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REVIEW OF THE HABILITATION THESIS "TRENDS OF THE EVOLUTION OF EPRIPHYOID MITES (ACARI, ERIPHYOIDEA) ON PLANTS" SUBMITTED FOR THE DEGREE OF DOCTOR OF BIOLOGICAL SCIENCES BY DR. FILIPP E. CHETVERIKOV

The topicality of the dissertation. The dissertation is focused on the evolution of eriophyoid mites (superfamily Eriophyoidea), a specious group of understudied plant feeding acariform mites with uncertain origin. Eriophyoid mites are considered to be a group of high economic importance due to their ability to cause growth abnormalities and transmit viruses in plants. The studies conducted by Dr. Filipp E. Chetverikov lead to better understanding of this important and poorly explored group of pests. *The topic of his dissertation "Trends in the evolution of eriophyoid mites (Acari, Eriophyoidea) on plants" is complicated enough to be a topic of a habilitation thesis submitted for the degree of doctor of biological sciences.*

Aims and methods. The key statement of the dissertation is presented in the Introduction where the author considers eriophyoid mites as a model object for evaluating the adaptive abilities of extreme morphologically simplified chelicerates and therefore touches an important philosophical problem of the impact of the process of simplification on the steadiness of a system. The basic narrative direction of the dissertation is aimed to elucidate the question: which features make eriophyoid mites highly adaptive despite the limited morphological material available for evolutionary changes. This sophisticated question is discussed through achieving several distinct goals: (a) analysis of the body plan, (b) reconstruction of phylogeny, (c) analysis of host plant associations of Eriophyoidea, and (d) descriptions of the key morpho-ecological trends marking the evolution of eriophyoid

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mites on plants. *The goals are relevant to the main idea of the dissertation and allow the author to cover the topic of the thesis comprehensively.*

The range of the applied methods is wide and includes different modern light microscopy techniques, including confocal laser scanning microscopy (CLSM), scanning electron microscopy, laser assisted microdissection, PCR and sequencing. The development of several new approaches for studying eriophyid mites, such as CLSM technique for studying topography of eriophyoid cuticle, detecting exuviae of the microarthropods in herbaria using UV-light, and a new mode of drawing microscopic objects using a video projector, are particular merits of the work.

General description of the dissertation structure. The thesis consists of Introduction, four chapters and six additional sections (Final remarks, Conclusions, List of publications on the topic of the dissertation, Main theses presented for defense, References, and Appendix). In the Introduction the author gives a general description of the thesis including presentation of the aim and the four goals of the study, as well as the applied methods. The four chapters, each corresponding to one of the goals, represent the main volume of the dissertation. The appendix includes three tables and 29 figures, perfectly illustrating the achieved results. The thesis is bilingual, the English version of the text is written on 183 pages all together. The structure of the dissertation conforms to the principles and structure of a scientific thesis. The author has studied and used an appropriate number of bibliography sources in the dissertation. *The thesis fulfils the formal requests on a satisfactory level.*

Evaluation of the research results and conclusions. The reviewed dissertation is an example of a multidirectional study of a group of microscopic phytophagous invertebrates with novel data obtained in different fields (comparative morphology, phylogeny, embryology, gallogenesis). Through a thorough analysis of the main evolutionary trends of eriophyoids on plants and the factors facilitating the successful colonization of vascular plants by these mites, the author demonstrated that evolutionary success of Eriophyoidea is based on various morpho-ecological reversals. The author showed that constraints on the eriophyoid evolution, created by miniaturization, high specialization and the morphological simplification of the ancestral morphotype, lead to canalized evolution. With cladistic methods, the author establishes the relationship between eriophyoids and Nematalycidae mites living between soil particles. This fact allowed the author to make an important conclusion that adaptations of the acariform mites to the interstitial life in the ancestral group

(called "protoeriophyoids" in the dissertation) may act as preadaptations for the subsequent successful evolution on plants. In the view of this hypothesis, the author proposed an interpretation of the transitions to endoparasitism in phylogenetically distant eriophyoid groups: they are considered as cases of ecological reminiscence of life inside the soil.

The category of "oscillation" was proposed as a key characteristic of morphological evolution of Eriophyoidea. The author shows that the evolutionary success of eriophyoids on plants were guaranteed by the dual nature of their ancestral morphotype and that during expansion on plants, repeated weakening and strengthening («oscillation») of different aspects of the ancestral morphotype formed the basis for the morpho-ecological reversals, which, in turn, ensured successful colonization of various niches and hosts.

Through this work, the author defined the main evolutionary trajectories of eriophyoids on plants. According to his results they include a) modifications of the mouthparts and genitalia, b) ever increasing reduction of chaetome and appendage modifications, c) body consolidation and pseudo-tagmatization, d) habitual transformations and morphotype reversals, e) life cycle simplifications and colonization of new host groups, f) acquisition of gall-inducing ability and phytopathogen transmission, g) adaptations to new niches, including transition to endoparasitism, h) formation of cryptic species complexes, and i) convergent formation of the large morphologically uniform polyphyletic genera.

The concept of "pseudotagmata" was used by the author to describe the variety of dorsal shields present in various lineages of Eriophyodea. The "pseudotagmata" terminology proposed in the dissertation creates an important basis for future taxonomic revisions and comparative studies of pseudotagmic taxa of Eriophyoidea.

Wide use of CLSM allowed the author to obtain novel data on the anatomy of eriophyoid mites as well as the 3-D reconstruction of internal genitalia which were crucial for further comparative analyses. Basal divergence of Eriophyoidea was reconstructed based on the results of molecular phylogenetic analysis of partial sequences of two genes (nuclear D1D2 28S and mitochondrial Cox1) combined with comparative anatomy of female internal genitalia. Although the author did not test monophyly of subfamilies and tribes of Eriophyoidea, the data clearly indicate that (a) phylogenetic structure of modern eriophyoid diversity includes three large clusters: basal paraphyletic group Pentasetacidae and two large sister clades – Phytoptidae s.l. (=Phytoptidae s.str. + Nalepellidae) and Eriophyidae s.l. (=Eriophyidae s.str. + Diptilomiopidae) and (b) the most important morphological traits, which mark these clades, include organization of the gnathosoma, genitalia, chaetotaxy of the

prodorsal shield, and sperm storage type. Comparison of these novel data on phylogeny of Eriophyoidea with that of vascular plants allowed the author to conclude that macrophylogeny of Eriophyoidea reflects the major steps of colonization of higher plants and corresponds with the key events of host phylogeny.

In cooperation with colleagues, this work also included a genetic study on the process of mite induced gall formations which showed that eriophyoids ability to induce gallogenesis is based on the manipulation of specific processes of normal hystogenesis of plant tissues. This process is achieved through alterations of the expression levels of regulatory genes via the effects of mite salivary components on plant epidermal cells.

New taxa of Eriophyoidea (7 genera, 16 species), including previously unknown endoparasites of the tissues of monocotyledonous plants were described, which is important contribution to investigation the world biodiversity of Eriophyoidea.

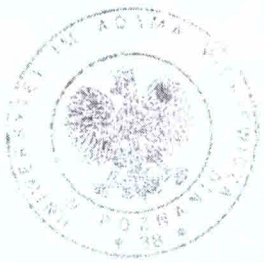
The results of the presented work are novel and will facilitate further understanding of the nature of symbiotic relations between mites and plants, which is particularly important for applied areas, given the injuriousness and great economic importance of eriophyoids. The dissertation is well structured, complete study with reasonable conclusions, clear goals, content, and abundant material involved in the analyses.

Criticism and discussion questions. According to the captions on figures 15 and 19, the data on sperm storage and musculature in Eriophyoidea obtained by F.E. Chetverikov have not been published, which in my opinion should be avoided in doctoral dissertations; however the author likely has reasons for doing that and he will probably comment on these during the official defense. Regarding the habilitation thesis, I have the following questions. (1) What exactly is called "evolutionary plasticity" in the Introduction, chapter III, and Conclusions? It is not clear from the text and needs more precise explanation. (2) Although the results of the molecular phylogenetic analyses described in the dissertation indicate that two hypotheses on the origin of Eriophyoidea are almost equally probable (sister relation with nematalycids and sister relation with eupodines), the author accepted only one hypothesis and built all his conclusions based only on the assumption that eriophyoids and nematalycids are sister taxa. This choice of the hypothesis needs better clarification. (3) As far as I know, along with other groups of acariform mites permanently associated with plants, eriophyoids usually are called "plant-feeding" or "phytophagous" mites in the literature. However the author of

the dissertation calls them "phytoparasites" which is slightly untypical. What was the basis for this terminological choice?

Conclusion. *The author of the dissertation summarized a broad range of data on comparative morphology, host-plant association, and molecular phylogeny of Eriophyoidea. He presented a solid retrospective description of the history of the association of eriophyoid mites with vascular plants and provided a new hypothesis on the origin of Eriophyoidea. The dissertation is an important contribution in the problem of the origin of phytophagy in Acari and morphoecological adaptations related to living on plants in Eriophyoidea. It makes a significant contribution to our understanding of canalized evolution in groups of highly specialized parasites constrained by miniaturization. It is a clear "step forward" not only in the improving our knowledge on eriophyoid mites, but also a strong methodological contribution due to the development, introduction and application of new techniques which will definitely be important for furthering progress in acarology in the near future.*

The dissertation meets all formal requirements given to full habilitation theses in natural sciences. It is based on papers with significant quality and their number notably exceeds minimal quantity for being permitted to doctoral defense, therefore I highly recommend accepting the thesis for the defense and, after oral presentation and discussion, to give the title of Doctor of Biological Sciences to Dr. Filipp E. Chetverikov.



Poznan, July 25, 2018

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