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EVOLUTIONARY PLASTICITY OF HIGHLY SPECIALIZED ORGANISMS: EVOLUTION OF ERIOPHYOID MITES (ACARIFORMES: ERIOPHYOIDEA) ON PLANTS

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Abstract

Eriophyoids are highly specialized plant-feeding acarifom mites. As a result of miniaturization and adaptation to phytoparasitism they lacked III and IV pairs of legs and acquired elongated vermiform body, unique structure of gnathosoma and peculiar anatomy. Despite the high degree of specialization eriophyoid mites demonstrate remarkable evolutionary plasticity which manifests itself in numerous morphoilogical reversia, parallelisms and modifications associated with occupying of a variety of niches, processes of gall formation, transitions to new groups of hosts and various adaptations to climate change.

KEY WORDS: miniaturization, specialization, chelicerate evolution, phytoparasitism

Introduction

There is a well-known and widely accepted classic thesis concerning the specialization process and adaptation abilities. According to Severtsov (2005) "... specialization is characterized by narrowing of the adaptive zone and intensive developing of the adaptations for surviving in that zone. In theory, it makes hard to develop adaptations to changing conditions. As a result the evolving group attains more and more specialized state...". The high degree of specialization is inherent for many parasitic organisms including phytoparasites (Shmalghauzen, 1939; Grant, 1985). With phytoparasitic mites of the superfamily Eriophyoidea as an example, I will discuss the question: to what extent in evolutionary terms may specialized organisms be plastic? Comparative analyses of various groups of highly specialized invertebrates are not within the scope of this review. Alternatively, I will focus on one group, the eriophyoid mites. Many ideas which I will discuss below originated in the end of XX in papers by Russian eriophyidologists (Sukhareva, 1992, 1994; Bagnjuk *et al*., 1995, 1998) from the group of phytoacarology of Biological Reseacrch Institute of Saint-Petersburg State University (Old Peterhoff) leaded by the late Prof. V.G. Shevchenko (Sukhareva & Chetverikov, 2010). Further developing of these ideas in the light of new data provided the basis for the invited talk which I gave in Serbian Academy of Sciences and Arts in October 2014. This review is an extended version of that public lecture.

There are several reasons why eriophyoids represent a good model to be discussed in this context. Firstly, it is a highly specialized group of mites, which possess a complex of unique adaptations for living on plants (see below). Secondly, the eriophyoid mites are morphologically very similar, so that members of different phylogenetically remote lineages look essentially the same and can hardly be differentiated based on their morphology. Thirdly, eriophyoids is an example of multicellular organisms, which underwent critical miniaturization in the course of their evolution. Remarkably, miniaturization might be considered as a "barrier" which constrains the evolution of the group (Polilov & Beutel, 2010). Among terrestrial euarthropods, only several tiny acariform mites (*e.g.* tydeoids), ptiliid beetles and parasitic hymenopterans are comparable in size to eriophyoids (Walter *et al*., 2009; Chetverikov *et al*., 2012a). And finally, eriophyoids belong to a very ancient group of mites. According to recent paleontological findings (Schmidt *et al*., 2012; Sidorchuck *et al*., 2014), eriophyoid mites or their relatives lived on gymnosperms and were abundant in early Mesozoic. Early steps of the evolution of this group of mites might have occurred in Paleozoic so that they had acquired their peculiar morphology by the middle of Mesozoic (Boczek & Schevchenko, 1996; Bagnyuk *et al*., 1998; Sidorchuck *et al*., 2014).

Results and Discussion

Adaptations of eriophyoids for living on plants

Eriophyoids have elongated body including two main parts: prosoma and opisthosoma. The prosoma bears prodorsal shield and includes mouth parts or gnathosoma and only two pairs of legs. That's why they are often regarded in the literature as "four-legged mites". Opisthosomal cuticle forms folds which are called opisthosomal annuli. In comparison to many other mites, eriophyoids have extremely reduced number of setae. The loss of two hind pairs of legs and chaetom reduction are often considered to be a result of neotenic hypomorphosis (Silvere & Shtein-Margolina, 1976).

Eriophyoids possess peculiar mouthparts which they acquired from their ancestors. Recently a sensational discovery of eriophyoid-like mites, the triasacaroids, has been made in ancient Triassic amber (Schmidt *et al*., 2012; Sidorchuck *et al*., 2014). Remarkably, they had freely projecting palpi and hypognathous proboscis including bluntly pointed chelicerae. It is assumed that these mites thrusted themselves into leaf stomata and feed on plant tissues within. In comparison to the Triassic mites, contemporary eriophyoids have much more evolutionary derived morphology of mouthparts. Their gnathosoma is adopted for piercing epidermal cells and sacking the plant sap: chelicerae and gnathosomal stylets are finely pointed and the palpi are closely appressed to each other, so that the stylets are hidden in the space between the palpi. Eriophyoid gnathosoma includes a unique structure, which is called motivator. It is a sclerotized muscle-activated structure articulated with cheliceral bases. Motivator makes pulsating back-and-forth movement (Silvere, Shtein-Margolina, 1976; Lindquist, 1996a,b). As a result, chelicerae gradually drill the plant tissue and penetrate inside.

In general, there are two principal morphotypes of eriophyoid mites differing in shapes and ecology. Usually, mites living in different shelters on plants possess worm-like body with equally annulated opisthosoma. Such mites can be found inside buds, leaf sheaths or galls. Free-living mites usually have more compact, fusiform and often flattened body which is considered to be an adaptation for living on exposed plant surfaces. Opisthosomal annuli are dorso-ventrally differentiated in these mites, that's why in literature they are often called "differently annulated" mites. They usually have large gnathosoma and prodorsal shield with large anterior extension called frontal lobe.

In comparison to other mites, eriophyoids have reduced sensory apparatus and several remarkably well-developed adhesive structures (Lindquist, 1996b; Nuzzaci, Alberti, 1996). They lack eyes and lost many setae typical for other mites. The highest concentration of sensory structures is observed in prosoma, especially in gnathosoma and legs, where we can find several tiny setae and solenidia. Opisthosomal setation is greatly reduced. Opisthosomal setae are mainly located on the ventral surface of the mite body. Eriophyoid mites use them as runners: the setae contact with the substrate during the movement, so that mite body slides along the substrate. In some cases, this results in significant thickening of the ventral setae. Adhesive apparatus includes tarsal empodia and two suckers – anal and palpal. Empodia are situated on the rear leg segment and provide tight contact with the underlay surface. Palpal sucker provides additional hermeticity between mouthparts and plant cell during feeding. Anal sucker is essential adaptation for dispersal by air. A mite attaches itself to a leaf by anal sucker, flips upside down to pose erect and leave the plant by wind currents.

Most eriophyoids can feed on and reproduce only on their specific host-plants. Eriophyoids are parthenogenetic animals. They possess arrhenotokous type of parthenogenesis when females develop from fertilized eggs while males appear from unfertilized eggs. Males lay spermathophores on leaves and females capturethem. Males often guard nymphs and lay spermathophores around them (Michalska *et al*., 2010).

Having described several specific traits of eriophyoid mites which they developed in the course of evolution as highly specialized phytoparasites, I will trace several evolutionary ways or tendencies in the evolution of eriophyoid mites which might be considered as their "attempts" to overcome the specialization constraints.

Modifications of mouthparts

Modifications of mouthparts is one of the most exciting innovations observed within superfamily Eriophyoidea. Mites with remarkably modified mouthparts belong to family Diptilomiopidae. These mites acquired strong, basally bent chelicerae and elongated oral stylet. The whole gnathosoma is directed downward or even posteriad. In comparison to other eriophyoid mites, diptilomiopid gnathosoma is two-four times longer and can be up to 80 micrometers long (Lindquist, 1996a; Amrine *et al*., 2003). Usually, eriophyoids suck the sap of epidermal cells. However, diptilomiopids have so strong gnathosoma that they can pierce through epidermis and feed on parenchyma or even of phloem tissues. For long time Diptilomiopidae has been considered as monophyletic family based on apomorphic morphology of their gnathosoma. But the results of recent molecular phylogenetic analyses suggest that it is a paraphyletic taxon which implies that diptilomiopid type of gnathosoma evolved convergently several times in different groups of eriophyoid mites (Li *et al*., 2014). Characteristics of the host-plant epidermis (such as the thickness of cell walls and the size of plant cells) might have been the most important factors which influenced on the modification of diptilomiopid mouth parts.

Endoparasitism and other examples of living under plant epidermis

In general, eriophyoid mites usually are considered as a group of ectoparasites associated with plant surface. In the course of evolution, these mites had colonized different parts of plant organisms. The majority of extant representatives are free-living; they live on the exposed parts of plants. However, in several phylogenetic lineages the hidden-living forms had evolved. They are adapted for living in confined spaces with easier access to soft tissues. Most clearly this trend appeared in the subfamily Novophytoptinae, whose members switched to endoparasitism. These mites live inside stems and leaves of herbaceous monocots like grasses, sedges and rushes. Most of their life cycle they spend under epidermis inside air-cavities where they reproduce and feed on the parenchymatous tissue. As a result of their activities the plant cells undergo necrosis and brown striae can be seen on the stem (Chetverikov, 2004; Flechtmann, 2004; Chetverikov, Sukhareva, 2007). It is an intriguing question how novophytoptines penetrate under epidermis? In the epidermis of leaves infested by novophytoptines I often observed circular pores, which were presumably made by mites. Although mouthparts of eriophyoids are specialized primarily for piercing plant cells but not for cutting holes in the epidermis, I suggest that novophytoptine actually make holes for penetrating under epidermis. A detailed analysis of the novophytoptine morphology is beyond of my speculations, but I suggest that the modification of their gnathosoma is one of the key adaptations for endoparasitism.

There are several other examples of eriophyoid mites which switched to living inside the plant tissues. Blister mites of the genus *Eriophyes* living on rosaceous plants penetrate inside a leaf and cause the formation of parenchymatous galls or blisters. Similar mites can also be found on conifers, for example one species of the genus *Trisetacus* lives inside needles of fir-trees and causes necrosis of needle parenchyma. *Trisetacus*, *Eriophyes* and *Novophytoptus* are phylogenetically rather remote genera. They belong to different families of eriophyoid mites. Therefore most likely endoparasitic forms have evolved independently in different phylogenetic lineages of eriophyoids associated with different groups of host-plants.

Defense mechanisms

Eriophyoid mites have lots of natural enemies. These are primarily predatory insects or other groups of mites and pathogenic fungi (Sabelis, 1996; Thistlewood *et al*., 1996; McCoy, 1996; Perring, McMurty, 1996). Eriophyoids are almost defenseless against them. The mite species living in various shelters on plants are in a somewhat better position. In this regard, mites of the subfamily Aberoptinae Keifer 1966 are remarkable. They have acquired the ability to produce web coating on leaves (Manson and Gerson, 1996). Aberoptines have two large anal glands which open to rectum. Actually all eriophyoid mites have such glands but in aberoptines these glands are especially well-developed. Aberoptines make twisting motions of the rear part of their body and weave web mats to protect themselves and their offspring. There are several remarkable defense mechanisms in free-living eriophyoid mites. Some of them climb the trichomes, as a result predators like phytoseids pass by and do not notice them. Several free-living eriophyoids (e.g. *Trimeroptes aleyrodiformis* Keifer, 1940) are capable of wax secretion. It is widely accepted that the wax may aid in water conservation or offer some protection of predators, and it may also assist during aerial dispersal (Sabelis and Bruin, 1996).

Gall formation and reverse evolution

Eriophyoid mites and their host plants constitute symbiotic systems with long history of relations. In the course of evolution of eriophyoid mites on plants intimate interactions between them had evolved. Biochemical mechanisms of these interactions are still largely unexplored. However, it is clear that the potential for these interactions can be overwhelming. Transmission of various microbial pathogens and horizontal gene transfer are often mentioned, when researchers speak about eriophyoid mites. Up to now it has been proved that eriophyoid mites are capable to transmit viruses and probably they are vectors of phytoplasmas (Oldfield & Proeseler, 1996). In the course of evolution in different lineages of eriophyoid mites, the ability to cause different damages, including galls, had evolved. De Lillo & Monfreda (2004) detected a gall-inducing compound in the eriophyoid saliva. This compound has cytokinin-like activity but its chemical structure remains unknown.

It is most likely that the ability to cause galls had been acquired and lost multiple times in Eriophyoidea. Presumably, it could have happened within a single generation. As a result, the mites adapted for living inside galls suddenly occurred in completely different conditions. Of course, the mites survived in rare cases. But when it happened, they had to adapt and possibly change their morphology by acquiring characters of vagrant mites. I think that the sequence of the events could be reversed when a vagrant mite acquired the ability to cause galls (Fig.1). Thus I suggest that gall formation might be one of the factors influenced on the evolution of eriophyoids and resulted in reverse morphological transformations in this group of mites. Mites of the genus *Fragariocoptes* Roivainen 1951 living on strawberries provide a bright example of this hypothesis. These mites can be found on the same plant, but one of the species lives inside gall whereas the other one is vagrant, it lives on the lower leave surface. There are minor morphological differences between these two species, but they are exactly the same as we usually observe between free-living and concealed mites. I suggest that *Fragariocoptes* mites may be a perspective model for future investigation of the morphological transformations related to gall formation.

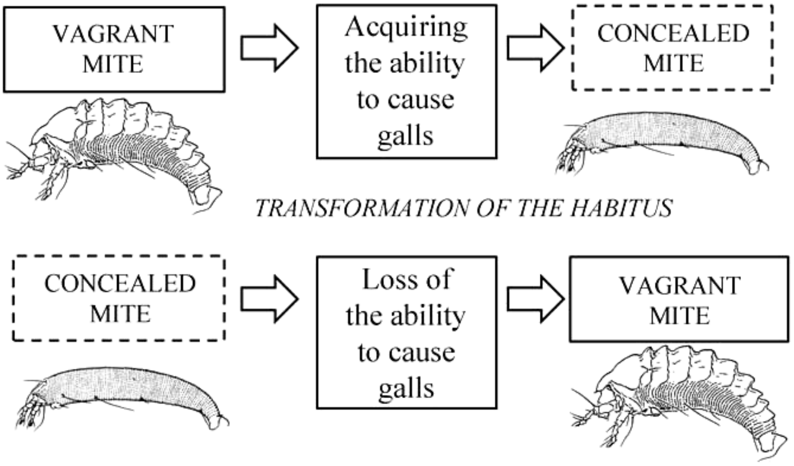

Figure 1. Scheme, illustrating possible role of the loss and acquiring the ability to cause galls in evolutionary transformations of habitus of eriophyoid mites.

A unique life cycle of pest mite *Phytoptus avellanae* (Nalepa, 1889) provides another intriguing argument in favor of the reverse evolution in Eriophyoidea. This mite can be found in various shelters on hazel nut in Europe, in North America, all over the world where its host plant grows (Ozman, 2000). Adults and immatures of this mite species have typical shapes of concealed mites: they are vermiform and equally annulated. But rarely an additional atypical nymph appears in their life cycle (Keifer, 1940; Ozman, 2000). This nymph looks like a vagrant mite as it is flattened and differently annulated. They can be found on the lower leaf surface in late spring and first half of summer. The uncommon shapes of these nymphs might be considered as morphological reminiscence of ancestor morphotype (Sukhareva, 1994; Sukhareva & Chetverikov, 2013). This implies that the ancestors of *P. avellanae* were vagrant mites which switched to living inside shelters and acquired corresponding morphology. Such evolutionary events might have occurred multiple times in different lineages of erioiphyoid mites, but a clear evidence to confirm that remained only in the life cycle of *P. avellanae*.

Deuterogeny and switches between morphotypes

Seasonal activity of eriophyoid mites is related to physiological rhythms of plants and is influenced by climate. Remarkably, many mites living on deciduous plants in temperate climate demonstrate great seasonal dimorphism. There are summer females, or protogynes, and winter females, or deutogynes (Keifer, 1942). Commonly, winter and summer females have morphological differences similar to those observed between free-living and concealed mites (Manson & Oldfield, 1996). It was hypothesized that morphological differences between protogynes and deutogynes may be a result of the climate change in past geological epochs (Sukhareva & Chetverikov, 2013): global climate cooling led to a transition to a hidden way of life in the protected habitats, on the contrary, in the course of global climate warming the vagrant mites might have flooded the exposed plant surfaces. Although this hypothesis requires further strict proof, it is evident that the eriophyoid mites are extremely plastic in relation to their two main morphotypes. Moreover, it is most likely that switches between these morphotypes had happened multiple times. It is interesting that some eriophyoid mites represent so an intermediate morphotype, for example, mites of the genus *Paraphytoptus* Nalepa, 1896. These amazing mites possess equally annulated anterior part of opisthosoma, whereas the annuli of the posterior part of their opisthosoma are distinctly dorso-ventrally differentiated. Mites of the genus *Paraphytoptus* inhabit various phylogenetically remote plants and most probably this genus is paraphyletic. On the one hand, *Paraphytoptus* mites can be unrelated forms that are in the process of transformation of their morphology. On the other hand, they can be aberrant forms. In this case molecular phylogenetic approach is the best tool to clarify this question.

Reduction of prodorsal shield chaetom and evolution of reproductive systems

Current classification of eriophyoids is based on morphology and was proposed by American acarologist Prof. J. Amrine (1996) and later revised by Amrine *et al* (2003). According to his classification, there are three families: Eriophyidae, Diptilomiopidae, and Phytoptidae. However, there are weak supports for monophylies of these families; moreover, phylogenetic relations between them are poorly understood (Lindquist 1996b). The results of recent molecular phylogenetic studies (Li *et al*, 2014; Chetverikov *et al*, 2014) show that Eriophyoidea comprises two large clades (Phytoptidae s.l. and Eriophyidae s.l.) and basal relict genera *Pentasetacus* and *Loboquintus*. Morphologically these groups differ in the anatomy of female internal genitalia and in the number of setae on their prodorsal shields (Sukhareva, 1994; Lindquist 1996a,b; Bagnjuk *et al*., 1995, 1998; Chetverikov *et al*., 2012a,b, 2013). Basal eriophyoids, like mites of the genus *Loboquintus*, possess the most complete set of prodorsal shield setae, including unpaired seta *vi* and paired setae *ve* and *sc*. In phytoptids inhabiting conifers setae *ve* were lost, whereas in phytoptids from angiosperms unpaired seta *vi* was lost. In Eriophyidae s.l. both setae *ve* and *vi* were lost. Most of eriophyids inhabit angiosperms but few of them live also on conifers and ferns, however, most likely angiosperms were their primary hosts. Therefore, the secondary associations with ferns and conifers had occurred as a result of host shift. Differences in reproductive anatomy clearly separate Phytoptidae s.l., Eriophyidae s.l. and basal relicts. The main differences are observed in the shape and direction of spermathecal tube, shapes of anterior genital apodeme and length of longitudinal bridge, these differences coincide with the clades found in molecular phylogenetic analyses.

Cryptic species and morphological canalization

For a long time, acarologists have been discussing a problem of host specificity of eriophyoid mites (Skoracka *et al.*, 2010). Usually in papers eriophyoids are mentioned as olygophagous or monophagous pests. However, several species are reported to be polyphagous as they have been registered on several hosts sometimes belonging to different genera. So, a question arises if all eriophyoids are actually highly host specific? Recent studies based on statistical analyses of morphometrics and molecular phylogenetic analyses address this question positively (Skoracka *et al.*, 2012). For example, for a long time the mite species *Aceria tosichella* Keifer 1969 has been considered as polyphagous species inhabiting various cereals. Actually this species is a complex of several cryptic species, and each of them is specialized for living on different grass species. Similar results were obtained in the course of some other studies (Vidovic *et al.*, 2008; Miller *et al.*, 2013), implying that cryptic speciation is a common way of Eriophyoidea evolution.

The problem of cryptic speciation of eriophyoids is closely connected with another phenomenon, namely morphological canalization. I will demonstrate this phenomenon with an example of the genus *Aceria* Keifer 1944. It is a huge genus comprising more than a 1000 species described all over the world from various dicot and monocot plants. Mites of this genus morphologically are so similar that if you accidentally do not know the host plant of the mite, most probably you will not be able to identify the species. This is the reason why this genus is so enormously large. Our molecular data suggest that this genus is paraphyletic. This means that mites from different phylogenetic lineages developed similar *Aceria*-like morphotype in parallel. I consider *Aceria*-like morphotype to be one of the main morphological canals within Eriophyoidea, which is evolutionarily highly successful. Actually there are several similar canals corresponding to large polyphyletic genera, for example, *Eriophyes* von Siebold 1851, *Aculus* Keifer 1959 or *Phyllocoptes* Nalepa 1887. This is not something new that the canalization of evolution had occurred in the course of evolution in highly specialized groups, it was demonstrated quite long ago (Grant, 1985). So it is quite expectedly that morphological canalization is one of the characteristics of the evolutionary process in Eriophyoidea.

Conclusions

Eriophyoids are extremely miniaturized and highly specialized animals. However, they demonstrate remarkable evolutionary plasticity in overcoming the constraints caused by specialization. Their plasticity is multicomponent and includes several important aspects, such as modification of mouth parts, reverse evolution, cryptic speciation, morphological canalization and others. Remarkably, in the course of evolution we do not see any “revolutionary” changes in morphology or ecology of eriophyoids resulted in surprising novelty. Quite the contrary, most of the discussed evolutionary ways are nothing more than further development of the ancestral characters which are typical for all eriophyoids including ancient mites found in Triassic amber. I mean that, quite expectedly, in the case of eriophyoids the overcoming of the specialization constraints was mainly based on preadaptations. Current achievements of molecular studies on Eriophyoidea indicate that soon we will have well-resolved phylogeny of Eriophyoidea. After that, it will be possible to map various morphological and ecological characters on the phylogenetic tree, perform precise analyses of coevolutionary patterns and test the hypotheses reviewed in this paper. And finally, I would stress, a great disproportion between applied and fundamental studies on eriophyoid mites. Because of this, many fundamental aspects, such as histology, embryology or phylogeny are greatly unexplored. I am convinced that further progress in eriophyoid studies needs fundamental approaches. In my opinion, eriophyoids is perspective model object for studying broad range of scientific problems which can be solved the best in the course of collaborative research by international groups of scientists.

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ЕВОЛУЦИОНА ПЛАСТИЧНОСТ ВИСОКО СПЕЦИЈАЛИЗОВАНИХ ОРГАНИЗАМА: ЕВОЛУЦИЈА ЕРИОФИДНИХ ГРИЊА (ACARIFORMES: ERIOPHYOIDEA) НА БИЉКАМА

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Извод

Ериофиде (Acariformes: Eriophyoidea) су високо специјализоване фитофагне гриње. Као резултат малих димензија њиховог тела и адаптације на фитопаразитизам, оне немају III и IV пар ногу, а имају издужено црволико тело, јединствене структуре гнатосоме и специфичну анатомску грађу. Упркос високом степену специјализације, код ериофидних грињa је присутна значајна еволуциона пластичност која се манифестује бројним морфолошким реверзијама, паралелизмима и модификацијама удруженим са заузимањем разноврсних ниша, процесом формирања гала на биљкама, преласком на нове групе биљних врста –домаћина и различитим адаптацијама на климатске промене. Предмет овог прегледног рада је расправа у вези са питањем: до које мере у еволуционом смислу могу специјализовани организми бити флексибилни, коришћењем ериофида као модел система.

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