



Homoplastic evolution and host association of Eriophyoidea (Acari, Prostigmata) conflict with the morphological-based taxonomic system



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ABSTRACT

The superfamily Eriophyoidea is exceptionally diverse and its members are highly host-specific. Currently, the taxonomy of this group is based on morphology only. However, phylogenetic relationships in this group could be incorrect if the diagnostic morphological characters are homoplastic. Therefore, the phylogeny of 112 representative taxa of Eriophyoidea from China was determined using 18S, 28S D2-5 and D9-10 rRNA. Phylogenetic relationships were inferred through Bayesian, maximum likelihood and maximum parsimony methods, and then a number of clades or major clades were defined according to robust phylogenetic topologies combined with morphological comparison. Tests of monophyly showed that two of three families of Eriophyoidea as well as one subfamily and four tribes were not monophyletic. Ancestral character state reconstruction (ACSR) showed that five diagnostic morphological characters evolved several times, confounding the current taxonomy. Additionally, reconstruction of the history of host plant colonization suggested host switching occurred in a limited range of host plants. The host association data made it possible to determine taxonomic relationships more accurately. These results show that by integrating morphological and molecular information and host plant choice, it is possible to obtain a more accurate taxonomy and a deeper phylogenetic understanding of Eriophyoidea.

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1. Introduction

Eriophyoid mites are distributed worldwide and, among phytophagous Acari groups, are second only to spider mites in their economic importance. They are exceptionally diverse and have a unique body structure compared to other groups of Acari (Lindquist, 1996). They are highly host-specific, with nearly 80% of the species reported from only one host plant (Skoracka et al., 2010). Some eriophyoid mites are agricultural pests while others are potential bio-control agents (Lindquist et al., 1996). As a result, there is a growing demand for a well-tested taxonomy and phylogeny of this group.

The traditional morphological-based taxonomic system for the superfamily Eriophyoidea has been used for over 100 years (Lindquist and Amrine, 1996). The monophyly of this superfamily is mostly accepted because of the distinct body structure (two pairs of legs with few setae, feathered or rayed empodium, absence of stigmata, peritremes or tracheae and transverse genital opening) (Krantz, 1978). On the other hand, the classification of families has been quite controversial. Currently, six taxonomic systems have

been established in Eriophyoidea (Boczek, 1966; Schevchenko, 1974; Nwekirk and Keifer, 1975; Boczek et al., 1989; Amrine and Stasny, 1994; Amrine et al., 2003). The revised system of Amrine et al. (2003) is widely used today. Boczek et al. (1989) defined five families while Amrine's group (Amrine and Stasny, 1994; Amrine et al., 2003) defined three. Both groups supported identifying the Diptilomiopidae (Rhyncaphytopidae) by their long-form oral stylet. In the current three-family system, the family Phytoptidae was considered ancestral because they retain the setae found in Triassic fossils (Schmidt et al., 2012). In contrast, the Eriophyidae has only scapular setae present or absent on the prodorsal shield. The diagnostic characters of the subfamilies, tribes and genera mainly include the morphology of the opisthosoma, the presence, position and direction of setae, the morphology of the genitalia, the morphology of the distal leg segments, and the shape of the empodium (Amrine et al., 2003).

However, these morphological-based systems were generally considered to be artificial (Lindquist, 1996; Lindquist and Amrine, 1996; de Lillo and Skoracka, 2010). In addition, the phylogeny would be expected to reflect host-specificity (Lindquist and Amrine, 1996). A critical problem has been the lack of consideration of the possibility of homoplastic evolution, which has been reported in many groups of animals, and would lead to misleading phylogenetic relationships among taxa and confusion in the

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literature (e.g. Mott and Vieites, 2009; Perkins et al., 2009; Schaffer et al., 2010; Urban and Cryan, 2009; Virgilio et al., 2009).

In view of this problem, de Lillo and Skoracka (2010) suggested a reconsideration of traits to evaluate the importance of characters used in the systematics of Eriophyoidea. Huang and Huang (1990) and Hong and Zhang (1996a,b, 1997) analyzed the cladistics of the superfamily Eriophyoidea, subfamily Diptilomiopinae and tribe Cecidophyini based on multiple morphological characters to test the phylogenetic relationships within these taxa. Both of these two groups of researchers supported the monophyly of three families, although Hong and Zhang (1996a) supported grouping *Sierraphytoptinus*, a Phytoptidae genus, with Eriophyidae. Kuang et al. (1992) examined the relationships among five eriophyoid mites based on the occurrence of esterase isozymes and Kuang et al. (1995) examined the relationships among three families of Eriophyoidea based on karyotypes. These two researches of Kuang et al. revealed that the relational sequence of three families was Nalepellidae (Phytoptidae)–Eriophyidae–Rhyncaphytoptidae (Diptilomiopidae).

In recent years, studies using a combination of morphological characters, molecular markers and ecological traits have helped to (1) revise taxonomic systems which were once confused by homoplastic evolution (e.g. Mott and Vieites, 2009; Perkins et al., 2009; Schaffer et al., 2010; Urban and Cryan, 2009; Virgilio et al., 2009), (2) enhance our understanding of biodiversity and (3) serve as a basis for answering important questions in evolutionary biology (Padial et al., 2009, 2010). Molecular-based technologies have been beneficial to the phylogenetic analyses of many natural groups including the Acari (e.g. Burger et al., 2012; Dabert et al., 2010; Schaffer et al., 2010; Solter et al., 2001). Among ecological traits of Eriophyoidea, the host plants should be given particular consideration. The reviews of Oldfield (1996) and Skoracka et al. (2010) illustrated high host-specificity of eriophyoid mites and their distributions in three major host ranges: conifers, monocotyledons and dicotyledons. Moreover, there are some molecular evidences of host-associated divergence and cryptic speciation in some *Abacarus* and *Aceria* species (Skoracka and Dabert, 2010; Skoracka et al., 2012, 2013, 2014; Miller et al., 2013). These observations show how an analysis of eriophyoid mite–plant relationships can provide substantial taxonomic information.

This study is the first to use molecular data to elucidate the phylogenetic relationships among the superfamily Eriophyoidea. One hundred twelve representative taxa from China were selected and three fragments of rRNAs (18S, 28S D2–5 and 28S D9–10) were used, which are widely used for phylogenetic analysis in Acari (Burger et al., 2012; Dabert et al., 2010; Klompen et al., 2007; Schaffer et al., 2010). Our aims were to (1) evaluate the validity of the current taxonomic system of Eriophyoidea by comparing it with molecular phylogeny; (2) test the possible homoplasy of diagnostic morphological characters and (3) test the possible host-associated evolutionary patterns and trace the histories of host plant switches within this group.

2. Materials and methods

2.1. Taxon sampling

Up to now, over 300 genera and 4000 species have been reported in the Eriophyoidea from all over the world (Zhang, 2011). Most of the genera are composed of few species. Here, the genera composed of more than ten members were given priority for selection. This study included a total of 112 species of Eriophyoidea from China, belonging to three families, six subfamilies, 12 tribes and 49 genera. The selected taxa were associated with host plants belonging to conifers (16 species of eriophyoid mites),

monocotyledons (12 species) and dicotyledons (84 species). A water mite species, *Mideopsis roztozcensis*, was chosen as the out-group. Sampling data including vouchers, localities and host plants are given in Table 1.

2.2. DNA extraction, PCR and cloning

Five to 30 mites were pooled for DNA extraction using a DNeasy Blood & Tissue Kit (Qiagen) following the protocol of the manufacturer as modified by Dabert et al. (2008). DNA samples were stored at -20°C until use. Because the mite bodies would be destroyed in different degrees by DNA extraction, secondary specimens (other individuals from the same population) were used as vouchers and deposited in the Arthropod/Mite collection of the Department of Entomology, Nanjing Agricultural University, Jiangsu Province, China.

Fragments of three ribosomal RNA genes (rRNAs) (18S, 28S D2–5 and 28S D9–10) were amplified by PCR using the primers and annealing temperatures (T_m) shown in Table 2. The internal transcribed spacers (ITSs) were found to vary greatly among different taxa, and it was hard to make an accurate alignment among them, and so they were excluded from the analyses. All PCRs were performed in 25 μL , containing 12.5 μL of Super Taq Mix (Pudi Biotech Co., Ltd., Shanghai, China), 5 μL of template DNA, 0.5 μL of each primer. Thermocycles consisted of an initial denaturation step at 96°C for 5 min, followed by 30 cycles of denaturation at 95°C for 30 s, annealing for 1 min and extension at 72°C for 1 min. The final extension was at 72°C for 5 min. After that, 5 μL of the PCR amplification production was run on a 1.5% agarose gel stained with ethidium bromide and visualized under UV light to ensure the correct size of the amplified fragment.

Cloning method was used to make sure one awarded sequence was from one individual. The amplified fragments were purified using a TIANGel Midi Purification Kit (Tiangen Biotech, Beijing, China). Distinct, single-band amplicons were cloned into pEASY-T3 Cloning Vector (pEASY-T3 Cloning Kit, TransGen Biotech, Beijing, China). One positive clone was randomly chosen and the inserts were sequenced by Meiji Biotech (Shanghai, China). Nearest matches to the sequences of Acari species were found by BLAST searches of the NCBI database. GenBank accession numbers of sequences are given in Table 1.

2.3. Alignment and phylogenetic analysis

Initial sequence alignment was made with Muscle (Edgar, 2004a,b) using the default settings. The obtained alignment was modified by eye according to sequence similarity among closely-related taxa. A final 3076-bp alignment was generated.

The 18S and 28S datasets were analyzed both separately and as a combined dataset. For each dataset, three different inferences, Bayesian inference (BI), maximum likelihood (ML) and maximum parsimony (MP) were applied. The best-fitting evolutionary models were assessed for two partitions (18S and 28S) using the Akaike information criterion (AIC) in jModeltest 0.1.1 (Posada, 2008), with the HKY + I + G model selected for 18S partitions and GTR + I + G model for 28S. BI trees were reconstructed with MrBayes 3.2.1 (Ronquist et al., 2012) with four chains (three heated, one cold) ran and by using the best-fitting evolutionary models for 18S and 28S partitions, respectively. Model parameters were unlinked and the overall rate was allowed to vary across partitions. The number of generations for the total analysis was set to 50,000,000 with the chain sampled every 5000 generations. The burn-in value was 25% and other parameters were set at the default values. To confirm convergence, ASDSF (average standard deviation of split frequencies) and PSRF (potential scale reduction factor) values were visualized in MrBayes, and ESS (evaluating

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