CALYPTOSTASY: ITS ROLE IN THE DEVELOPMENT AND LIFE HISTORIES OF THE PARASITENGONE MITES (ACARI: PROSTIGMATA: PARASITENGONA)

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ABSTRACT: The paper presents a review of available data on some aspects of calyptostasy, i.e. the alternation of active (normal) and calyptostasic (regressive) stages that is characteristic of the life cycles in the parasitengone mites. There are two different, non-synonymous approaches to ontogenetic and ecological peculiarities of calyptostasy in the evaluation of this phenomenon and its significance for the development and life histories of Parasitengona. The majority of acarologists suggests the analogy between the alternating calyptostasy in Acari and the metamorphic development in holometabolous insects, and considers the calyptostase as a pupa-like stage. This is controversial with the opposite view emphasizing the differences between calyptostases and pupae in regard to peculiarities of moulting events at these stages. However both approaches imply the similar, all-level organismal reorganization at them. The same twofold approach concerns the ecological importance of calyptostasy, i.e. its organizing role in the parasitengone life cycles. The main (parasitological) approach is based on an affirmation of optimizing role of calyptostasy through acceleration of development for synchronization of hatching periods in the parasitic parasitengone larvae and their hosts, while the opposite (ecophysiological) approach considers the calyptostasy as an adaptation to climate seasonality itself through retaining the ability for developmental arrests at special calyptostasic stages evoked from normal active stages as a result of the life cycle oligomerization. Both of these approaches share the understanding of calyptostasy as a tool for synchronization of particular steps in the parasitengone life cycles with seasonal events of physical or biological origin.

KEY WORDS: Parasitengona, life history, seasonal adaptations, dormancy, diapause, quiescence, calyptostasy.

INTRODUCTION

All representatives of parasitengone mites (Acariformes: Prostigmata:Parasitengona) are characterized by the unique modified type of life cycle, in which active developmental stages (normal both morphologically and functionally) alternate with inactive stages (regressive morphologically and functionally). These inactive regressive stages are called usually as the calyptostases (Grandjean 1938) that means «hidden (or veiled) stages», inasmuch as they are retained within the egg shell or the cuticle of the previous instar (Walter and Proctor, 1999; Walter 2006). Such a phenomenon of alternation of active and inactive stages has received the term of «alternating calyptostasy» (Kethley 1991).

The life cycle of parasitengone mites consists of an egg and six postembryonic stages — regressive calyptostasic prelarva, active parasitic heteromorphic larva, regressive calyptostasic protonymph, active predatory deutonymph, again regressive calyptostasic tritonymph, and, finally, active predatory adult mite (Fig.1). This specialized type of development is characteristic of all terrestrial Trombidia with their soil- and litter-dwelling postlarval active stages (Wharton and Fuller 1952; Johnston and Wacker 1967; Robaux 1974; Proctor 1998; Wohltmann 2001; Shatrov and Kudryashova 2006)*, and of water mites group, Hydrachnidia, with an aquatic

life style of all developmental stages (Sokolow 1940; Böttger 1977; Tuzovsky 1987; Proctor and Harvey 1998; Di Sabatino et al. 2000, 2003; Peyrusse and Bertrand 2001; Smith et al. 2001)** . The same alternation of overt active and covert calyptostasic stages is characteristic not only of the whole cohort of Parasitengona, but also of two smaller taxons of prostigmatic mites, namely the family Pterygosomatidae, all the active stages of which — larva, deutonymph plus adult stage in females, and larva plus adult stage in males are parasitic (Goodwin, 1954), and the plesiomorphic genus *Neonanorchestes* (the family Nanorchestidae) with its amphibiotic style of life and plesiotypic traits of free-living overt stages (Kethley 1991). As against the mentioned mites with their alternating calyptostasy, the majority of acariform mites possesses only the single calyptostase presented by prelarval stage (the embryonalized first larva) at the start of postembryonic development, consisted of active stages only. The calyptostasic prelarva is revealed in Oribatida, Astigmata and some Prostigmata (Lange 1960; Sitnikova 1960; Grandjean 1962; Alberti 1975; Wainstein 1978; Fain and Herin 1979; etc.).

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* It is necessary to add that in some terrestrial Trombidia predatory larvae are known, and in one species (*Microtrombidium hirsutum*) deutonymphs emerge from eggs due to calyptostasic character of larvae (Wohltmann 2001). There are known also some cases of additional moults in nymphs and adults of Microtrombidiidae (Michener 1946).

** Some species of Hydrachnidia also manifest deviations from the general scheme of life histories expressed either in the terrestrial habits of parasitic larvae, or in the transformation of parasitic larva into predatory or non-feeding stage (Davids 1997; Smith 1998; Wohltmann 2001), often inactive and united together with prelarva into the complex calyptostase. Some water mites (e.g. *Limnochares aquatica*) reveal also the possibility for additional moults of nymphs and adults (Böttger 1972a, Wohltmann, personal communication).
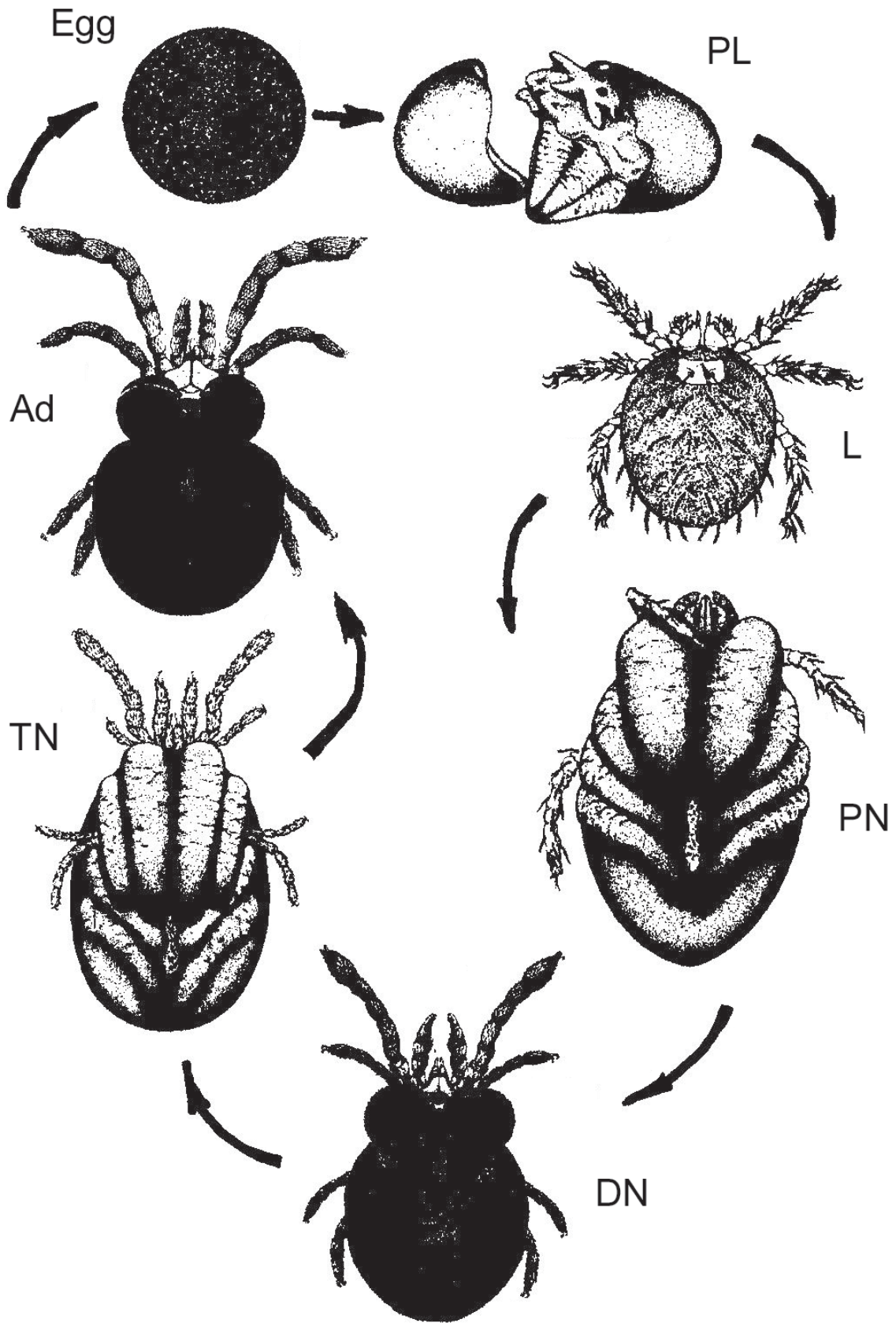
Fig.1. Life cycle of the parasitengone mites (on the example of the trombiculid mite, *Leptotrombidium akamushi*, with figures of stages from Neal and Barnett (1961).

PL — prelarva, L — larva, PN — protonymph, DN — deutonymph, TN — tritonymph, Ad — adult mite.

There are some problems concerning both designation and nature of stages received in acarological literature the name of calyptostases. Quite different terms are used for designation of these calyptostasic stages (regressive, quiescent, resting, immobile, non-feeding, covert, hidden, veiled etc.), but only some of them are appropriate for this purpose. There are essential differences also in an understanding the nature of such stages and their role in regard to the evolution of ontogenesis in Acari, and to the control of seasonal life cycles, due to those important aspects still need special attention. These different, non-synonymous approaches to ontogenetic and ecological peculiarities of calyptostasy in the evaluation of this phenomenon and its significance for the development and life histories of the Parasitengona are the main topics of the presented paper**.** Their consideration is the subject of the paper based on an analysis of available acarological literature. Special attention is paid here to the important, but unclear problem concerning the calyptostasic stages of the parasitengone mites as a possible tool in seasonal control of their life cycles.

TERMINOLOGY OF REGRESSIVE STAGES IN PROSTIGMATIC MITES

Some different terms mentioned in the introduction concern the phenomenon of calyptostasy in regard to its different aspects — ontogenetic (calyptostasic*), morphological (regressive), functional (immobile, non-feeding), ecophysiological (quiescent, resting) and virtual (covert, hidden, veiled). Undoubtedly, there are no objections for application of the original, precise and meaningful terms «calyptostasy» and «calyptostases» in their ontogenetic meaning. The same concerns the term «regressive» in its morphological sense, and «covert, hidden, veiled» in their virtual sense due to their adequacy and compatibility with corresponding traits, that makes these adjectives to be understandable both *sensu stricto,* and *sensu lato.* However, I have essential doubts in regard to the authorization for using the terms «quiescent» (used by many authors, e.g. by Shatrov 1999, 2000; Shatrov and Kudryashova 2006; etc.) and «resting» (Di Sabatino et al. 2000; etc.) for calyptostasic stages within their ontogenetic continuity. The usage of both these ecophysiological terms in the meaning of

«calyptostasic» results in some confusions and misunderstandings, inasmuch as they both are used erroneously by many acarologists for the immobile developmental state occurring in mites and ticks (as well as in other arthropods) during the last part of an intermolt period and connected with molting processes from their first steps (apolysis) through hatching (ecdysis), i.e. for the so called pharate stage. It is necessary to note also that the terms «quiescent» and «resting» are used already by entomologists and other biologists (quite adequately!) in connection with special consecutive type of dormancy (i.e. quiescence) participating in the control of seasonality of life cycles by means of temporary state of developmental and behavioral inactivity (resting) caused through direct impact of adverse external conditions (see Tauber et al. 1986; Danks 1987; Koštal 2006). Correspondingly, the other, prospective type of dormancy, the so-called diapause, is an anticipated arrest of development or activity aroused according to internal programs, usually under effect of token factors signalling an approach of unfavourable conditions, and eliminated by special mechanisms of reactivation.

Thus I guess that the terms «regressive» and «covert (hidden, veiled)» are appropriate in acarological literature for both designation and characteristics of calyptostasic stages (*i.e.* stages with calyptostasic traits), while the terms «quiescent» and «resting» (as well as «immobile» and «non-feeding») may be used for the supplementary characteristic of such stages only. Some additional special reasons concerning two terms of ecophysiological character will be considered below in the section on the role of calyptostasy in seasonal adaptations of the parasitengone mites.

CALYPTOSTASY AND ITS ROLE IN ONTOGENETIC EVENTS

Unfortunately, little is known about the organization of the calyptostasic stages in mites, as well as about the detailed developmental processes in them. Apparently the only essential studies of these questions belongs to Jones (1951, 1954) and Shatrov (1999, 2000) who have analyzed the moulting processes in calyptostasic instars of trombiculid mites (Acariformes: Trombiculidae). There is a great need, therefore, for further research and analysis of acariform mite's ontogenesis in order to understand the exact nature of calyptostases and the essence of alternating calyptostasy.

There are meanings that the life cycle of Parasitengona (in particular of Hydrachnidia) with their

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* I think that the term «calyptistasic» used in this paper is more correct grammatically and sounds better than the commonly used in acarological literature the term «calyptostatic».

heteromorphic larva and two pupa-like resting nymphal stages is similar to that of holometabolous insects (Walter and Proctor 1999; Di Sabatino et al. 2000; Smith et al. 2001). It is mentioned by Shatrov (1999), that the same analogy with respect to proto- and tritonymphs in Trombidia has been postulated earlier by Jones (1954), Johnston and Wacker (1967) and several other authors. I can add that Southcott (1961) used the terms «pupa I and II» for these stages. But Shatrov (1999, 2000) himself declared persistently, that «the quiescent instar» in the parasitengone mites with its specific mode of development (two moults at each nymphal calyptostase) couldn't be regarded as a pupa due to different, one-moulting traits in typical development at the pupal stage of holometabolous insects. However, there are known numerous examples of non-typical, complex nature of insect pupae that present an association of two successive pharate stages (pupal and adult) expressed particularly conspicuously in Diptera (Hinton 1976) and reminding the situation in nymphal calyptostases of parasitengone mites.

According to Hinton (1946, 1976), each new stage (or instar) in arthropods is initiated while the animal is still enclosed within the cuticle of the previous stage, and this part of its development represents the pharate stage (pharate larva, pupa, or adult in insects). Thus, every stage of an arthropod consists of a pharate stage (from apolysis through ecdysis) and a non-pharate stage (from ecdysis through the next apolysis). It is essential that Johnston and Wacker (1967) have regarded the «quiescent instars» (calyptostases) in trombiculid mites as the entire inactive periods within the cuticle of the previous instars, e.g. as the pharate instars as a whole. From my point of view, this approach is quite authorized, though nymphal calyptostases in mites are undoubtedly not homologous, but only analogous to insect pupae.

At the same time, while the pupa in insects can be really regarded as a progressive intercalary stage that ensures the strong metamorphosis of the wingless larva into the winged adult, the nymphal calyptostases are considered as regressive stages enabling only the shortening and optimization of ontogenesis (Shatrov 2000). Such evolutionary trends in trombidiiform mites manifesting the tendency to reduce the number of active stages were noted earlier by Knülle (1961) and Böttger (1977), and are accepted by many recent acarologists (Wohltmann 2001; Wohltmann et al. 2001; etc.). But calyptostasic stages in parasitengone mites might really be termed progressive, inasmuch as they serve the considerable structural reorganization that are most conspicuously manifested between heteromorphic larva and deutonymph (Wohltmann, personal communication).

In general, the difference between the opposite approaches to the nature of calyptostases in the parasitengone mites is quite virtual, inasmuch as they both imply the similar, all-level organismal reorganization at calyptostasic and pupal stages.

CALYPTOSTASES AND THEIR PARTICIPATION IN SEASONAL ADAPTATIONS OF THE PARASITENGONE MITES

1. Significance of calyptostasic stages in the parasitengone life histories

The main attention in investigations of life histories of the parasitengone mites has been paid to the phenomenon of larval parasitism in this group of Acari (Ewing 1949; Robaux 1974; Shatrov 2000; Shatrov and Kudryashova 2006; etc.) due to essential medical importance of trombiculid larvae as vectors of some rickettsioses and agents of dermatitis.

The other aspects of the parasitengone life histories, particularly the role of alternating calyptostasy and calyptostases themselves in the control of life cycles of these mites and their seasonal synchronization, have attracted much less attention of acarologists. It is significant that «only the active stages are considered» in the remarkable paper of R Mitchell (1957) on major evolutionary lines in water mites, and the same situation retained until now. Perhaps, the only exception is presented by the recent reviews of A. Wohltmann (2001), as well as of Wohltmann et al. (1999, 2001) with a comprehensive analysis of the life history evolution in terrestrial Parasitengona (including the available information on their seasonal adaptations with some data on calyptostasic stages in these mites). The seasonal aspects of trombiculid life cycles are reviewed shortly by Shatrov and Kudryashova (2006) also, who made the conclusion that the seasonal patterns of development in trombiculid mites and their hibernating stages are still unclear, inasmuch as the biology of these mites has been studied mainly in laboratory. I should add here that the most unclear is the role and function of calyptostasic stages in this regard due to the lack of thorough respective field and laboratory investigations.

According to Wohltmann (2001) and Wohltmann et al. (2001), the calyptostasy in parasitengone mites evolved to ease synchronization of their life cycles with optimal host availability. Such an

affirmation is quite correct for temporary parasites and phoretics (see Siepel 1994), especially in connection with the other Wohltmann's conclusion that the larval parasitism of these mites on flying insects and other mobile arthropods has derived from a predatory life style, and main advantage of this transformation was connected with an increased ability to disperse via the host. Wohltmann (2001) affirmed also that synchronization of life cycles by means of calyptostasy evolved for enabling the best conditions for meeting both sexes to mate. It is remarkable, however, that there are no indications in his review in regard to the possibility for evolving of calyptostasy in parasitengone mites due to direct effects of climate seasonality itself. Nevertheless the Wohltmann's considerations and data reviewed in his paper (2001) permit to attribute regulatory functions of seasonal adaptations (diapause and other forms of dormancy) to calyptostasic stages. Though the role of them in synchronization of parasitengone life cycles with hosts is less evident, the available data give manifold confirmation for their important role in adaptation to climate seasonality. More detailed consideration of calyptostasic stages in this regard is presented below.

2. Seasonal patterns in life cycles of the parasitengone mites

It is worth mentioning here that both terrestrial Trombidia (Wohltmann 2001, etc.) and aquatic Hydrachnidia (Di Sabatino et al. 2000, 2003; etc.) are characterized by the conspicuous regularity of seasonal patterns in life cycles of these mites and their control. As it follows from data compiled by Wohltmann (2001), most species of parasitengone mites display the uni- to semivoltine* life cycles completed in one (annually) or two years (biennially) respectively. Namely these life cycles of plesiotypic character, peculiar for the most Trombidia, in particular for trombidiid (Zhang 1999), microtrombidiid (Wohltmann 1996) and trombiculid mites (Sasa 1961), 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/year is apotypic and more derivative. This type of voltinism being not so common in Parasitengona is known for

some water mites (Lanciani 1969, 1971; etc.), in Trombidia only for the erythraeid mite *Balaustium putmani* (Putman 1970) and some trombiculid species (Sasa 1961). Life-cycles in Erythraeidae, as a rule, are strictly univoltine, with the appearance of their active instars in the field within rather short particular periods of the year, while most of the year erythraeids spend as resting eggs or calyptostases (Southcott 1961 — cited by Wohltmann 2001). In other Trombidia, the life cycle may be also univoltine (e.g. in *Johnstoniana rapax*) or uni-semivoltine (*J. errans*), when some individuals complete their development within one year, while others need two years.

According to Wohltmann (2001) and Wohltmann et al. (2001), the high degree of life cycle synchronization found in most species of parasitengone mites and expressed in synchronous appearance of larvae with their hosts, as well as in the simultaneous abundance of males and females during the mating period, is ensured mainly by diapause of obligatory character at particular developmental stage, such as the egg (Johnstonianidae; Eggers 1995), the protonymph (*Leptus ignotus, Leptus sp.*; Wohltmann 1995) or the pre-reproductive adult (*Eutrombidium trigonum*; Wohltmann et al. 1996). However, as it follows from the available data (Tables 1–2), this obligatory diapause is often supplemented also by some other dormant states (quiescence or facultative diapause) with different ontogenetic localization. There is known a case also (*Johnstoniana parva* — Wohltmann, personal communication) with facultative diapauses at two different stages (an egg diapause and adult reproductive diapause), when the respective developmental arrest of eggs (in the female ovary or after egg-laying) is determined both at the adult stage in dependence on the time of female insemination or oviposition, and eliminated by the prolonged chilling. It is quite probable that such a combination is not a single case in the parasitengone mites.

Among the **Trombidia** (Table 1), representatives of the family Microtrombidiidae (with uni-semivoltine development) are characterized usually by hibernating dormancy in nymphal and adult instars, but sometimes with an additional third instar (eggs). The state of obligatory diapause is equally peculiar for egg and adult instars of these mites. In the family Johnstonianidae with uni- and uni-semivoltine development the hibernation is known at one (egg or adult), two (egg and adult) or three stages (egg, nymph and adult). The number and distribution of hibernating stages in the family

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* In literature instead of terms «multivoltine» , «univoltine» and «semivoltine» there are often used their synonyms «polyvoltine», «monovoltine» and «biennial».

Table 1

Some examples of hibernating and diapausing stages in life cycles of terrestrial parasitengone mites
(Trombidia) (after Wohltmann 2001 with supplements)

Species 1	Hibernating stages 2	Voltinism 3	References 4
Microtrombidiidae			
1. *Camerotrombidium pexatum*	**adult**	−	Wohltmann, Makol and Gabrys 2003
2. *Camerotrombidium rasum*	nymphs, **adult**	uni-semi	Wohltmann 1996a
3. *Campylothrombium boreale*	**egg**, nymphs, adult	uni-semi	Wohltmann 1996a
4. *Dactylothrombium pulcherrimum*	**egg**, nymphs, adult	uni-semi	Wohltmann 1996a; Wohltmann and Gabrys 2003
5. *Enemothrombiium bifoliosum*	DN, **adult**	uni-semi	Wohltmann and Gabrys 2006
6. *Echinothrombium rhodinum*	**egg**, adult	uni-semi	Gabrys and Wohltmann 2003
7. *Echinothrombium spinosum*	**egg**, adult	-	Wohltmann (pers.comm.)
8. *Eutrombidium locustarum*	DN, **adult**	uni-semi	Huggans and Blickenstaff 1966
9. *Eutrombidium trigonum* *	PN, DN, TN, **adult**	uni-semi	Wohltmann et al 1996
10. *Georgia pulcherima*	**egg**, DN, adult	uni	Wohltmann 1996a
11. *Microtrombidium pusillum*	nymphs, **adult**	uni-semi	Gabrys and Wohltmann 2001
12. *Platytrombidium sylvaticum*	nymphs, **adults**	uni-semi	Gabrys, Wohltmann and Makol 2005
13. *Platytrombidium fasciatum*	nymphs, **adults**	uni-semi	Gabrys, Wohltmann and Makol 2005
14. *Valgothrombium valgum*	DN, **adult**	uni-semi	Wohltmann and Wendt 1996; Wohltmann 1996a
Johnstonianidae			
1. *Centrotrombidium schneideri*	**adult**	uni	Wohltmann and Wendt 1996
2. *Diplothrombium longipalpe*	**egg**, adult	−	Wohltmann, Gabrys and Makol 2004
3. *Johnstoniana errans*	**egg**, nymphs, adult	uni-semi	Wohltmann 1996b
4. *Johnstoniana eximia* (= *J. tuberculata*)	**egg**, adult	uni	Wohltmann et al.1994
5. *Johnstoniana parva*	(egg), nymphs, (**adult**)	uni-semi	Wendt et al.1994; Wohltmann et al. 2001
6. *Johnstoniana rapax*	**egg**	uni	Eggers 1995
Trombidiidae			
1. *Allothrombium fuliginosum*	nymphs, **adult**	uni-semi	Wohltmann 2001
2. *Allothrombium mitchelli*	**adult**	uni	Wiggins et al. 2001
3. *Allothrombium pulvinum*	**adult**	uni	Zhang, Xin 1989; Saboori, Zhang 1996
4. *Allothrombium ovatum*	**egg**	uni	Dong et al.1996
5. *Podothrombium filipes*	egg, **DN**, adult	uni-semi	Wohltmann 2001
6. *Trombidium brevimanum*	nymphs, **adult**	uni-semi	Wohltmann 1999
7. *Trombidium holosericeum*	nymphs, **adult**	uni-semi	Makol and Wohltmann 2000
Trombiculidae			
1. *Neotrombicula autumnalis* *	**egg, L**, PN, DN, (adult)	uni-semi	Daniel 1961; Scholer 2002
2. *Hrsutiella zachvatkini*	**egg, L**, nymphs, adult	uni-semi	Daniel 1961; Vasil'eva1977; Shatrov 2003
3. *Leptotrombidium pallidum* *	L, DN, TN, **adult**	uni-semi	Takahashi et al. 1993
4. *Leptotrombidium akamushi*	L, DN, **adult**	uni-semi	Takahashi et al. 1995
5. *Leptotrombidium deliensis*	**adult**	multi (?)	Mehta 1948
6. *Eutrombicula alfreddugesi*	par.L	multi (?)	Williams 1946
7. *Trombicula hylae*	par.L	multi (?)	Ewing 1926
Calyptostomatidae			
1. *Calyptostoma velutinus*	L, nymphs, **adult**	uni-semi	Vistorin-Theis 1975; Wohltmann et al.1999
Smarididae			
1. *Hirstiosoma ampulligera*	**egg**, nymphs, adult	−	Wohltmann (pers. comm.)
Erythraeidae			
1. *Abrolophus brevicollis*	**adult**	uni	Wohltmann 2001
2. *Abrolophus longicollis*	**egg**	uni	Wohltmann 2001

Table 1 (continued)

1	2	3	4
3. *Abrolophus rudaensis*	**egg**	uni	Wohltmann 2001
4. *Curteria southcotti*	**egg**	uni	Wohltmann, Makol and Gabrys 2007
5. *Erythraeus alpendiculatus*	**egg**	uni	Wohltmann (pers. comm.)
6. *Erythraeus cinereus*	**adult**	uni	Wohltmann 2001
7. *Erythraeus phalangioides*	**egg**	uni	Wohltmann 2001
8. *Erythraeus regalis* (= *E. nivalis*)	**DN**	uni	Wohltmann (pers. comm.)
9. *Erythraeus rupestris* *	**PN**	uni	Wohltmann (pers. comm.)
10. *Leptus beroni*	**DN**	uni	Wohltmann 1995
11. *Leptus fernandezi* *	egg, **PN**	uni	Wohltmann 1995
12. *Leptus ignotus* *	**PN**	uni	Wohltmann 2001
13. *Leptus* sp.*	**PN**, TN	uni	Treat 1979
14. *Leptus trimaculatus* *	PN, **adult**	uni	Wendt et al. 1992
15. *Balaustium murorum*	**egg**	uni	Wohltmann 2001
16. *Balaustium putmani*	**(egg)**	multi	Putman 1970

Notes: The column 1: Species of mites with hibernating nymphal calyptostases are marked with an asterisk (the number of such species may be much higher than cited in the Table at the cost of species with hibernating «nymphs»). The column 2: The mites hibernating in the state of diapause (according to published data and Wohltmann's personal communication) are marked in bold; the other mites hibernating in the unknown dormant state are given in common prim. The case of facultative diapause is given in bold with brackets. Abbreviations in the column 3: uni — univoltine, semi — semivoltine, multi — multivoltine development.

Trombidiidae with its uni-semivoltine development are both variable and similar to the johnstonianid mites — one (egg or adult), two (nymph and adult) or three stages (egg, nymph and adult) also. In the Trombiculidae with uni-semivoltine development the number of dormant stages is much more (3–5) than in tropical multivoltine mites (with only one dormant stage presented by adults or parasitizing larvae. Three hibernating stages (larva, nymph and adult) enable the regulation of uni-semivoltine development in Calyptostomatidae. However, the most species of Erythraeidae with their univoltine development are characterized by the single species-specific winter diapause at any developmental stage (usually as egg, but also as deutonymph, adult or calyptostasic protonymph), though some *Leptus* species possess the dormant state at two stages (calyptostasic protonymph plus egg or adult). However the bivoltine *Balaustium putmani* has its control by means of facultative egg diapause adapted after egg-laying firstly for aestivation and later for hibernation (Putman 1970). The related species *B. murorum* has the hibernating egg diapause of obligatory type synchronizing the univoltine life cycle of this species, similarly with the majority of erythraeid mites (Wohltmann 2001).

According to A. Wohltmann (personal information) in semivoltine species the capacity to survive winter in quiescence is present in all postlarval instars, sometimes even in eggs or larvae. In strictly univoltine species, at least the nondiapausing active instars are not able to overwinter (but inactive instars might be, as *Leptus fernandezi* in an example).

Aquatic **Hydrachnidia** (Table 2) in regard to the number and localization of dormant stages are similar with terrestrial Trombidia. The hibernating dormancy can involve both one and some stages of their life cycles. As mentioned by Wohltmann (2001), the water mites reveal the diapause mostly as deutonymphs or adults (before reproduction), or as larvae inside the egg-shells (*Eylais extendens*) or at the host (*Eylais discreta*). In general, the first larval case (*E. extendens*) may be considered as a prelarval calyptostase. It is quite probable that this type of seasonal dormancy controlling the synchronized hatching of parasitic larvae is common in parasitengone mites (both aquatic and terrestrial) not less than an egg diapause. In its turn the latter case (*E. discreta*) corresponds the feeding delay of terrestrial trombiculid larvae (*Neotrombicula autumnalis* and *Hirsutiella zachvatkini*) attached to their mammalian hosts in winter (see below). Among fresh-water mites this type of life cycle synchronization is known not only in the genus *Eylais,* but also in some species of *Hydrachna*. There are known also some species of Hydrachnidia with hibernating calyptostasic stages, e.g. some water mites from temporary waters like *Arrenurus planus* (Wiggins et al. 1980) with long resting protonymphal calyptostase.

Table 2

Some examples of hibernating stages in life cycles of aquatic parasitengone mites (Hydrachnidia)

Species	Superfamily, Family	Hibernating stages	Voltinism	References
1	2	3	4	5
1. *Hydrachna conjecta*	Hydrachnoidea, Hydrachnidae	Egg, par L	multi	Davids 1973
2. *Hydrachna globosa*	Hydrachnoidea, Hydrachnidae	par L	uni-semi	Bottger 1972 a,b
3. *Hydrachna maramauensis*	Hydrachnoidea, Hydrachnidae	par L	uni	Davids 1973
4. *Eylais infundibulifera*	Eylaoidea, Eylaidae	Egg, DN	multi	Bottger 1962; Nielsen and Davids 1975
5. *Eylais extendens*	Eylaoidea, Eylaidae	Egg	?	Nielsen and Davids 1975
6. *Eylais discreta*	Eylaoidea, Eylaidae	par L	bi	Nielsen and Davids 1975
7. *Eylais setosa*	Eylaoidea, Eylaidae	Egg, par L	?	Nielsen and Davids 1975
8. *Limnochares aquatica*	Eylaoidea, Limnocharidae	Ad	uni	Bottger 1972a
9. *Neoacarus hibernicus* *	Arrenuroidea, Neoacaridae	Egg, TN, Ad	uni-semi	Gledhill 1969
10. *Arrenurus planus* *	Arrenuroidea, Arrenuridae	PN, TN	uni ?	Wiggins et al.1980
11. *Arrenurus globator*	Arrenuroidea, Arrenuridae	Egg	uni	Bottger 1962
12. *Feltria romijni* *	Hygrobatoidea, Feltriidae	DN, TN, Ad	uni-semi	Efford 1965
13. *Unionicola crassipes*	Hygrobatoidea, Unionicolidae	DN, Ad	uni-semi	Bottger 1972b
14. *Piona nodata*	Hygrobatoidea, Pionidae	DN	multi	Bottger 1962
15. *Limnesia maculata*	Hygrobatoidea, Limnesidae	Ad?	uni	Bottger 1972b

Notes. The column 1: Species of mites with hibernating nymphal calyptostases are marked with an asterisk. The column 2 shows the taxonomic position (superfamily and family) of species (according to Cook 1974). the abbreviations in the column 3 mean: parL — parasitic larva attached to the host; PN, DN, TN — proto-, deuto- and tritonymph; Ad — adult mites, in the column 4: uni — univoltine, semi — semivoltine, multi — multivoltine development

As it is seen from this review, the diapausing instar (or instars), being species-specific in parasitengone mites, as well as in other Acari and all arthropods, may reveal, nevertheless, considerable peculiarities in their localization along the life cycle even between related species. Besides that, the hibernation of some trombiculid mites is known to take place even at different steps of the same instar. For instance, larvae of the above-mentioned *N. autumnalis* and *H. zachvatkini* can overwinter both in unfed and engorged state, as well as during their attachment to the host (Keay 1937; Daniel 1961; Shoshina 1965; Vasil'eva 1977; Klumpen 2002). The hibernation of attached larvae (corresponding the special form of diapause known in ixodid ticks, see Belozerov 1982) is known also in the North American species, *Eutrombicula alfreddugesi* (Williams 1946). It is of interest that delayed feeding of larvae on their hosts (that evidences their participation in seasonal control of life cycles) was observed not only in trombiculid mites from temperate climate, but also in subtropical trombiculids parasitising on terrestrial Amphibia (Ewing 1926) and in tropical trombidiids parasitising on insects

(Michener 1946). As was noted above, some water mites (*Hydrachna, Eylais*) can hibernate also as larvae attached to their insect hosts (Table 2).

3. Calyptostasic stages as tools of seasonal control in the parasitengone life cycles

It was marked by Wohltmann (2001), that the diapause both in terrestrial and aquatic Parasitengona might involve not only eggs and the so called active stages (larva, deutonymph and adult mites), but also inactive covert stages (proto- and tritonymphal calyptostases, and probably prelarval calyptostase). This is really confirmed by available data, though not very numerous (Tables 1–2). Nevertheless, we need more confirmations for this conclusion, because in literature there were expressed affirmations, as mentioned above, that evoke some doubts. I mean the conspicuous feature of the life cycles in Parasitengona expressed in the constant and shorter duration of calyptostasic stages (prelarva, proto- and tritonymph) as contrasting to the variable and longer duration of mobile stages, i.e. larva, deutonymph and adult mite (Shatrov 2000, Wohltmann 2001, Wohltmann et al. 2001; Shatrov

and Kudryashova 2006, etc.). Some examples of this contrast are given in the above-mentioned publications. For instance, the proto- and tritonymphal calyptostases in the microtrombidiid *Eutrombidium trigonum* last 23–28 days, while its active deutonymph — from 21 up to 220 days, in the johnstonianid *Johnstoniana errans* — 15–23 and 15–97 days, and in the trombiculid *Eutrombicula cinnabaris* — 9–10 and 59 days respectively (Wohltmann 2001). Similar data of the same character are given by some other authors, *e.g.* by Michener (1946a) for tropical *Eutrombicula batatas* (5–7 and 16–45 or more days respectively), and by Simonová (1983) for two boreal trombiculids, *N. autumnalis* and *H. zachvatkini* (11–17 days in calyptostasic proto- and tritonymphs, while from one to 7–14 months in active deutonymphs). Not less conspicuous data for tritonymphs and deutonymphs of *H. zachvatkini* (7–26 and 9–597 days) and four other trombiculids (*Lepototrombidium orientalis, L. schlugerae, Neotrombicula vulgaris, Euschoengastia rotundata*) are presented in the Shatrov's monograph (2000). These data say as if for non-diapausing properties of calyptostasic stages due to their short duration. Shatrov (2000) assumed therefore that calyptostases might play the stabilizing and optimizing role within dynamics of development in chigger mites. The same meaning is expressed by Wohltmann (2001) and Wohltmann et al. (2001). However, there are quite opposite data concerning the longevity and variability of calyptostasic stages. For instance, protonymphal and tritonymphal stages in *Leptus* (Parasitengona, Erythraeidae) are «of unpredictable duration, lasting from a few weeks to several months» (Treat 1979) that gives the direct confirmation for the presence of diapausing arrest in nymphal calyptostases. The function of calyptostasic stages may enable not only the stabilization of life cycles (their acceleration according to the Shatrov's meaning) by means of «condensation» of two (or even three*) developmental stages, but also the synchronization of the life cycle steps with certain seasonal events (of either physical, or biological character) by means of developmental or behavioral arrests. The results of my experimental investigations on diapause in ixodid ticks (Parasitiformes: Ixodidae) evidence that in tick species with a hereditary predisposition

for diapause at the particular stage (e.g. adults of *Ixodes ricinus*), the duration of this stage due to its capability for developmental arrest is markedly more, than at the same stage in ticks (*I. persulcatus*) lacking these properties (Belozerov 1976), whereas their difference in regard to its variability (depending upon many environmental and internal factors) is neither essential, nor regular. Naturally, the duration of development in diapausing specimens is much more than in non-diapausing specimens, as known for the thoroughly studied acarines (ticks, as well tetranychid and phytoseiid mites).

Theoretically it is possible to conclude that in dependence on evolutionary circumstances the calyptostasic stages in parasitengone mites may reveal either the retarding, or accelerating function due to the control of their life cycles, inasmuch as in both cases it is the function of synchronization. However, the recognition is more reliable about two opposite approaches to ecological importance of calyptostasy, i.e. its organizing role in parasitengone life cycles. The main (parasitological) approach is based on recognizing the optimizing role of calyptostasy through acceleration of development and synchronization of hatching periods in parasitic larval mites and their hosts, while the opposite (ecophysiological) approach considers the calyptostasy as an adaptation to climate seasonality itself through retaining the possibility for developmental arrests at particular calyptostasic stages evoked from normal, non-calyptostatic ancestral stages (with adaptations for dormancy) as a result of oligomerization of life cycles (see Dogiel 1954). In spite of the mentioned differences, both approaches are similar in emphasizing the seasonal events (of biotic and abiotic character respectively).

It is necessary to add here that obligatory diapause as a main tool of seasonal regulation, mainly at the egg or adult stages, is often supplemented by dormancies of different type at some other stages that are capable for hibernation and enable the control of seasonality in life cycles also (Tables 1–2). In the mentioned erythraeid *L. fernandezi* (according to personal information of A. Wohltmann it is a *nomen nudum*), the obligatory diapause in the protonymphal calyptostase is supplemented, for instance, by facultative hibernation at egg stage that may result in semivoltine development of this mite (Wohltmann 1955, 2001). The more multiple set of hibernating stages of similar complex composition is characteristic for terrestrial *Eutrombidium trigonum* (Fig.2) and aquatic *Fel-*

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* There are parasitengone species (*Piona nodata* — Böttger 1962, *Microtrombidium hirsutum* —Wohltmann 2001), in which the calyptostasic stage involves prelarva, larva and protonymph, due to that the stage hatching from egg is represented by active deutonymph.
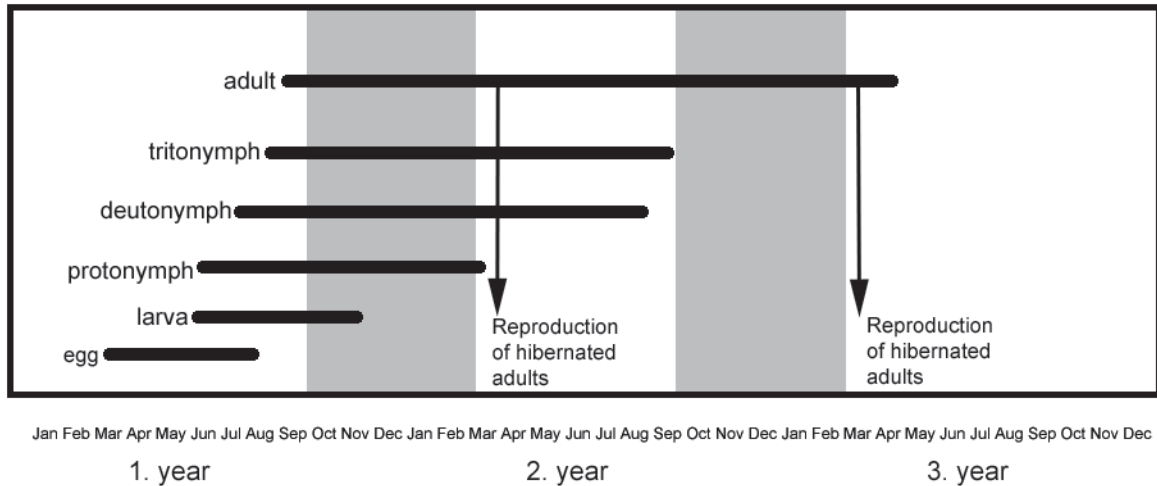
Fig.2. Phenology of development in the terrestrial trombidiid *Eutrombidium trigonum* (from Wohltmann et al. 1996).
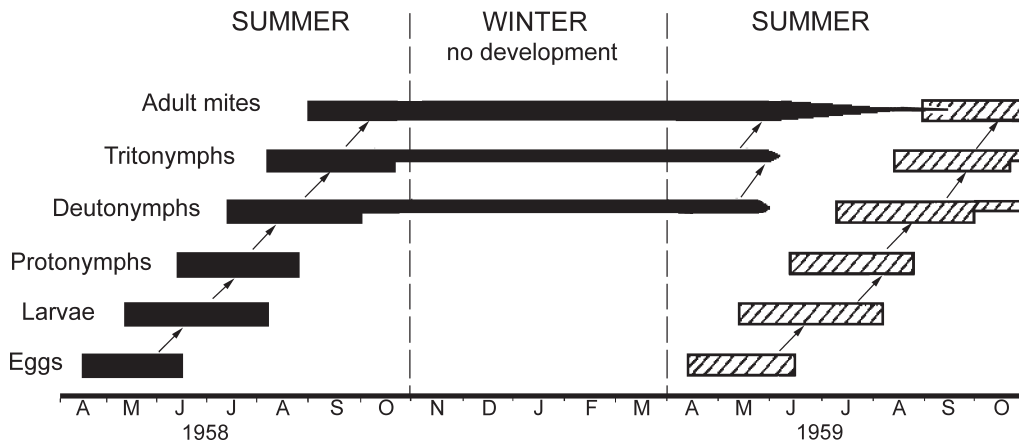

Fig. 3. Phenology of development in the aquatic hydrachnid *Felria romijni* (from Efford 1965).

tria romijni (Fig.3). The adult stage with obligatory diapause is supplemented in these species by non-diapause dormant states at some nymphal (calypto-stasic and non-calyptostasic) stages.

Being forced by the direct temperature decrease, this type of supplementary dormant state can be classified undoubtedly (according to Müller 1992) as a consecutive dormancy, i.e. quiescence. The same concerns apparently some other numerous cases of supplementary dormant stages in terrestrial and aquatic parasitengone mites (Tables 1–2). Both these groups of Parasitengona are undoubtedly similar in regard to the presence of different types of dormant state (diapause and quiescence) both at normal and calyptostasic stages within their life cycles.

4. Ecophysiological traits of calyptostasic and normal stages confirming their similarity in synchronizing the seasonality of parasiten-gone life cycles

Essential information that confirms the synchronizing function of calyptostasic stages in the life cycle control is granted by the available (however very limited) data on their ecophysiological properties. First of all, I mean the similarity in mechanisms controlling the termination of dormant state at calyptostasic and normal, non-calyptostasic stages. According to Wohltmann's conclusion, the overwhelming majority of parasiten-gone mites reveals the dominance of uni- to semi-voltine life cycles with rigid control through obligatory diapause, often at egg stage, but in some cases

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at adult and nymphal stages (Table 1–2). The main role in synchronization of these life cycles is ensured, as a rule, through elimination of dormant state at diapausing stage by external environmental factors, in most cases by prolonged (2–4 months) chilling followed by return of reactivated eggs (or other stages) from low temperatures (0–6ºC) into incubating conditions (15–25ºC). Such a mechanism was revealed in and explained for the johnstonianid mite *Johnstoniana rapax* (with univoltine development and obligatory diapause at egg stage), whose diapausing eggs receive a capability for normal fast development after 2- or 3-month chilling followed by an increase of temperature to 15–20ºC (Eggers 1995). Under field conditions of North Germany this mechanism ensures the synchronized simultaneous hatch of overwintered eggs at the beginning of May with the following development of larvae through adults by the end of summer (July–August) completed with laying of diapausing eggs by adult females in September–October. Similar seasonal course of univoltine development controlled by the same temperature-dependent mechanism for synchronization of larval hatch from overwintered diapausing eggs in spring was demonstrated also in the closely related species, *Johnstoniana tuberculata* (= J. *eximia*) (Wohltmann et al., 1994).

The control of seasonal development in the mentioned univoltine johnstonianid species with obligatory egg diapause depends in full on temperature, being independent on photoperiod (Wohltmann, 2001). The same situation is known in some microtrombidiid mites with egg (*Campylothrombium boreale* and *Georgia pulcherima*) or adult diapause (*Camerotrombidium rasum*), as well as in the erythraeid *Leptus beroni* with diapause at the deutonymphal stage (Wohltmann, 1995, 1996b, 2001). It is of interest, that the specialized erythraeid mite *Balaustium putmani* (with predatory larva and bivoltine development) has the facultative diapause in eggs laid by females of the second generation in July–August. Its termination with a receipt of a capability for fast spring development is enabled also by 2-month chilling followed by watering of overwintered eggs (Putman, 1970), while its induction is likely determined here by photoperiodic response of adult females to decreasing day-length during the second half of summer. There are preliminary unpublished data also that some trombidiid (*Allothrombium fuliginosum, Trombidium holosericium*) and erythraeid mites (*Erythraeus cinereus*) reveal both temperature- and

photoperiod-determined termination of diapause at the non-calyptostasic nymphal and adult stages (Wohltmann, 2001). Apparently this twofold mechanism of reactivation is characteristic of some other univoltine erythraeids, e.g. of *Erythraeus rupestris* diapausing as a calyptostasic protonymph (Wohltmann, personal communication).

The erythraeid mite *Leptus fernandezi* (nom. nud.) (with its uni- or semivoltine development and obligatory protonymphal hibernation) represents the only case investigated in regard to ecophysiological control of life cycle seasonality in parasitengone mites at the calyptostasic stage. As was shown by Wohltmann (1995), the termination of dormant state in protonymphs of this species is realized by the same temperature-dependent mechanism, likely to the most parasitengone mites diapausing at the non-calyptostasic stages (eggs, deutonymphs and adults). Prolonged chilling of dormant protonymphs of *L. fernandezi* under temperature of 5ºC followed by its increase to 15–20ºC, results in the fast development of reactivated nymphs and highly synchronized emergence of deutonymphs with the following development through the adult stage, though there is no controlling effect of photoperiod. There is no doubt, therefore, that protonymphal dormancy in *L. fernandezi* (similar to seasonal arrests of development at the egg, deutonymphal or adult stages in the above-mentioned parasitengone mites) corresponds the category of obligatory diapause and ensures the main regulatory function in seasonal synchronization of life cycles in this mite. It is understandable, as well, that the model for functional responses of parasitengone mites in regard to the diapause control (developed by A.Eggers for *J. rapax* in 1993 and mentioned in the Wohltmann 2001 review) seems really to be valid for temperate Parasitengona diapausing at egg or calyptostasic stages.

The additional data on ecophysiological properties of calyptostasic stages as tools in life cycle control of Parasitengona are supplied by an investigation of eggs and protonymphs in some species of the Erythraeoidea and Trombidioidea in regard to their resistance for humidity deficiency (Wohltmann 1998). These experiments have shown that the erythraeoid mites adapted to dry conditions are more resistant to drought (due to reduced water loss) than the hygrophilic trombidioid mites retaining properties of hygrobiotic stem species of terrestrial Parasitengona. The most essential result of this study (in regard to the problem under consideration) concerns the recognition of real resistance of calyptostasic stages (prelarvae and protonymphs)

in all the investigated erythraeoid mites (*Leptus ignotus, Erythraeus sp., Hirstiosoma ampulligera, Charletonia cardinalis*) to low humidities (73–76% RH), while the trombidioid mites (*Johnstoniana errans, J .parva, J. tuberculata, Trombidium holosericeum, Calyptostoma velutinus* and some others) at the same stages need to be submerged in water or maintained at the humidity of 98–100% RH. It is of special interest that eggs and prelarvae of the erythraeoid mites have revealed the temporary arrest of development at the humidity of 73–76% RH, with its retaining during one month and a renewal of development after the transfer of eggs into humidity increased up to 98–100% RH. These data show that the seasonal control of life cycles in terrestrial Parasitengona can be really enabled by resistant calyptostases, inasmuch as at least two calyptostasic stages in the erythraeoid mites (prelarva and protonymphs) possess the capability to survive the periods of drought in the state of humidity-dependent quiescence. Quite possible, that nymphal calyptostases in some other trombidioid mites, not revealing the capability for humidity-dependant arrest of development (Wohltmann 1998), may possess the ability for the temperature-dependent quiescence (alike to the non-calyptostasic stages of terrestrial Trombidia).

DISCUSSION AND CONCLUSION

The parasitengone mites (Acariformes: Prostigmata) are characterized by the modified type of life cycles revealed in the alternation of normal, functionally active ontogenetic stages (egg, larva, deutonymph and adult) and regressive calyptostases (prelarva, protonymph and tritonymph). The main function of calyptostases consists of ensuring the events of organismal reorganization between non-calyptostasic stages (alike the pupal stage between larval and adult stages of the holometabolous insects). The analogy between calyptostasic stages in the parasitengone mites and pupal stage in insects recognized by the majority of acarologists (Jones 1954; Southcott 1961; Johnston and Wacker 1967; Smith and Cook 1991; Walter and Proctor 1999; Di Sabatino et al. 2000, etc.) is denied by some others (Shatrov 1999, 2000; Shatrov and Kudryashova 2006). But the prevailing view has the more reliable foundation from anatomical studies of entomologists (Hinton 1946, 1976), and even of acarologists (Jones, 1954), concerning the pharate nature of the mentioned stages in Insects and Acari.

According to Wohltmann (2001), the overwhelming majority of the extant parasitengone mites, both terrestrial (Trombidia) and aquatic (Hydrachnidia), retain three correlated traits evolved in the stem-lineage of Parasitengona (the nymphal calyptostasy, larval parasitism and dominance of semi- to univoltine life cycles with rigid control through obligatory diapause). The need in synchronized annual life-cycles is considered as a major selection pressure leading to the transformation of active to calyptostasic instars and promoting the simultaneous emergence of parasitic larval mites with their hosts, as well as the meeting of adult mites during the mating period (Wohltmann 2001; Wohltmann et al. 2001). The same meaning about optimization of life cycles (through acceleration of development in nymphal calyptostases) is expressed by Shatrov (2000) and Shatrov and Kudryashova (2006). More correct interpretation can be represented, however, by recognizing the calyptostasy as a result of oligomerization in the parasitengone life cycles according to this leading principle of morphological evolution (see Dogiel 1954), as well as of evolution of life cycles (Beklemishev 1970).

It is well known that in insects and other arthropods the seasonal synchronization involves special adaptations revealed as the dormancy (diapause or quiescence) at particular (single or multiple) stages of the life cycle (Lees 1955; Danilevsky 1961; Müller 1970, 1992; Tauber et al. 1986; Danks 1987; Saunders 2002). The same is characteristic of representatives of the Acari lacking the alternating calyptostasy, e.g. in the blood-sucking ixodid ticks, plant-inhabiting tetranychids and eriophyids, as well as in predatory phytoseiids (Belozerov 2006, 2007). In the parasitengone mites this synchronizing function belongs, as a rule, to the normal, non-calyptostasic stages, mainly to eggs and adult mites (Tables 1 and 2). However, as it was marked by Wohltmann (2001), and confirmed by data of the presented paper, this function both in terrestrial and aquatic Parasitengona may involve not only eggs and the so-called active stages (larva, deutonymph and adult mites), but also inactive regressive stages (proto- and tritonymphal calyptostases, as well as prelarval calyptostase).

In spite of some doubts aroused due to the above-mentioned incorrect interpretation of differences in the duration of calyptostasic and normal stages, the participation of calyptostases in the life cycle synchronization through arising the developmental or behavioral arrests at these stages, is well confirmed by results of the life cycle monitoring in some trombidioid and hydrachnoid mites under field conditions (Daniel 1961; Efford 1965; Put-

man 1970; Takahashi et al. 1993; Wendt et al. 1994; Eggers 1995; Wohltmann 1995, 1996; Wohltmann and Wendt 1996; Wohltmann et al. 1996), as well as of experimental ecophysiological investigations of these mites in laboratory (Putman 1970; Wohltmann 1995, 1998; Eggers, 1995; Wohltmann et al. 1996). Of special interest are data from experiments that ascertained the similarity of physiological mechanisms for maintenance and termination of obligatory diapause (the parapause according to Müller 1970, 1992) in calyptostasic protonymphs of the erythraeid *Leptus fernandezi* (Wohltmann 1995) and in prelarvae of the erythraeids *Leptus ignotus* and *Erythraeus sp.* (Wohltmann 1998) with those in non-calyptostasic stages. In both cases the elimination of diapause (i.e. reactivation) needs long chilling (during 2–4 months) followed by keeping the state of quiescence (at low temperatures or humidity) that is interrupted afterwards by an increase of temperature in quiescent protonymphs or by watering of quiescencent prelarvae inside the egg shell. The similar temperature-dependent mechanism for termination of obligatory diapause seems to be peculiar also for termination of facultative egg diapause in the erythraeid *Balaustium putmani* with the photoperiod-dependent mechanism of its induction. Besides that, both temperature- and photoperiod-dependent termination of nymphal and adult diapauses mentioned by Wohltmann (2001) for some trombidiid and erythraeid mites, and likely related to the category of the eudiapause, is also probable in their calyptostasic stages. Such a similarity between calyptostasic and normal, non-calyptostasic stages in regard to mechanisms controlling the diapause and, respectively, to their role for the life cycle synchronization, seems to be quite possible due to the analogous role and ecological importance of insect pupae (at the pharate adult stage) (see Danks 1987).

The analysis of published data on alternating calyptostasy in the parasitengone mites (Tables 1–2) permits to conclude that the function of nymphal calyptostases as tools for seasonal synchronization is characteristic of them in the same extent, as for non-calyptostasic, normal instars in the life cycle of these mites. This function is very important, but nevertheless quite less than their main function of organismal reorganization and unionization of some neighbouring stages for a decrease in number of the life cycle instars (that is in full correspondence with the Dogiel's rule about the oligomerization as a leading pathway of evolutionary changes in polymeric biological systems). It is notable that evolu-

tionary reorganizations in lifecycles of ixodid ticks follow the same rule (Belozerov 1991).

There are some additional aspects of the problem to be approached in the conclusion due to my previous papers on these aspects (Belozerov 2006, 2007). The analysis of data on alternating calyptostasy in the parasitengone mites do permit to make no definite conclusions yet, concerning the evolution in their systems of seasonal control (in regard to changes in the number and distribution of instars that are capable for dormancy) and its relationships to the phylogeny of the Parasitengona. The present materials say more for independence and discrepancy of these events, though some data support the conformity in their pathways. This idea is confirmed by the dominance of uni- to semivoltine development in plesiotopic mites with multiple dormant stages (e.g. in the Microtrombidiidae and Johnstoniidae) in contrast to the presence of multivoltine development in more derivative, apotypic mites with a single dormant stage (e.g. in Erythraeidae). The problem needs more large-scale and thorough studies for its solution.

The same concerns another problem, common not only for the parasitengone mites, but for the almost all Acari. I mean the necessity in more thorough investigations to understand and differentiate the nature of different kinds of their dormancies that may be either of prospective type (diapause), or of consecutive type (quiescence), as well as the evolution of these adaptations.

ACKNOWLEDGEMENTS

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