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OVOVIVIPARITY, PRELARVA AND THE PECULIARITIES OF ECLOSION IN FRESH-WATER ORIBATID MITES *THRYPOCHTHONIELLUS SETOSUS* (WILL.) AND *HYDROZETES LEMNAE* (COGGI)

ЯЙЦЕЖИВОРОЖДЕНИЕ, ПРЕДЛИЧИНКА И ОСОБЕННОСТИ ВЫЛУПЛЕНИЯ ПРЕСНОВОДНЫХ ПАНЦИРНЫХ КЛЕЩЕЙ *TRHYPOCHTHONIELLUS SETOSUS* (WILL.) И *HYDROZETES LEMNAE* (COGGI)

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ABSTRACT

The peculiarities of formation of the prelarva, as well as the eclosion process in hydrophilous oribatid mites *Trhypochthoniellus setosus* (Willmann, 1928) and *Hydrozetes lemnae* (Coggi, 1899) were described as a result of observations on the embryogenesis *in vivo*. The prelarvae of species studied are immotile and fetal. They belong to two known types according to the classification of Lange, 1960: in prelarvae of *T.setosus* the appendages are represented by sheath-like structures, whereas those appendages in *H.lemnae* are not morphologically developed. The prelarva of *H.lemnae* has a sack-like form as many higher Acariformes. The ontogeny of mentioned species is accompanied by the lecital and the uteral embryonization [Lange, 1960; Lange, Sokolova, 1992], but at different degrees. In *H.lemnae* the eggs are deposited at the early phases of embryogenesis, whilst in *T.setosus* the process of the embryonization goes further, and the eggs are deposited with the larva ready to eclose (ovoviviparity). The eclosion of *T.setosus* goes in two steps: the partial eclosion ("semi-eclosion") of the prelarva, and the final eclosion of the larva. It is found that the frontal peak of the prelarva functions as the "egg tooth". In *H.lemnae* the prelarva does not tear the egg coverings, and the larva is the eclosion stage.

The development of studied species of mites demonstrates different degrees of both the lecital and the uteral embryonizations with their most derived state in *T.setosus* where it includes the embryogenesis, the prelarva and the formation of the larva.

РЕЗЮМЕ

Особенности формирования предличинки и процесс вылупления гидрофильных панцирных клещей *Trhypochthoniellus setosus* (Willmann, 1928) и *Hydrozetes lemnae* (Coggi, 1899) изучены *in vivo*. Предличинки изученных видов неактивны и представляет собой *foetus*. В соответствии с классификацией А.Б.Ланге [1960], предличинки принадлежат к двум типам: у предличинки *T.setosus* конечности представлены чехловидными придатками, тогда как у *H.lemnae* они морфологически не выражены. Предличинка *H.lemnae* имеет мешковидную форму, подобно большинству высших Acariformes. Онтогенез изученных видов сопровождается лецитальной и утеральной эмбрионизацией [Ланге, 1960; Ланге, Соколова, 1992], но в различной степени. У *H.lemnae* яйца откладываются на ранних фазах эмбриогенеза, тогда как у *T.setosus* процесс эмбрионизации заходит дальше, и яйца откладываются с личинкой, готовой к вылуплению (яйцеживорождение). Вылупление *T.setosus* проходит в две стадии: частичное вылупление предличинки ("полувыклев") и последующее окончательное вылупление личинки. Показано, что фронтальный козырек предличинки функционирует как "яйцевой зуб". У *H.lemnae* предличинка не разрывает покровы яйца, и стадией вылупления является личинка.

Развитие изученных видов клещей демонстрирует различные степени лецитальной и утеральной эмбрионизации, наиболее далеко зашедшей у *T.setosus* и охватывающей эмбриогенез, предличинку и формирование личинки.

A number of acariform mites inhabit fresh-waters. Except to a considerably extent aquatic Parasitengona and Halacaroidea, fresh-water mites can be found in such higher taxa as Oribatei, Astigmata and Eleutherengona most representatives of which are terrestrial [Tolstikov, 1996]. In oribatid mites the secondarily aquatic species are the representatives of the hydrobiontic families Hydrozetidae, Limnozetidae and Aquanothridae, and also of Trhypochthoniidae, Malaconothridae, Zetomimidae etc. The taxonomic distribution of oribatid mites along the aquatic-terrestrial ecocline, which include the fresh-water body, is dispro portionate, with the shoreline and the drift zone being the most diverse taxonomically. Only a few species of oribatid mites, such as *Hydrozetes parisiensis* Grandj., according to our observations, can be found far from the shoreline in a relatively large number [Tolstikov, 1997].

Some adaptations of respiratory system, osmoregulation, sense organs, locomotion etc are known in the aquatic mites [Tolstikov, Petrova, 1996]. The thelytokous parthenogenesis can be considered as a preadaptation [Norton, 1994], as well as the ovoviviparity (see below).

In the present paper the development and morphology of prelarvae and larvae and the peculiarities of eclosion in two species of fresh-water oribatid mites *T.setosus* and *H.lemnae* are discussed. The observations were made on alive mites with the application of the original methods [Lange, 1996]. Mature eggs obtained from alive females were kept in a suspended water drop until the eclosion of a larva, which makes it possible to observe the process of early mite development continually, step by step. The alive objects were drawn by the first author using the camera lucida "RA-4". Later on, the second author inked the drawings.

Trhypochthoniellus setosus (Willmann, 1928)

Widely distributed in the Palaearctic. The species is reproduced parthenogenetically (by thelytoky) which is a rule for the whole cohort Desmonomata [Palmer, Norton, 1991]. Males are not known, and yet have never been observed in our three-year culture.

T.setosus was obtained in the fresh-water lake Marukhinskoye (southern part of Tyumen Province) where it occurs in great numbers in the algal mats (mostly *Oedogonium* sp.) on well-heated sandy shallows. The standard methods of collecting were applied [Tolstikov, Petrova-Nikitina, 1997]. The species has been cultivated for more than three years in aquaria on *Riccia fluvitans* at a room temperature. The mites were mostly associated with the decaying plant material on the bottom of aquaria. The larva hatches very soon after the egg deposition. This explains why the eggs are found rarely in a culture.

About 200 specimens were studied. The mites were selected by the presence of eggs and developmental stages that could be seen through the semitransparent coverings. Paired ovaries each presenting one ovariole with hermarium and follicles at different stages of development were extracted from females. It is possible to observe stages of embryogenesis from the beginning of cleavage to the formed active larva encased by the egg and prelarval coverings in one ovariole. Eggs are normally deposited at this stage, and almost immediately the larvae hatch. The mean number of eggs (at different stages of development) in both ovarioles reaches six.

Until the prelarva is formed the embryo reaches the stage of well-developed segmented limbs (Fig.1). The chelicerae possess hardly outlined chelae, and the pedipalps are with a coxendite and a segmented palp (telopodite). The legs are distinctly segmented, but pretarsi and surface ("cutaneous") sense organs are not developed. The coxal region is weakly outlined. The hypoderma of segments is represented by columnar epithelium. Internally the segments are filled with oblong mesoderma cells. There is a frontal peak (projection) with a rudimentary eye. The anal valves are outlined. Later on, quite before the excretion of the prelarval cuticle, the limb segmentation disappears, the cell boundaries become unclear, and tissue of limbs and body hypoderma acquire syncytial structure with very small nuclei (Fig.2).

At this moment the prelarval cuticle appears. Correspondingly, the prelarva has a sack-like body oval in shape (Fig.3). Its chelicerae, pedipalps and three pairs of legs correspond in size to limbs of the future larva, but look like unsegmented cases narrowing at tips, with no any sense organs. The

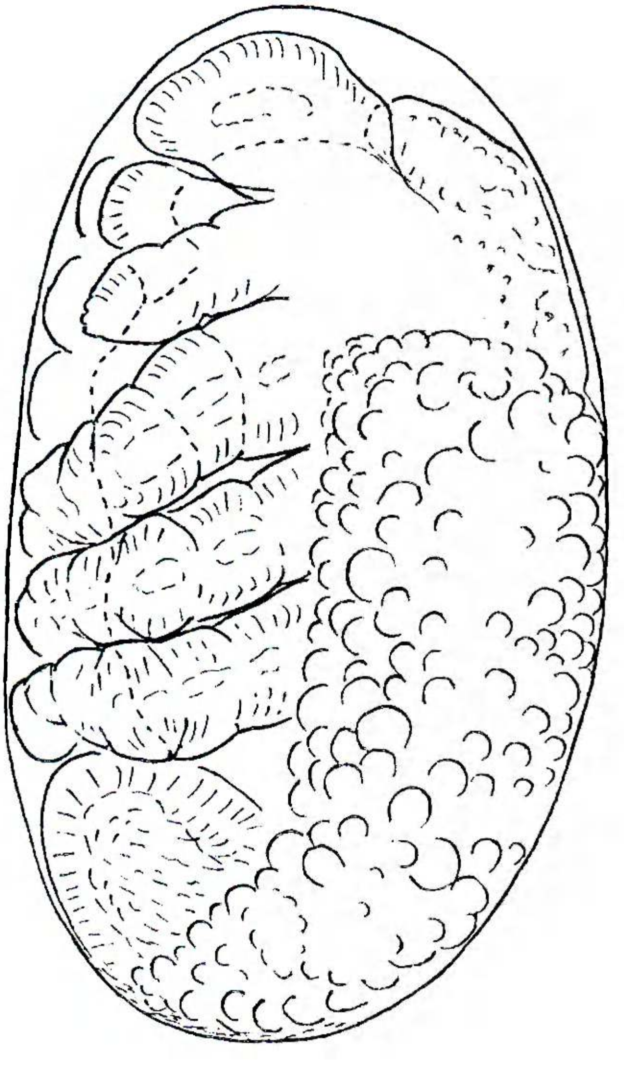

Fig.1. *Trhypochthoniellus setosus* (100×7). Embryo. The stage with "segmented appendages".

Рис.1. *Trhypochthoniellus setosus* (100×7). Эмбрион. Стадия "с расчлененными конечностями".

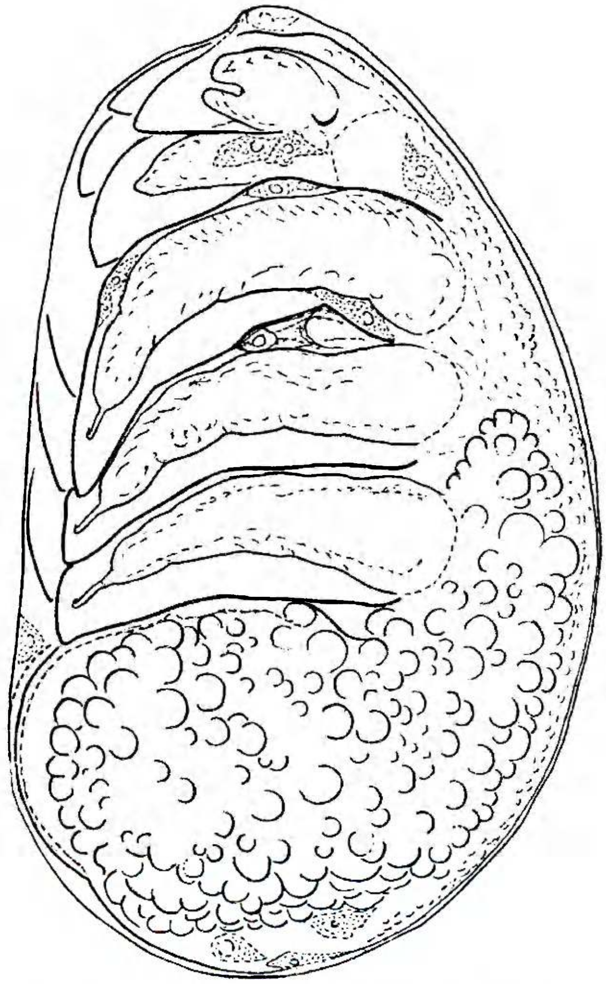

Fig.2. *Trhypochthoniellus setosus* (100×7). Prelarva formation.
Рис.2. *Trhypochthoniellus setosus* (100×7). Формирование предличинки.

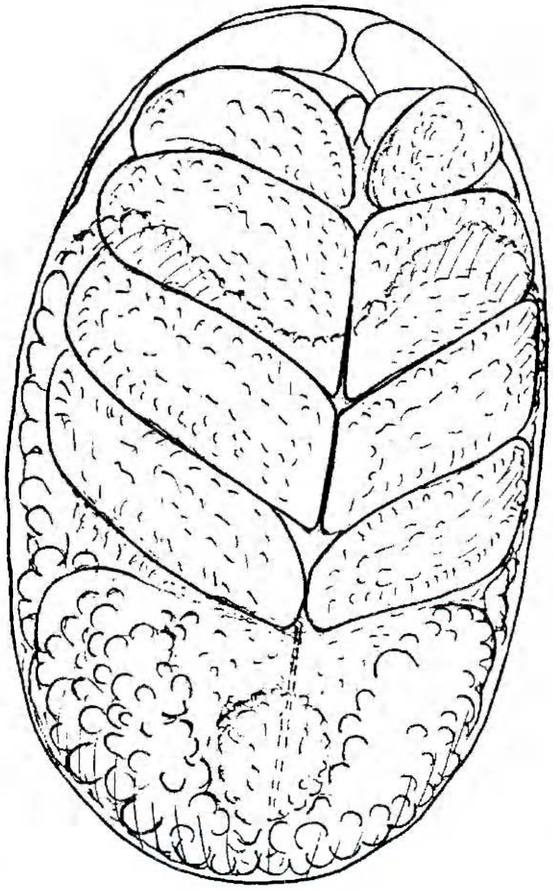

Fig.3. *Trhypochthoniellus setosus* (100×7). Prelarva cuticle formation.
Рис.3. *Trhypochthoniellus setosus* (100×7). Формирование предличиночной кутикулы.

epistoma is present, as well as the rudiments of the hypostomal complex with a rudimentary pharynx. The anal valves are outlined by a longitudinal furrow. The coxal organs are more sclerotized than the rest of the cuticle, rounded at the base, in form of membranous bulb, with a slit-like opening at the end (Fig.4). Typically located "egg teeth" are semi-crescent, strongly sclerotized, having a sharp external edge. The frontal projection is sharp at the end, in form of a sclerotized triangular, split medially denticle, which is primarily pressed by egg coverings to the frontal part of the body. The frontal eye is situated, as usual, on the ventral side of the projection, with a semi-spherical thin lens and a small granular congestion under the latter, probably, of pigment. Later the frontal projection protrudes piercing the egg coverings, which become torn laterally to the level of the pedipalpal bases. As a result the frontal part of the prelarva becomes free. Consequently, the prelarva *per se* hatches out by its frontal region yet in oviducts of a female, i.e. is a first stage of the eclosion. According to our observation, the tearing of egg coverings by frontal projection usually takes place when the formation of the larva in the prelarval cuticle begins, but occasionally a little earlier. The latter, however, might be a result of the preparation.

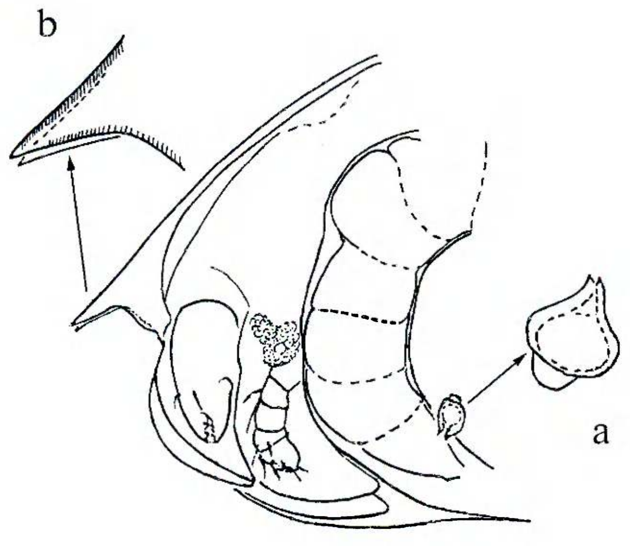

Fig.4. *Trhypochthoniellus setosus* (100×7). Immotile larva formed. a — Claparede's organ (100×20) (left, lateral view); b — frontal projection.
Рис.4. *Trhypochthoniellus setosus* (100×7). Сформировавшаяся неподвижная личинка. а — орган Клапареда (100×20) (слева, латерально); b — ростральный выступ.

Fig.5. *Trhypochthoniellus setosus* (100×20). Motile larva: active movements of legs, palpi, and chelicerae.
Рис.5. *Trhypochthoniellus setosus* (100×20). Подвижная личинка: движение ног, пальп, подъем и опускание хелицер.

The formation of the larva lasts for about 48 hours. The limbs are formed inside the case-like coverings of the prelarva (Fig.5). The narrowing and segmentation of mouthparts and legs is observed in the larva. They firstly retain the syncytial structure, but then the limb hypoderma becomes columnar. Myoblasts are formed in the inner part of limbs. The morphogenesis, segment differentiation, the growth of pretarsi and trichogenous cells (forming setae) etc. are easy to observe *in vivo*.

The yolk occupies almost all the hysterosoma in the prelarva. Its globules are well developed. The solitary ameba-like moving ecdysial cells which are called exuviocytes [Lange, 1960] because of their role in prelarval cuticle coming off in the process of the larva formation are clearly seen under the prelarval cuticle of the body and limbs of the prelarva.

The larva is quite typical for the family. After the completing the sclerotization, it begins to move actively in the egg under the prelarval coverings. In such a condition the egg is laid.

The larva continues the intensive movements with its appendages. Quite after the egg is laid the larva tears the prelarval cuticle up by its claw-like leg empodia along the semi-spherical ecdysial cleavage line, presenting a pattern known in Desmonomata [Norton, Kethley, 1994]. Then it pulls legs out and throws off the prelarval cuticle together with the residues of egg coverings dorsally. After the hatching of the larva the yolk is still remaining in its gut. During this period the larva obviously is a fetal stage – *foetus*. After the yolk is completely utilized, the larva gets started an active feeding.

Hydrozetes lemnae (Coggi, 1899)

H.lemnae is a cosmopolitic species. It is found in different fresh-water bodies especially shallow and lotic ones. The species is very common in aquaria and hothouse pools. It reproduces by parthenogenesis (thelytoky). Males are known, but extremely rare [Grandjean, 1948]. Some other species of the genus have the sex ratio close to 1:1. Females deposit eggs in different hidden places on plants (leaf vaginae of aquatic macrophytes, aeriferous parenchyma etc.).

H.lemnae for the research was obtained in the pond of the Moscow Lomonosov State University Botanical Gardens, Vorobyev Hills, Moscow, during the period 1–20.06.1996. The culture of this species was maintained on the duckweed *Lemna minor* and *Riccia fluvitans*.

The methods of dissecting, obtaining of eggs and making observations on the development of *H.lemnae* were the same as for the previous species. According to data obtained for about 200 dissected females, the eggs develop in ovaries till the stage of the germ band formation and in the normal condition are deposited at this stage. According to two microphotographs presented in the paper of Baker [1985], he also observed the egg being deposited at the germ band stage that has reached the stage of the limb formation.

Our observations revealed that in eggs placed in a suspended water drop the stage of "segmented limbs" appears approximately on the third day after the egg deposition (Fig.6). The shortening of the limbs and their gradual complete merging with coverings take place. Moreover, tissues on this stage also acquire the syncytial structure. At this time the prelarval cuticle is secreted by hypoderma. Correspondingly, the prelarva is sack-like having no appendages as in most higher oribatid mites [Grandjean, 1962 etc.]. Mostly the prelarva has a smooth, transparent cuticle only with some oblique wrinkles on the lateral sides. The coxal organs and the "egg denticles" have a structure typical for Oribatei Superiores. The first are in a form of conical papillae with the pore on the ring-like cuticular basis (Fig.7a). The second are in a form of sclerotized denticles, hollow inside. The frontal projection is absent. The rudiments of the pharynx are expressed. The prelarva *per se* does not tear the egg coverings up, but the denticles press them by their tips.

After the prelarval histolysis, the formation of larva goes on under the coverings. Its limbs develop

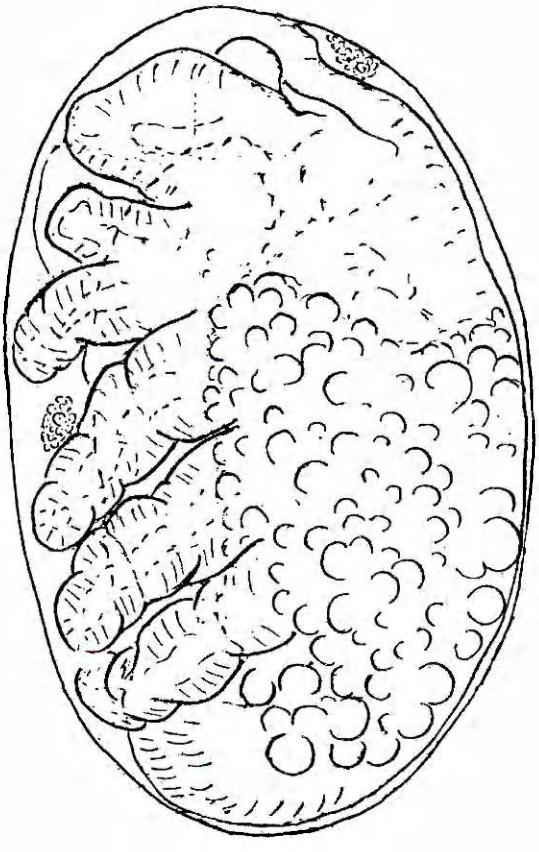

Fig.6. *Hydrozetes lemnae* (100×7). Embryo. The stage with "segmented appendages".
Рис.6. *Hydrozetes lemnae* (100×7). Эмбрион. Стадия "расчлененных конечностей".

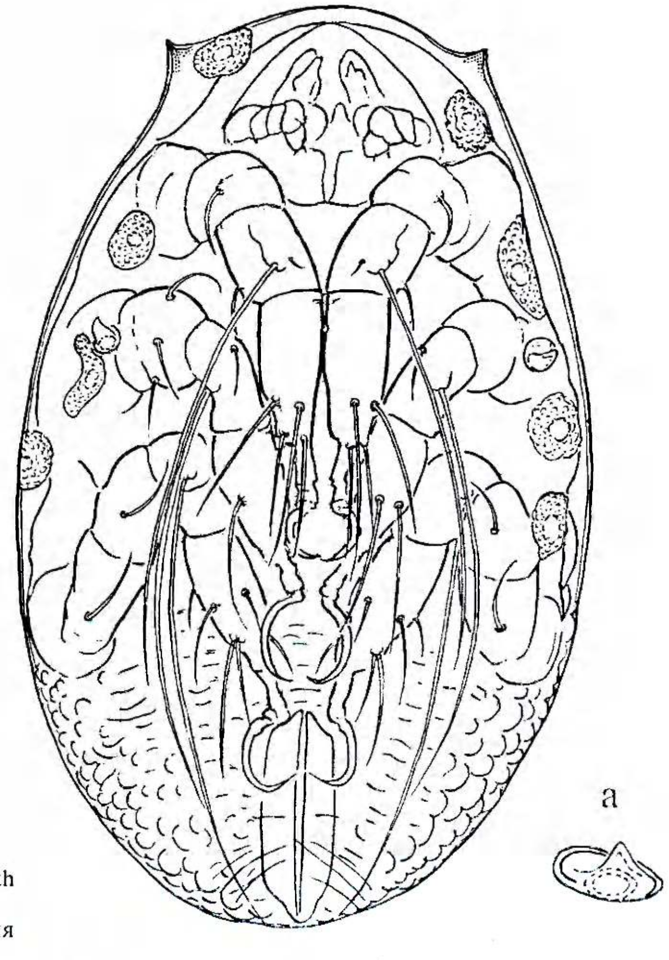

Fig.7. *Hydrozetes lemnae* (100×7). Larva in egg and prelarval coverings. a — Claparede's organ (100×20).
Рис.7. *Hydrozetes lemnae* (100×7). Личинка в яйцевой и предличиночной оболочках. a — орган Клапареда (100×20).

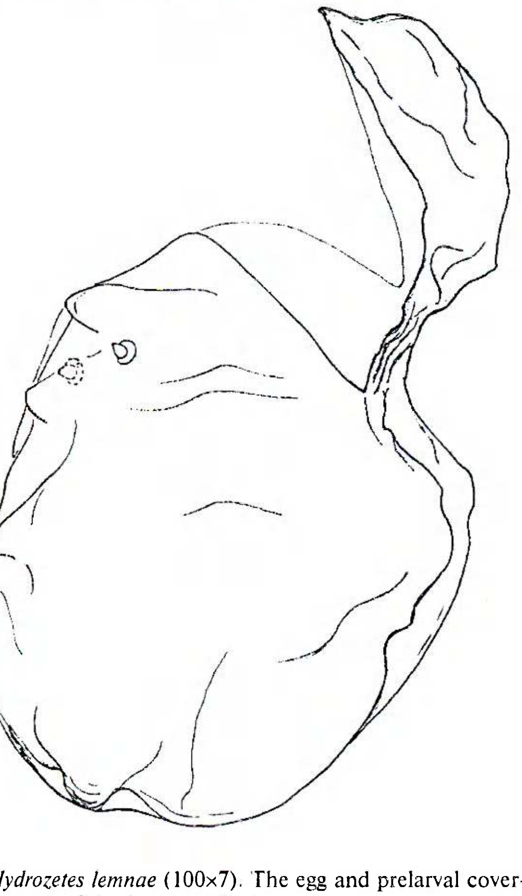

Fig.8. *Hydrozetes lemnae* (100×7). The egg and prelarval coverings (exuviae) of the larva hatched.
Рис.8. *Hydrozetes lemnae* (100×7). Сброшенные яйцевые и предличиночные оболочки вышедшей из яйца личинки.

folded and held tight to each other ventrally. It is also possible to observe the differentiation of the leg setae. The yolk occupies the hysterosoma, and reaches the level of the second pair of legs by its front edge. As in the previous species, the yolk residues are retained until the larva starts feeding by its own. Large elongated and rounded mobile ecdysial cells are well seen on the sides of the prelarva when observing from the ventral aspect (Fig.7).

Quite before the eclosion, in a result of active movements of the larva, the egg coverings become pierced, probably by "egg denticles" of the prelarva, and the cuticle of the latter is torn by empodia of the larva from the front along the ring-like equatorial ecdysial line. The larva hatches out as in the previous species shedding the prelarval cuticle and the residues of the egg coverings on the dorsal side (Fig.8).

DISCUSSION

For the understanding of the peculiarities of the prelarva, ovoviviparity and the eclosion process of the described species and their position within Acariformes in accordance to these features, it is necessary to discuss some general regularities of the evolution of prelarval stage and the ontogenetic level of the offsprings' appearing in mites of this ordo, by drawing some data on the ontogeny of Chelicerata and Arthropoda in general. Some aspects of the nature of the prelarva in Acariformes and the offsprings' appearing level were discussed in our earlier papers [Lange, 1957, 1960, 1992].

Major trend in the evolution of the arthropod ontogeny, including chelicerates, is the embryonization of development [Lange, 1966 a,b]. We distinguish three forms of the embryonization: lecital, uteral, and pupal one.

Lecital embryonization in arthropods takes place on the border of embryonic and postembryonic development by enrichment of eggs with yolk and the consecutive transition of early postembryonic stages to feeding with yolk, their transformation to not actively feeding *foetus*, and the following embracement of the latter by embryogenesis. Speaking of the embryonization of development as "a leading factor in the origin of multi-cellular organisms and the evolution of Metazoa", A.Zakhvatkin [1949, 1953a, 1953b, Zakhvatkin, Lange, 1953] discussed namely this type of embryonization.

Uteral embryonization is observed when eggs are retained in the female's reproductive system, and is accompanied by ovoviviparity, up to adult stage. In arthropods this form of embryonization occurs sporadically and never is a leading trend attributed to large taxa. Within Chelicerata it is not infrequent in systematic groups of different level. Often it does not change the course of the embryogenesis and the postembryonic development, but sometimes (Scorpiones, Pseudoscorpiones in part) the placental type of relations between the maternal organism and the embryo is established that leads to strong changes of the latter.

Pupal embryonization normally appears in the end of the postembryonic development when an exceeding feeding is observed in certain developmental stages, resulted in the aphagy and the histolytic metamorphosis in the following stages. The classic example of the completing of this process by forming the only stage of histolytic metamorphosis (the pupa) is the Holometabola within insects.

The evolutionary mechanism of embryonization is the morpho-trophic relations. According to our definition, they present a ratio between the rhythm of feeding and the morphogenesis*. In the early-derivative state the postembryonic growth and the morphogenesis in arthropods are accompanied by periodical ecdyses, and the development is divided into several stages.

In the ecdysial process the evolutionary leading morpho-trophic element ("phagy" — "aphagy") is present. At every stage arthropods feed and then move on to a period of "aphagic rest" that includes pre-ecdysial period, ecdysis (apolysis of the old cuticle, producing a new cuticle and shedding the old cuticle), and postecdysial rest when the new cuticle is completely hardened. The ecdysis *per se* is rather complex and usually accompanied by differently expressed histolytic and histogenetic processes, especially in the hypoderma. As it is known, the ecdysial process is regulated hormonally.

The change in morpho-trophic rhythm lies in the basis of the embryonization both lecital and pupal, in the first case — on the border between the embryogenesis and the postembryonic development, and in the second case — in the middle part or in the end of postembryonic development [Lange, 1970].

In mites of the ordo Acariformes the processes of maturation of eggs and their further deposition go on according to two types, with some possible intermediates. In most species of mites eggs become mature and are laid one after another (uni-oval type) which is the result of the closeness of eggs and adult mites in size as a consequence of miniaturization [Lange, 1976]. In some species (second type) eggs are accumulated in the female body (from several to hundreds) (multi-oval type), and are laid in clutches or disperse (for example, Anystidae, some Parasitengona).

The ontogenetic level of the appearing offspring in acariform mites varies greatly (from egg to adult). Mostly mites are oviparous, and all three above-mentioned types of the embryonization occur within the ordo: lecital, uteral, and pupal one.

Only the prelarva is liable to lecital embryonization. It is active in some early-derivative forms, but in most acariform mites is embryonized to different extent and reduced to embryonic ecdysis, that is observed in species of oribatid mites described heretofore. The possible existence of an active prelarvae in Endeostigmata was suggested by the first author [Lange, 1960]. Presently, an active prelarva is found in *Saxidromus delamarei* (Adamystidae) [Coineau, 1977, 1979], *Chaussieria venutissima, Erythracarus* sp., *'New genus'* (Anystidae) [Otto, Olomski, 1994; Otto, 1997].

In *Speleorchestes* sp. (Nanorchestidae) a motile prelarva was obtained by the first author in 1963 using methods of the egg incubation in a suspended water drop [Lange, 1964]. Later on, it was found again in *Speleorchestes poduroides* [Schuster, Potsch, 1989]. The embryogenesis and the prelarva of *Speleorchestes* sp. are of great evolutionary interest. Its full description has been recently published [Lange, 1996]. The complete equal cleavage with the traces of spiral one in the first three divisions (the polar commissures of blastomeres, the alternation of leo- and dexiotropic bends of division spindles, the clear larval segmentation (in the understanding of P.P.Ivanov [1928]), the simultaneous formation of four larval segments and primordial appendages (the recapitulation of *protaspis,*

*The notion of *morpho-trophic relations* is the extension of the notion of *gono-trophic relations* of females (gono-trophic cycle) to all the ontogenesis.

the primary larva of trilobites)) were recorded in the course of the embryogenesis.

In these mites the stage with long segmented legs with coxendites on all coxae, and minimal histolytic process, is precursory to prelarva. The prelarva *per se* is very interesting in many respects, and, due to its preservation, demonstrates the appearance very close to ancestral and primary for the Acariformes. It is segmented and tagmotized: proterosoma — trilobite's head (acron plus 4 larval segments), metapodosoma — thorax (segmetns of third and further fourth legs), well-developed seventh (pregenital) segment, opisthosoma (segments 8-10). The eighth (genital) segment forms the genital cone as in all the other chelicerates. Chelicerae are with acute chelae. Palps are segmented. Strong, typically segmented legs are with claw-like empodia on pretarsi. Coverings are "coriaceous", closely-scaled, bearing chetoids. Setae and solenidia on legs are well developed. Famulus is ball-like, with small spines, having a pedicel. Eyes present (frontal and lateral). Coxal organs are in a form of flexible erectile pipes with a ring-like tenidium and a funnel-like pneumatic cupule at the end. The prelarva uses them for touching the substrate sucking in to it. It can be observed, for example, when the prelarva attaches itself to the cover slip after leaving the suspended water drop in the cavity slide. These structures serve as the hydroreceptors providing the information on the surface moisture, and osmoregulators as in other Acariformes [review in Evans, 1992]. The gut is filled with yolk. The segmental system of paired diverticules of the middle gut is of interest because it corresponds to a number of hysterosomal segments of the larva. Quite before the eclosion the prelarva ingests the fluid inside the egg. At the moment of hatching it presses the eggshell with the paraanal "egg teeth", pierces it with chelicerae, tears egg coverings ventrally with the leg empodia and throws them dorsally. The actively moving prelarva ingests water from a suspended water drop that helps in the digestion of the yolk. This is probably the long-term surviving stage in the life cycle. In the laboratory prelarvae lived up to two weeks, but it was impossible to observe the ecdysis. Its transformation to the larval stage is connected with the transition to the ephemeral life form with thin coverings, which is very hygrophile, that is also characteristics for all subsequent stages. The prelarva of *Speleorchestes* serves as a proof that the ephemerity of many Acariformes is newly derived, though it probably occurred long back in the history of the ordo.

Inactive aphagous prelarvae with well-developed but sheath-like appendages demonstrate the next step of the lecital embryonization. They can be often found in Endeostigmata and in the lower Oribatei, Parasitengona etc. They partially eclose from the egg coverings. The mouthparts and legs are usually protruded outside but sometimes left under the coverings which are left torn only in the frontal part. According to a degree of the lecital embryonization, such level of the prelarval reduction is seen in *Trhypochthoniellus tectorum* [Taberly, 1952], *Palaeacarus histricinus* [Lange, 1960], and also in *T.setosus*, described heretofore.

The following embryonization of a prelarva leads to a reduction of the appendages in the process of histolysis. As the prelarva is a replica of the embryo condition at the moment of the cuticular covering formation, it has a sack-like appearance. The prelarva in most "higher" Acariformes, including Oribatei, is of this type, and that is well demonstrated by *H.lemnae*.

Often the prelarva has a thin cuticle but in some cases the latter becomes firm and functions as an additional egg covering protecting the forming larva, for example, in Phthiracaroidea [Lange, 1960; Grandjean, 1962].

Originally the prelarva is an eclosion stage. In species where the prelarva is active, it tears the egg coverings apart with claw-like empodia. With the transition of the prelarva to inactive state, when it's living and further transformation into the larva is provided by yolk accumulated in the egg, the prelarva forms one or another provisional organs of eclosion quite different in various groups of Acariformes: set of erectile dorsal setae (some Endeostigmata), two pairs of erectile frontal setae tearing the egg coverings apart in the front (*Palaeacarus* spp.), hollow frontal projections, or "prodorsal spines" (some Prostigmata), "egg teeth" (Oribatei including *Hydrozetes* spp., and free-living Astigmata), which by most part serve as supports when the larva ecloses. We demonstrated the role of the "frontal peak" in *T.setosus* which functions as the "egg tooth".

Thus, in Acariformes the eclosion process *per se* is a subject of the evolution. Originally the active (motile) prelarva ecloses. Then, when the prelarva becomes a passive fetal stage it firstly ecloses in part, tearing the egg coverings apart in the front and often protruding the legs. This process can be referred to as the semi-eclosion. In such forms the next step is the appearing of an active larva which is an eclosion stage *per se*. In mites where prelarval stage is reduced to an embryonic molt, the function of the eclosion is fulfilled by the larva.

The highest level of regression of the prelarval instar is observed in the Astigmata [Fain, Herin, 1978] both parasitic and free-living. *Sarcoptes scabiei* is an example, where the numerous exuviocytes surrounding the embryo before the larva formation can serve as a good proof of the prelarva existence [Sokolova, Fedorovskaya, Lange, 1989].

The embryogenesis may undergo the uteral embryonization to one or another extent when the eggs are laid at its different phases, up to the egg containing the larva ready to hatch. The postembryonic development may also undergo this type of embryonization that is accompanied by *viviparity*, an the development to the adult stage within the body of the female. Those cases when the eggs are laid with embryos, and especially with the formed larva are called *ovoviviparity*.

This phenomenon can be seen in secondarily aquatic oribatid mites described heretofore. In *T.setosus* the ovoviviparity occurs at the phase of larva that is ready to eclose (*in situ* the second, final eclosion). In *H.lemnae* the eggs are laid at the early phase of the embryogenesis, and the eclosion stage is the larva.

The pupal embryonization is especially obvious in terrestrial Parasitengona, with the hypertrophic parasitic larva and two pupal (calyptostasic) stages: the protonymph and the tritonymph [Shatrov, 1998]. In aquatic Parasitengona the parasitic larva reaches the colossal hypertrophy, the protonymph develops under the larval coverings as a calyptostase, the deutonymph is active, and under coverings of the latter and the calyptostasic tritonymph the adult is formed [Bottger, 1977]. Here we deal with the repeated pupal embryonization which is seemingly explains the imaginal gigantism, especially in fresh-water mites.*

The ovoviviparity at later stages of the postembryonic development, up to the adult stage, is rare, and is demonstrated by only a few species in different taxonomic groups. *Pediculoides ventricosus* Newport can be referred to as the classical example (Herfs, 1926).

It can be added that in females of some acariform mites, normally oviparous, the progeny at different stages of postembryonic development can occasionally be found. In some cases, there probably occurred the pathologic retaining of eggs in the body of the female either alive or dead. The phenomenon of the progeny's escape from the dead female body is well described, and is referred to as "aparity" [Michael, 1884].

When studied the embryogenesis, we obtained the prelarvae from oviparous species by incubation both laid eggs and eggs retained in the dead female bodies (Endeostigmata, Palaeosomata, Brachypylina, Astigmata, and Parasitengona). It was observed that the progeny going out is possible. However, in most cases it is not likely to happen. This phenomenon was called as the "post-mortal pregnancy" by the first author and was experimentally demonstrated for *S.scabiei* [Lange, 1992].

Consequently, a relatively deep lecital embryonization is observed in secondarily aquatic oribatid mites, and *T.setosus* and *H.lemnae* show the successive steps of this process. This statement is also true for the uteral embryonization, which concurrent, and reaches different degrees. In *T.setosus* all the process of the embryogenesis, the formation of the prelarva and the larva take place in the reproductive ducts of the female, and latter immediately eclose after the egg is laid. In this species the eclosion includes two steps: partial eclosion of the prelarva, and the final — of the larva. In *H.lemnae* the eggs are deposited at the stage of the embryonic germ, the prelarva does not eclose, the larva hatches.

In the conclusion, it can be noted that the uteral embryonization in oribatid mites, at different degrees, can take place in aquatic and semi-aquatic forms [Norton, 1994], and in *T.setosus* it embraces the embryogenesis, the prelarva and the larval formation. The adaptive significance of this phenomenon is unclear, but it is attributed namely to aquatic forms.

*The finding of so-called alternating calyptostasy that evolved independently in *Neonanorchestes* (Endeostigmata) [Kethley, 1991] is of major interest, and might serve to explaining the more complex forms of this phenomenon.

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