann 1998). The quiescent state in response to humidity deficit presents a case of special interest for solving the origin and evolutionary trends in dormancy and life-history strategies of terrestrial arthropods (Emme 1953; Ushatinskaya 1973, 1990; Jönsson 2005; etc.). This can be ascertained through study of their dormant states, and through comparison with similar forms of latent life, particularly anhydrobiosis. Of great necessity in the same regard is to learn and understand the real (but still unclear) nature of winter dormancy in temperate- and polar-climate oribatid mites due to their general plesiotypic traits. It is necessary to add to the Norton's (1994) note about "full set of conservative plesiotypic traits concerning their life history", that the Oribatida are characterized by positive conformance of plesiotypic characters in both biological (life history) and ontogenetic aspects.

Among free-living **Astigmata** (Acaridia) diapause, combined usually with phoresy, is a dominant form of dormancy for survival during temporary periods between colonizations of their ephemeral habitats, as well as during adverse seasons. It relates usually to the deutonymphal heteromorphic instar (hypopus) with adaptations for phoretic or non-phoretic dispersal (but in some cases to the non-phoretic tritonymphal instar). In contrast, Psoroptidia, as permanent parasites of vertebrate animals, are deprived usually of dormant stages due to dominance of close host-parasite relationships, especially in mammalian parasites, while feather mites, as more plesiotypic parasites of birds, may retain sometimes the capability for dormancy (rather as quiescence, though in literature suggested as diapause). The number of dormant stages that participate as regulators of

Table 6. Summary of data on dormant stages and their types in different groups of the acariform mites.

Taxons	Voltinism or hostal specifity	Number of dormant stages	Number of species	Types of dormancy		
				Quiescence	Diapause	Unknown
1	2	3	4	5	6	7
ORIBATIDA						
Oribatida	perennial	4–6	4	3 (all stages)	0	1
	semivoltine	3–5	12	1 (all stages)	6 (alm. all stages)	5
	uni/bivoltine	1–3	6	1 (TN, Ad)	5 (DN, TN+AD)	0
ASTIGMATA						
Acaridia	multivoltine	1 or 2	16	1 TN	12 DN + 1 TN	2
	uni-bivoltine	1 or 2	8	1 (TN+Ad)	6 DN + 1 TN	0
Psoroptidia	on mammals	no	4	–	–	–
	on birds	1–3	7	1 (?)	4 (?)	2
	dust mites	?	5	5	0	0
PROSTIGMATA						
EUPODINA						
Eupodoidea	multi/univoltine	1	4 mv, 1 uv	0	5 aestiv. Eggs	0
Bdelloidea	univoltine	1	1	0	1 aestiv. Eggs	0
Tydeoidea	multivoltine	1	1	0	1 hibern. Ad female	0
Halacaroidea	univoltine	2	6	6 Ad	6 DN	0
	bivoltine	6	3	3 all stages	0 ?	0
PARASITENGONA						
Erythraeina	univoltine	1–2 (usual 1)	16	Ad, Eg, PN	3Ad, 7Eg, 4PN, 2DN	0
Trombidiina	uni/semivoltine	1–5 (usual 2)	39	Ad, Eg, La, N.	19Ad, 13Eg, 6La, 1N	0
Hydracarina	uni/semivoltine	1–3 (usual 1)	15	La, DN, TN	4Ad, 6Eg, 3La, 2Nm	0
ANYSTINA						
Anystidae	multivoltine	1	1	0	hibern. Eggs	0
ELEUTHERENGONA						
Raphignathoidea	multivoltine	1	1	0	1 hibern. Ad female	0
Tetranychoidea	multivoltine	1	17	0	10 Ad female and 7 Eggs	*
Eriophyoidea	gall/bud mites	0–4 (usual 1–2)	11	0	N2, N2+Ad, Eg+NN+Ad+Deut	0
	arboreal vagrants	1–4 (usual 1)	8	0	Eggs, N3, Deutog.	0
	grass inhabitants	1 or 4	2	Protogynes or Eg+N1+ N2+ Protog.	?	0
HETEROSTIGMATA						
Tarsonemoidea	Mycetophags etc.	?	3	?	?	3
	Insect associates	Ad, Ad female, La female	6	?	?	6
Pygmephoroidea	Mycetophags etc.	Ad female	5	–	3 Ad female	2
	Insect associates	Ad female	4	–	1 Ad female	3

Note: Data were compiled from Tables 1–5 of this paper and Tables 1–2 of the paper on the calyptostasy in Parasitengona (Belozerov 2008a). An asterisk in the last column opposite to Tetranychoidea means the presence of some exclusions in regard to their dormant stages (see text). Numerals in columns 5, 6 and 7 mean the number of mite species with corresponding traits. Numerals in the column 3 mean the number of dormant stages in life cycles of investigated mite species. The compilation presents very approximate results on relationships, but more definite results on distribution of dormancy types in different taxa of the acariform mites.

life cycles in the acaridian mites is limited usually to the single diapausing instar (deutonymphal hypopus) characterized by special morphological adaptations due to phoresy and aphagy. Quite possible, that post-diapause quiescence ascertained in hypopodes of *Lepdoglyphus destructor* (Knülle 1991b; Danks 1994, 1999) may be the common dormant adaptation in the acaridian mites for synchronous moult of their DN to TN. The acarid mite *Naiadacarus arboricola* presents a unique case of life cycles with the TN for winter diapause (followed by post-diapause quiescence), phoretic DN for summer dispersal and other instars, probably, for winter quiescence. The number of resting stages (of indefinite nature) in feather mites may be one to three. The Astigmata, as well as Oribatida, are characterized by the conformance of biological and ontogenetic traits, though in contrast to Oribatida (due to derivative position and specialization of astigmatid mites) they reveal apotypic trends in both aspects (biological and ontogenetic). Some peculiarities and properties of diapause in acaridian hypopodes are rather ingenious and want special separate investigations in spite of great insight into the general life history of these mites (Athias-Binche 1991; Houck and OConnor 1991; Houck 1994).

Quite a different picture is characteristic of the complex taxon **Prostigmata** with its biological, ontogenetic and morphological diversity. The main life-history peculiarity, deserved special consideration in this taxon, concerns the combination of diapause and quiescence in life cycles of its representatives either at different instars, or at the same ontogenetic instar (this is unknown in plesiotypic Oribatida and practically absent in apotypic Astigmata). For instance, in terrestrial Eupodina the combination of diapause and post-diapause quiescence occurs at the same instar (eggs in penthaleid and bdellid mites, or adult females in tydeid mites), but in marine halacarid mites this control includes deutonymphal diapause with post-diapause quiescence, followed by common cold-enforced quiescence in adult females. The combination of diapause and quiescence at different stages of life cycle is characteristic of most Parasitengona (terrestrial Trombidiina and freshwater Hydracarina with uni-semivoltine development), though representatives of Erythraeina differ from them usually by a single dormant stage of diapausing character (at different species-specific instars), that give evidences (together with rigid univoltinity of these rather xerophylic mites) for more apotypic traits of their life histories, than in other Parasitengona (see Wohltmann 2001). At last, Eleutherengona comprise taxa with very different relationships between their traits, concerning the life-cycle seasonality and morphology/ontogeny. If the four-legged mites (Eriophyoidea) reveal plesiotypic and variable systems of seasonal control (including both diapause and quiescent stages) in contrary to apotypic morphological and ontogenetic reduction, the relationships between these trends in true spider mites (Tetranychoidea: Tetranychidae) is perfectly opposite (the apotypic uniformity of regulatory systems presented by either embryonic, or reproductive diapause, and quite plesiotypic traits in morphology and ontogeny), while in false spider mites (Tetranychoidea: Tenuipalpidae) both trends coincide as apotypic (the single dormant stage of diapausing adult females and obvious traits of deep morphological reduction). In this regard they are quite comparable with astigmatic Acaridia (especially in regard to the single dormant stage, presented by diapausing adult female in tenuipalpid mites and by diapausing deutonymphal hypopus in almost all free-living acaridian mites). The mentioned differences between biological and morpho-ontogenetic trends in taxa of Eleutherengona support the meaning of entomologists (Danilevsky 1961; Ushatynskaya 1976; Tyshchenko 1983; etc.), that evolution of seasonal adaptations in insects does not correspond their phylogenetic evolution, though phylogeny may influence on biological features through the life style, which is peculiar for taxonomic groups. This corresponds also to a statement that location of diapause at definite ontogenetic instar depends mainly on the ecology of species and has slow connections with its taxonomic position (Danilevsky 1961), that is well illustrated by various species-specific position of diapause in Erythraeina mites (see above). These data quite agree with my opinion that evolutionary events of seasonal adaptations have occurred in different animal taxa according to and depending on their organization, manner of life, geographic distribution and historic changes in conditions of their existence (Belozerov 2006, 2007, 2008b).

At last, among **Heterostigmata** with their extreme ontogenetic and morphological reduction (as well as with r-selected attributes), some many representatives of tarsonemoid and pygmophoroid mites reveal associations with insects as their phoretics, parasites and parasitoids, sometimes with synchronized appearance and hibernation of both

associates. The last trait favours for diapausing nature of their dormant and phoretic stages. Some heterostigmatids (*e.g. Scutacarus acarorum*, hibernating on bumblebee females), reveal the obvious probability of combination of diapause and post-diapause quiescence. All known cases of dispersal through phoresy relate to adult females in heterostigmatid mites (usually due to extreme reduction and condensation of their life cycles). Many parasitic representatives of this taxon are deprived of dormant stages (*e.g.* the endoparasitic tracheal bee mite *Acarapis woodi,* enabling infestation of hosts by its adult females, which are not capable for long off-host survival). In spite of low knowledge of life histories in heterostigmatid mites, it is possible, nevertheless, to see their essential convergent similarity in some regards with free-living astigmatid mites, especially associated also with insects through phoresy and parasitism.

The diversity of quiescence types and their functions in life cycles of acariform mites

According to the common meaning, the main (if not the unique) function of quiescence in arthropods concerns their survival during adverse environmental conditions, due to high general and specific tolerance obtained in this state, while quiescent stages are hardly capable to be of use for the seasonal control of life cycles. However, such an opinion concerns only the most common type of quiescence, that arises as a direct response to adverse environmental conditions at any life-cycle stage and ceases just after elimination of unfavorable factors.

This opinion, accepted by almost all ecologists, has obtained theoretical support from a group of entomologists and mathematicians from USA (Gurney et al. 1991). They showed by means of mathematical modeling that this form of enforced dormancy, received from these authors the term "the stage-independent quiescence", acting alone (with no diapause) and independent of any developmental stage, can never synchronize insect life cycles to the seasons. Undoubtedly, this is characteristic of the acariform mites also. Thus, the theoretical analysis has confirmed the common meaning about the enforced quiescent dormancy ascertained by biologists in field and laboratory.

The same authors revealed later (Gurney et al. 1994) another modified type of quiescent dormancy, called by them as "the stage-specific quiescence" due to its functional connection with some ontogenetic stage, differing from other stages by developmental thresholds. The main significance and peculiarity of this special quiescence is presented by its capability not only to provide higher tolerance, but also to synchronize life cycles and, thus, to replace diapause as a means of seasonal synchrony. This is a very interesting result based also on mathematical modeling that is consistent with empirical data of some entomologists. Nevertheless the stage-specific quiescence still requires thorough evaluations through special biological (hopefully also acarological) investigations, because the authors themselves consider their results as abstractions, hoping that "their analysis encourages further empirical documentation of these patterns".

The most important perspective on the problem of quiescence and its relations to diapause is represented, undoubtedly, by the third type of quiescent dormancy, ascertained by Czech entomologists (Hodek 1996, 2002; Koštal 2006)[*] as "the post-diapause quiescence" after their comprehensive analysis of successive physiological stages of diapause in insects. This form of quiescence, representing the terminal phase of diapause development (Fig. 3), ensures both vital functions attributable for diapause (survival and synchronization), though not through replacing diapause (as in previous case of the stage-specific quiescence), but by means of diapause supplementation for an increase of accuracy in seasonal synchronization of life cycles. This is enabled firstly through the enforced maintenance of post-diapause dormant state under adverse conditions (together with the covert developmental potentiality received at the end of diapause), and then by realization of this potentiality through resumption of overt development after adequate environmental changes. According to Koštal (2006), the potentiality for development may be realized either immediately after the end of diapause, if the conditions are permissive, or after some delay in the state of quiescence until favorable environmental changes.

Some cases with traits of the post-diapause quiescence were demonstrated before and after the mentioned publications of Hodek and Koštal by

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[*]The first entomological data on diapause followed by quiescence in accordance to traits of post-diapause quiescence were obtained by Hodek (1971, 1973) in *Pyrrhocoris apterus* and in coccinellid beetles, as well as by Krysan (1978) in *Diabrotica virgifera.* The first case of the same type in Acarology with aestivatng egg diapause followed by quiescence was described for the spider mite *Petrobia apicalis* by Zein-Eldin (1956).
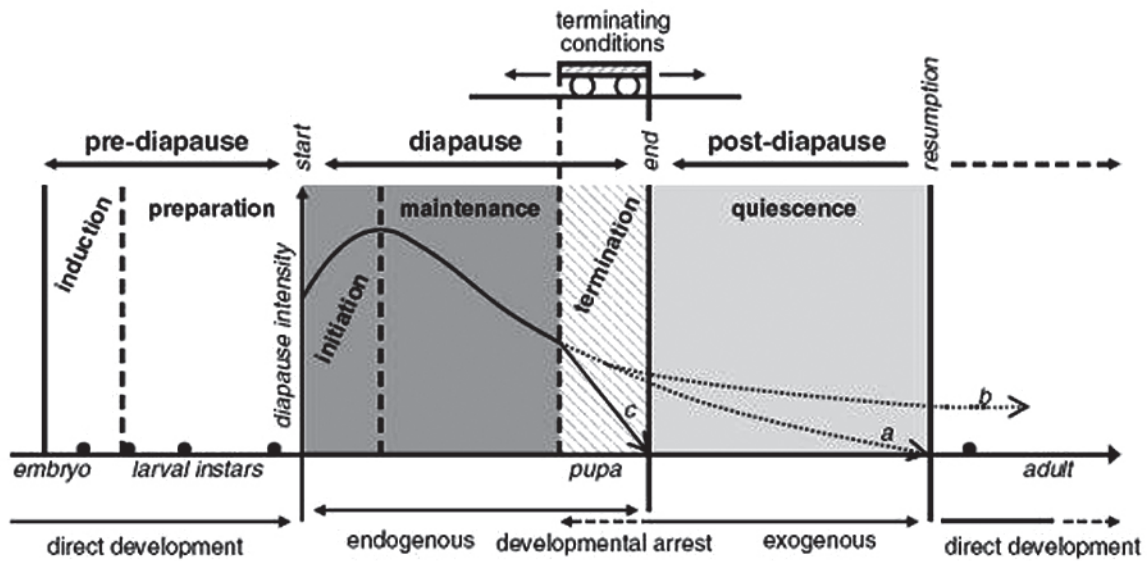
Fig. 3. Schematic depiction of phases in diapause development during ontogenesis of one hypothetical insect individual. The points on the line delineate major ontogenetic stages. Three major phases, namely pre-diapause, diapause and post-diapause, are distinguished during the diapause including ontogeny. Further division to sub-phases, namely induction, preparation, initiation, maintenance, termination and quiescence, is indicated by vertical lines Changes in diapause intensity are schematically presented: dotted branches (a and b) apply to the constant conditions, while solid branch (c) applies to the change of environmental conditions (specific terminating conditions/stimuli coming at different physiological times-movable carriage) (after Koštal 2006).

entomologists and zoologists of other specialties. For instance, this type of quiescence was shown also in Crustaceans, particularly in some branchiopods, where the larval hatch from reactivated cysts may occur either just after diapause termination, or after temporary delay in the state of post-diapause quiescence affected by external conditions (Brendonck 1996), as well as the larval hatch in insects and mites from reactivated eggs.

Essential data on this peculiar form of dormancy were obtained at the same time and even earlier by acarologists working on phenology and seasonal adaptations (particularly on diapause) of different acariform mites. A. Veerman (1985) from the Amsterdam University was perhaps the first who emphasized the great adaptive significance of the post-diapause quiescence for "fine" time-adjustment (as a supplement for "coarse" diapausing adjustment) of hatch in overwintered eggs of spider mite *Panonychus ulmi,* though initially the traits of this quiescence in spider mites were discovered in aestivating eggs of *Petrobia apicalis* by Zein-Eldin (1956), and confirmed later for *P. harti* by Koveos and Tzanakakis (1991)**.** The maintenance of developmental arrest in aestivating eggs (together with retaining the developmental potentiality after the end of diapause) is enabled by summer conditions (high temperature and relatively dry atmosphere), but is broken (with restoring the

embryonic development) in autumn by decreasing temperature and increasing humidity. Similar relationships with temperature and moisture in maintenance and termination of developmental arrest during and after aestivating diapause were recorded also in eggs of the predaceous eupodine mite *Bdellodes lapidaria* from Australia (Wallace 1971), and in especially well investigated Australian plant pests, phytophagous eupodine mites, *Halotydeus destructor* and some cryptic species of *Penthaleus* (Prostigmata: Eupodina) with aestivating diapause of egg also (Wallace 1970a,b; Ridsdill-Smith 1997; Umina et al. 2003, 2004; etc.). Something similar is revealed in marine halacarid mites with summer-autumn deutonymphal diapause followed by post-diapause quiescence (*Metarhombognathus armatus* etc.), as well as in TN of the water acarid mite *Naiadacarus arboricola,* and in adult females of predatory stigmaeid mite *Zetzellia mali* (Eleutherengona: Raphignathoidea) with winter diapause and cold-dependent quiescence in both latter cases. The described mechanisms with participation of post-diapause quiescence enable the accurate synchronizing effect in seasonal adjustment of life cycles in mentioned mites with aestivating diapause.

The role of post-diapause quiescence as a synchronizing agent, being quite appreciable in species with aestivating diapause, is less obvious and received less attention (as self-evident event) in

cases of hibernating diapause, as far as the resting state is maintained and terminated here mainly by temperatures (with its reactivating chilling effect and recovering effect of increase of temperature).

It is quite usual for insects and mites that developmental potentiality in overwintering specimens (*i.e.* their cold-reactivation according to Danilevsky 1961) is achieved long before the end of cold weather (see Hodek 2002), and the dormant state retains rather long time until the start of warm weather, enforcing the synchronized renewal of development. In acariform mites this is characteristic of many spider mites, overwintering both as adult females (*Tetranychus urticae*, *T. kanzawai* etc.) and eggs (*Panonychus ulmi*, *Bryobia rubrioculus, Oligonychus ununguis* etc.), of some eriophyid mites with winter egg diapause (*Nalepella haarlovi* etc.), and of many parasitengone mites with hibernal diapause at egg stage (*Johnstoniana rapax, J. tuberculata, Campylothrombium boreale, Georgia pulcherima* and *Balaustium putmani),* at adult stage (*Camerotrombidium rasum*), as deutonymphs (*Leptus beroni)* and even as calyptostasic protonymphs (*Leptus fernandezi*) (see Eggers 1995; Wohtmann 2001; Belozerov 2008a). The same mechanism is quite probable in the astigmatid mite *Naiadacarus arboricola,* diapausing in winter at resistant tritonymphal stage (Fashing 1977). Mechanisms of adequate character associated with post-diapause quiescence are quite possible in most terrestrial acaridian mites.

Thus, the post-diapause quiescence, ascertained in insects, is an important device for "fine" seasonal synchronization of life cycles in representatives of acariform mites, irrespective of diapause type (aestival or hibernal) and its ontogenetic location (egg, immatures or adult stage). Unfortunately, it is impossible yet to clarify the definite relationships of diapause with post-diapause quiescence. It is not unlikely, however, that the post-diapause quiescence, being displayed at the end of diapause only (*i.e.* after reactivation), may arise much earlier, at the beginning of diapause (on phases of its initiation or maintenance — see Fig. 3), joining their common tolerant capabilities. There are many important and interesting questions for further investigations of properties, ecophysiological and evolutionary relationships of quiescence, diapause and active state, proposed by the remarkable Russian ecologist and evolutionist, A.M. Emme (1953) more than half a century ago, which still need comparative study. A discussion of one of these follows.

The origin and evolution of dormancy in arthropods

There are many hypotheses about both the origin and evolution of dormancy in living beings on our planet, but the problem remains unresolved. It is frequently proposed that quiescence, as the simplest form of dormancy, represents the starting point for the evolution of diapause. One of the first proponents of this view, as noted by Tauber et al. (1986), was Emme (1953), who suggested that diapause has arisen from quiescence (firstly temporary, but then evolved to long-termed and cold-resistant arrest) due to moisture deficit. The close suggestion was given by Ushatinskaya (1976) that diapause evolved not from torpidity, but from "sleep" with its basic inherent preconditions. It is necessary, of course, to remember H.J. Müller (1992), who considered quiescence as an initial pra-form of all forms of dormancy. Numerous opponents of these views suggest that the origin of diapause resides in responses other than those involved in quiescence. For instance, Tyshchenko (1973, 1983) and Tauber et al. (1987) proposed comprehensive hypotheses of diapause evolution in connection with the evolution of photopeiodism and the perception of seasonal token stimuli.

In regards to the origin of diapause *per se*, its capability is considered by some authors as a primary feature, inherited by arthropods from their ancestors. According to Alekseev and Starobogatov (1996), diapause has originated only once in the animal kingdom and in any new case has "dependent, evolutionary transferred origin" based on original reactions of ancestors (*i.e.* monophyletically). Similar opinions about diapause origin are characteristic of entomologists C. and M. Tauber and S. Masaki, who consider each new diapause acquired in the course of insect evolution as a modification of an ancestral diapausing response, inherent for their ancestors (Tauber et al. 1986, p. 219). In contrast, other authors favor the hypothesis of polyphyletic origin of diapause (Danilevsky 1961; Cáceres 1997; etc.), in correspondence with the idea of great lability of evolutionary processes concerning diapause and "phenological strategies". This idea is very resistant in entomological literature (Kozhanchikov 1959; Alexander 1968; Masaki 1978; etc.) and admits *de novo* formation of diapause even in specialized taxa. According to Cáceres (1997, p. 371), "dormancy has most likely arisen multiple times in invertebrate life histories, both within and between phyla".

The opinion, that capability for dormancy in arthropods was received from their ancient remote ancestors, and its further evolution occurred on the basis of their ancestral responses and properties (with possibility to display their retention someway later also) seems more correct. My analysis of the distribution of dormant stages in life cycles of Insects, Crustaceans and Acari (Belozerov 2006, 2007) suggests that adaptations enabling the seasonal alternation of active and dormant periods in life cycles of arthropods arisen at the earliest occurrence of life and developed afterwards in different animal taxa according to their organization, manner of life, geographic distribution and historic changes in ecological conditions of their existence. This is well supported by the above recorded examples with differences either in correspondence, or in inconsistency of ecophysiological and morpho-ontogenetic evolutionary trends among different lineages of Eleutherengona and other prostigmatid mites (pp. 100, 109, 112, 114), which evidences the non-conformity of phylogenetic and ecophysiological evolution in insects (Danilevsky 1961; Ushatynskaya 1976; Tyshchenko 1983), in spite of some influence of phylogeny on biological features through the life manner, that is peculiar for taxonomic groups.

Now, on the basis of materials presented above (especially in the previous part of the Discussion, emphasizing the role of post-diapausing quiescence), it is possible to give more reasonable suggestions, itemizing the initial state of dormancy in ancestors of acarines and other arthropods as a complex adaptation to both predictable and unpredictable environmental changes.

The tight-connected association of diapause and quiescence (namely of the post-diapause type) is characteristic, as we have seen, of many extant species of insects, mites and some other invertebrates. The diapause in penthaleid and tetranychid mites considered earlier as the single dormant stage controlling their seasonal life cycles, represents really a complex involving a diapause and post-diapause quiescence (as was ascertained in investigations of diapause termination). Thus, the seasonal synchronization of life cycle in these prostigmatid mites is ensured by a combination of both kinds of dormancy — by real diapause and by post-diapause quiescence. An advantage of this association has two essential aspects. It ensures not only accurate time-adjustment of both arrest and resumption of development (before and after an inappropriate season respectively), but also

population survival in the state of quiescence during such a season.

This phenomenon, with the association of two different adaptive responses, gives a reasonable basis for the solution of both general and particular problems concerning the origin and evolution of dormancy in arthropods (*e.g.* for Oribatida as an important taxon among acariform mites with uncertain nature of their seasonal dormancy and its contradictory interpretation). The combination of post-diapause quiescence and diapause may be considered as an initial ancestral state of dormancy enabling universal adaptation in the acariform mites to any environmental changes. This opinion allows a reasonable suggestion for the presence of the double nature of dormancy in ancestral Oribatida and the same explanation for retention of this feature in extant oribatid mites (in contrast to contradictory interpretations of their winter dormancy as a result of either quiescence, or diapause only). The hibernal dormancy in extant oribatid mites, in my view, begins from the state of induced diapause and ends with the state of enforced post-diapause quiescence followed by events of direct development. The ascertainment of such double mechanisms in hibernating oribatid mites from different habitats and taxonomic groups will give the real confirmation of the idea of ancestral nature of their initial double dormancy. This helps also to understand the evolutionary pathways of life-cycle control in acariform mites from the initial combination of diapause and post-diapause quiescence, with further changes of their control into three main functional directions: (1) either being retained in their descendants as a double controlling mechanism of plesiotypic character with both types of dormancy; (2) or being modified into one of the specialized mechanisms of apotypic character with diapausing or quiescent response; (3) or being transformed into active stage with no capability for dormancy (this is well corresponds to general evolutionary transformations of life cycles and their controlling systems in all Acari — Belozerov 2007, 2008b). All these hypothetical versions seem probable, but need, of course, serious theoretical evaluation through the study of ecologically and taxonomically different acariform mites.

Conclusion: some results and tasks for further study of dormancy in acariform mites.

The analysis of data on dormant stages in three main taxa of acariform mites (Oribatida, Astigmata and Prostigmata) has confirmed the

main conclusions made in my previous papers (Belozerov 2006, 2007, 2008b) concerning regularities in evolution of systems controlling the seasonality of acarine life cycles from a plesiotypic state (with numerous diapausing stages) to apotypic states (with single or limited number of such stages). These conclusions are supplemented now by the statement that seasonality control of life cycles is enabled not only by diapause, but also by some forms of quiescence, particularly by the post-diapause quiescence ascertained by entomologists (Hodek 1996; Koštal 2006), and emphasized by an acarologist Veerman (1985). The most important conclusion is that the combination of diapause and post-diapause quiescence, characteristic of many extant acariform mites, corresponds the ancestral initial state of dormancy in adaptations (particularly of Oribatida) to any environmental changes.

The ascertainment of the cooperating combination of diapause and post-diapause quiescence reveals a facility of great ecophysiological significance in insects, acarines and other arthropods, which obtained with its help the efficient capability for adaptations to predictable and unpredictable environmental changes, for adaptations to long-termed climatic changes, and for preadaptations to more adverse and extreme conditions. Investigations of this quiescence, tightly connected with diapause, give real basis for better understanding the evolutionary pathways of dormancy in arthropods (in general), as well as for understanding the initial and real nature of dormancy in the Acari, and especially the Oribatida in particular.

Dormancy in ancestral Oribatida was probably represented, as it is now in many extant prostigmatid mites (Eupodina, Eleutherengona etc.), neither by the single quiescence, nor by the single diapause, but was based on cooperating combination of both kinds of dormancy, giving real advantages for coordinated survival of populations and their seasonal developmental synchrony under different climatic conditions. The solution of problems, arisen from conclusions of the presented analytical review on acariform mites, needs further investigations of different forms of quiescence, their properties and relationships with diapause, *i.e.* of the same problems that were proposed by A.M. Emme (1953).

Besides the question on the nature of dormancy in Oribatida, which is extremely important for the problem of dormancy evolution in acariform mites, there is another controversial question concerning the peculiarities of dormancy in free-living Astigmata, some properties of diapause in which are not clear enough. There is a serious inconsistency of diapausing traits of deutonymphal hypopodes in these mites with the common unpredictability of their ephemeral habitats. The best way to address both these issues may be further experimental study of dormancy termination in resting stages of acaridian hypopodes and overwintering dormancy in oribatid mites, *i.e.* by means of the same efficient procedures which helped to ascertain the post-diapause quiescence in prostigmatid mites.

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