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The phylogenetic position of eriophyoid mites (superfamily Eriophyoidea) in Acariformes inferred from the sequences of mitochondrial genomes and nuclear small subunit (*18S*) rRNA gene

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ABSTRACT

Eriophyoid mites (superfamily Eriophyoidea) comprise >4400 species worldwide. Despite over a century of study, the phylogenetic position of these mites within Acariformes is still poorly resolved. Currently, Eriophyoidea is placed in the order Trombidiformes. We inferred the high-level phylogeny of Acari with the mitochondrial (mt) genome sequences of 110 species including four eriophyoid species, and the nuclear small subunit (*18S*) rRNA gene sequences of 226 species including 25 eriophyoid species. Maximum likelihood (ML), Bayesian inference (BI) and Maximum parsimony (MP) methods were used to analyze the sequence data. Divergence times were estimated for major lineages of Acari using Bayesian approaches. Our analyses consistently recovered the monophyly of Eriophyoidea but rejected the monophyly of Trombidiformes. The eriophyoid mites were grouped with the sarcoptiform mites, or were the sister group of sarcoptiform mites + non-eriophyoid trombidiform mites, depending on data partition strategies. Eriophyoid mites diverged from other mites in the Devonian (384 Mya, 95% HPD, 352–410 Mya). The origin of eriophyoid mites was dated to the Permian (262 Mya, 95% HPD 230–307 Mya), mostly prior to the radiation of gymnosperms (Triassic-Jurassic) and angiosperms (early Cretaceous). We propose that the placement of Eriophyoidea in the order Trombidiformes under the current classification system should be reviewed.

1. Introduction

Mites and ticks (subclass Acari) represent the most diverse group within the class Arachnida (spiders, scorpions, pseudoscorpions, mites, ticks, solifuges, etc.) with ~55,000 described species (Zhang, 2011). Acari has two superorders, Parasitiformes and Acariformes (Lindquist et al., 2009). Within the Acariformes, the Eriophyoidea is the most species-rich superfamily in the Acari with >4400 described species (Zhang et al., 2011). Eriophyoid mites can be distinguished from other mites by their body shape (vermiform or fusiform), body colour (usually white or light yellow), small body size (average 200 μm), two pairs of legs, reduced setae on the opisthosoma and legs, and ringed opisthosoma (Amrine et al., 2003). Most eriophyoid mites have high host-plant specificity (Skoracka et al., 2010) and weak dispersal abilities (Michalska et al., 2010). Some species of eriophyoid mites are economic pests in crops (Duso et al., 2010) and forests (Castagnoli et al., 2010).

The affinities of eriophyoid mites at higher levels (order or cohort level) in the Acari remains poorly resolved. Reuter (1909) divided the Acari into four suborders: Parasitiformes, Trombidiformes, Sarcoptiformes and Eriophyiformes (Reuter, 1909); eriophyoid mites formed the Eriophyiformes, separate from Trombidiformes. Kishida (1937) divided the Acari into five suborders: Acariformes, Parasitiformes, Trombidiformes, Eriophyiformes and Opilioacariformes. Lindquist et al. (2009) reduced the Acari to two superorders: Parasitiformes and Acariformes; the Acariformes includes two orders: Trombidiformes (comprising Prostigmata plus the small suborder Sphaerolichida) and Sarcoptiformes. Eriophyoid mites are still considered part of the Trombidiformes. Based on having four legs (instead of eight legs as in other mites and ticks), eriophyoid mites were grouped in the cohort Tetrapodili (Oudemans, 1923; Schevtchenko, 1971; Woolley, 1988). In the current classification system (Lindquist et al., 2009), however, Tetrapodili is rarely used, except by some Russian acarologists (Schevtchenko, 1971; Sukhareva, 1994). Whether eriophyoid mites

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should be in the order Trombidiformes or in the order Sarcoptiformes, however, has been controversial. Eriophyoid mites lack a tracheal system, which is a defining character of the Sarcoptiformes (Lindquist et al., 2009). On the other hand, eriophyoid mites also have characters of the Trombidiformes, e.g. legs with empodium and an opisthosoma lacking paired lateral glands. Based on the comparison of morphological characters with other mites, Lindquist (1996) suggested that eriophyoid mites could also be treated as an order or suborder of their own. Nevertheless, morphological evidence was weak for this hypothesis, and the high level affinities of eriophyoid mites have not been well resolved.

All eriophyoid mites were grouped in the superfamily Eriophyoidea by Amrine et al. (2003). Recently, however, a new superfamily, Triasacaroidea, was created for four fossil eriophyoid mites (Schmidt et al., 2012; Sidorchuk et al., 2015). The oldest fossil records of Eriophyoid mites were dated to 230 million year ago (Mya) (Schmidt et al., 2012; Sidorchuk et al., 2015). However, the origin and the divergence time between eriophyoid mites and other mites remains unclear. The ancestor of eriophyoid mites had similar morphology to extant species, such as four legs, reduced setae on the opisthosoma and legs, anal parts forming a sucker, and a prodorsal shield with two to five setae. The monophyly of Eriophyoidea has been widely accepted (Lindquist and Amrine, 1996; Lindquist et al., 2009), however, the monophyly of the new superfamily Triasacaroidea and its phylogenetic relationship with extant Eriophyoidea is not known.

In the past decade, the phylogeny of various mite groups has been studied using molecular markers such as mitochondrial (mt) gene sequences (Dabert et al., 2010), mt genome sequences (Chen et al., 2014; Gu et al., 2014; Palopoli et al., 2014) and nuclear gene sequences (Dabert et al., 2010; Domes et al., 2007a, 2007b, 2008; Klompen et al., 2007; Kreipe et al., 2015; Murrell et al., 2005; Pachl et al., 2012; Pepato and Klimov, 2015). The Acariformes were always recovered as monophyletic in these studies, as were the Parasitiformes. The monophyly of Acari, however, was not always recovered (Arabi et al., 2012; Dabert et al., 2010; Dunlop and Alberti, 2008; Ovchinnikov and Masta, 2012; Pepato et al., 2010; Pepato and Klimov, 2015). The sister group of Acariformes recovered in these studies varied from the Solifugae (Arabi et al., 2012; Dabert et al., 2010; Dunlop and Alberti, 2008; Pepato et al., 2010; Pepato and Klimov, 2015), the Pseudoscorpines (Ovchinnikov and Masta, 2012) and the Ricinulei (Shultz, 1989, 1990; Weygoldt and Paulus, 1979). Dunlop and Alberti (2008) reviewed in detail the phylogeny of mites and ticks from morphological, developmental and molecular evidence, and support the polyphyly of Acari. Eriophyoid mites, however, were not included in any of these analyses and the phylogenetic position of Eriophyoidea within Acari remained unresolved.

Sequences of multiple genes or genomes have been used in phylogenetic studies in recent years and provided insights into the higher-level relationships in insects (Behura, 2015; Misof et al., 2014), worms (Andrade et al., 2014) and fungi (Chang et al., 2015). Mitochondrial genomes, usually 16 kb in size with 37 genes for animals (Boore, 1999), have been shown to be a useful marker for inferring higher-level phylogeny (Bourguignon et al., 2015; Fenn et al., 2008; Li et al., 2015; Song et al., 2010; Wei et al., 2014). In a previous report (Xue et al., 2016), we found that two species of eriophyoid mites did not group with other trombidiform mites in a phylogenetic analysis of mt genome sequences. To better elucidate the phylogenetic position of Eriophyoidea, we sequenced the mt genomes of two additional eriophyoid mites, representing two families (Eriophyidae and Diptilomiopidae), and conducted phylogenetic analyses with mt genome sequences of 110 species of arachnids. We also conducted parallel analyses using the nuclear small subunit rRNA (*18S*) gene from 226 species of arachnids to infer the phylogenetic position of eriophyoid mites.

2. Materials and methods

2.1. Data collection

Both eriophyoid mites were collected in Nanjing, China: *Leipothrix* sp. from the juniper, *Juniperus chinensis* (Cupressaceae) (China savin, May 2013) and the *Rhinotergum shaoguanense* from the elm, *Ulmus* sp. (Ulmaceae, May 2014). Mite samples were either used immediately for DNA extraction or were preserved in 100% ethanol at −20 °C prior to DNA extraction. Samples of each species was also slide mounted as vouchers, using modified Berlese medium (Amrine and Manson, 1996) for morphological checking with a Zeiss A2 (microphoto camera AxioCam MRc) microscope. All of the specimens and vouchers were deposited in the Arthropod Collection, Department of Entomology, Nanjing Agricultural University, China.

The mt genome sequences of 110 species of Arachnida and two outgroup species were retrieved from GenBank (Table S1). The dataset includes two Amblypygi, 26 Araneae, two Opiliones, five Scorpiones, two Solifugae, one Thelyphonida, two Pseudoscorpiones, four Ricinulei, 39 Parasitiformes mites, and 27 Acariformes mite species. The outgroups used were the horseshoe crab, *Limulus polyphemus* (Lavrov et al., 2000) and *Carcinoscorpius rotundicauda* (Baek et al., 2014).

Sequences of nuclear small subunit (*18S*) rRNA gene (~1800 bp) of 229 species were retrieved from GenBank (Table S2). These species include 140 families from 14 orders: 83 species of Trombidiformes (including 25 eriophyoid mites from all three families, Phytoptidae, Eriophyidae and Diptilomiopidae); 81 Sarcoptiformes; 31 Parasitiformes; four Amblypygi; five Araneae; five Opiliones; five Pseudoscorpiones; four Ricinulei; four Scorpiones; four Solifugae; and three Merostomata, which were chosen as outgroups.

2.2. DNA extraction, mt genome amplification and sequencing

For *R. shaoguanense*, genomic DNA was extracted from individual mites, using a DNeasy Blood and Tissue Kit (Qiagen), following a modified protocol (Dabert et al., 2008). A 658-bp fragment of *cox1* was initially amplified by PCR with the primer pair LCO1490–HCO2198 (Folmer et al., 1994) (Table 1). The PCR amplicon was purified and sequenced directly using Sanger method at Majorbio (Shanghai, China). A pair of specific primers for *R. shaoguanense*, X4COIF1–X4COIR1, was designed from the sequence of the *cox1* fragment. PCR with this pair of specific primers amplified a 13 kb amplicon. This amplicon was sequenced with Illumina Hiseq 2000 platform at the Beijing Genomics Institute, Hong Kong (BGI-HK).

Table 1
PCR primers used in this study.

Primer	Sequence (5′–3′)	Source
LR-J-122887	CCGGTCTGAACTCAGATCACGT	Simon et al. (1994)
LR-N-13398	CGCCTGTTTAACAAAAACAT	Simon et al. (1994)
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (1994)
X4COIF1	CATGCGATTTGTAGGTTTATACACTGAGCGGTTTC	This study
X4COIR1	AATCGTATCACAAGGCTTAAAGAAGATCCGTAGAA	This study
COIEb5F1	AATCAACCTCAGGCCTGAACCATAA	This study
16SEa1R1	TCTGCTCATTGCCGAGACAAGGTAAAA	This study
EA1F6R	GAGCAGAAGCAAGCTTCTAATAAGAGGCCT	This study
EA1R6R	CGTTACCATGGTAGGGGTTGTGTCTGTTTTCG	This study