



The phylogeny of acariform mites: what brought us here and perspectives*

ALMIR R. PEPATO^{1,2}, SAMUEL G. DOS S. COSTA^{1,2,4} & PAVEL B. KLIMOV^{2,3,5}

¹Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Departamento de Zoologia, Laboratório de Sistemática e Evolução de Ácaros Acariformes, Av. Antonio Carlos, 6627, Pampulha, Belo Horizonte - MG ZIP: 31270-901, Brazil

✉ apepato@gmail.com; <https://orcid.org/0000-0002-2944-4209>

²Tyumen State University, X-BIO Institute, 10 Semakova Str., 625003 Tyumen, Russia

³Purdue University, Lilly Hall of Life Sciences, G-226, 915 W State St, West Lafayette, IN 47907, United States

⁴<https://orcid.org/0000-0003-1686-1406>

⁵<https://orcid.org/0000-0002-9966-969X>

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Recent years have witnessed an increasing availability of DNA sequence data from acariform mites. However, compared to Hexapoda, a clade to which the mite diversity rivals, the amount of acariform molecular data estimated in cells in supermatrix alignments (Fig. 1) is lagging behind by approximately one decade, since insect datasets reached 10^7 cells in 2010 (reviewed in Kjer *et al.* 2016). The studies published to date progressed from Sanger sequenced data where ribosomal RNA (rRNA) played a predominant role (Maraun *et al.* 2004, Pahl *et al.* 2012, 2021, Krause *et al.* 2016, Schaefer *et al.* 2010, Pepato & Klimov 2015), often combined with a smaller locus, such as nuclear coding *elongation factor 1- α* (EF1 α) gene (Domes *et al.* 2007, Klimov & O'Connor, 2008); mitochondrial *cytochrome c oxidase subunit 1* (COI) (Dabert *et al.* 2010, 2016, Pepato *et al.* 2018, 2019), or morphology (Pepato *et al.* 2010). More recently, Sanger datasets have added additional single-copy markers, such as *signal recognition particle 54* (SRP54) and *heat shock protein 70* (HSP70) (Klimov & O'Connor 2013, Klimov *et al.* 2018, Pepato *et al.* 2022). Furthermore, new generation sequencing (NGS) was employed to sequence mitochondrial acariform genomes (Xue *et al.* 2016, Li & Xue 2019, Arribas *et al.* 2020), phylogenomic studies addressing the chelicerates large picture included an increasing number of members of the group (*e.g.* Lozano-Fernandez *et al.* 2019), and the first phylogenomic studies addressing the internal relationships of Acariformes were recently published (Dong *et al.* 2018, Klimov *et al.* 2022). The use of Ultra Conserved genomic Elements (UCEs) is a promising approach waiting for being further explored (Van Dam *et al.* 2019).

The use of molecular data led to settle long held debates among acarologists, provided new evidence for ongoing debates, or rejected long held ideas. For the former we can mention the inclusion of Astigmata and *Paralycus* among Oribatida. In the latter, the main division of Acariformes in Sarcoptiformes and Trombidiformes, and placement of all Endeostigmata among Sarcoptiformes, with increasing evidence of lineages that diverged previously to the Sarcoptiformes-Trombidiformes split. Finally, there are new hypotheses with an increasing support, for example that marine mites (Halacaridae), traditionally included in Eupodina and regarded as a sister group to Bdelloidea, are better placed within Anystina, close to Parasitengona, and the phylogenetic placement of the vermiform plant associates, Eriophyoidea, among basal Endeostigmata. Here we discuss the insights from a recently published, representative timetree (five genes, 9,200 bp aligned, 367 terminals belonging to 150 ingroup plus 15 outgroup families, 23 fossil calibration points). Concerning the Acariformes internal relationships, our phylogeny recovered the lineage alicid endeostigmatid + eriophyoid (Alycidae, Nanorchestidae, (Nematallycidae, Eriophyoidea)) diverging prior to the remaining Acariformes: (proteonematallycid Endeostigmata, alicorhagiid Endeostigmata, Trombidiformes, Oribatida (including Astigmata)). Trombidiform relationships had the following novel rearrangements: (i) traditional Eupodina lacked support for the inclusion of Bdelloidea; (ii) Teneriffidae, traditionally placed among Anystina, was consistently recovered in a clade including Heterostigmata in Eleutherengona; (iii) several lineages, such as Adamystidae, Paratydeidae, Caeculidae and Erythracaridae, were recovered in a large clade along other Anystina and Eleutherengona, suggesting single origin of several fundamental character states, such as the reduction of the cheliceral fixed digit and development of the palpal thumb-claw complex.

Our phylogeny points to future directions for the Acariformes phylogenetic studies: (i) inclusion as many family-level clades as possible; (ii) addressing the basal relationships among the Trombidiformes and Parasitengona; (iii) using the Birth-Death class of models in timetree inference requiring a more evenly distributed sampling of the acariform diversity, and (iv) including morphological datasets to better integrate fossils into timetree inference (a tip dating approach). Finally, the Sanger heritage and morphological studies must be integrated to the phylogenomic analyses, not just by guiding the sampling, but also by adding new terminals to the already assembled datasets of Sanger sequenced markers and mitochondrial genomes, since this data may be easily obtained from NGS data (Azevedo *et al.* 2022). As the Sanger legacy continues playing an important role, future research will certainly move toward phylogenomic approaches using whole genome sequencing data.

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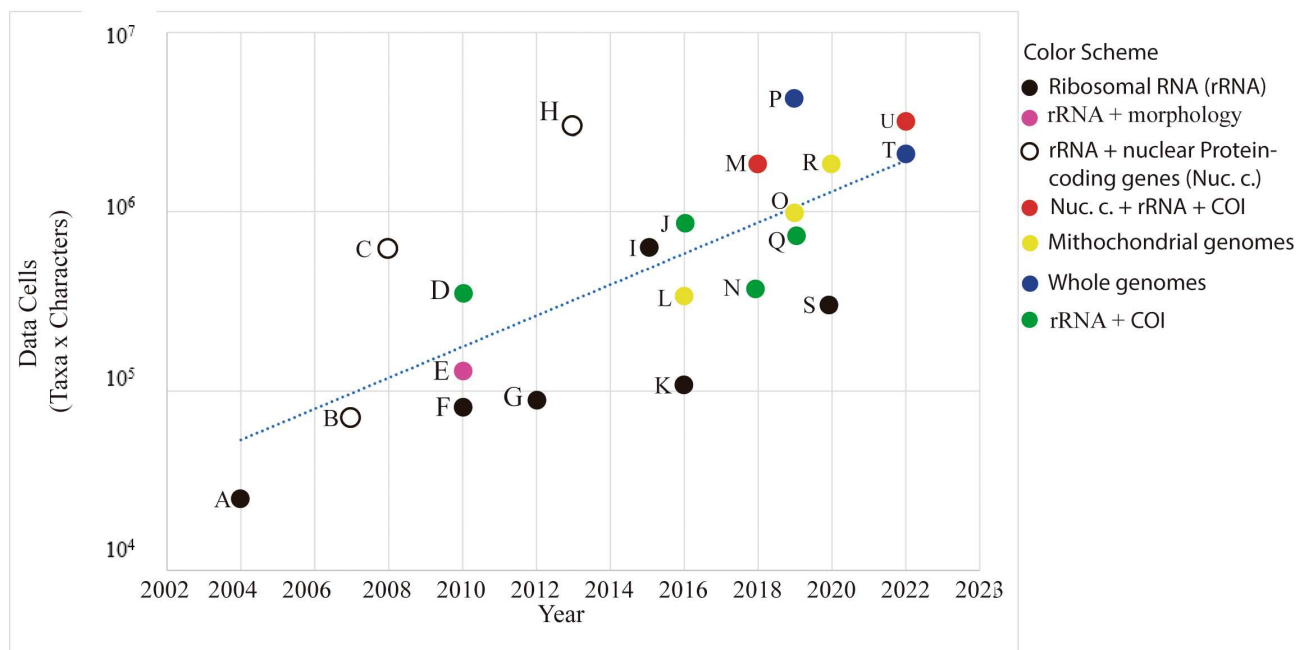


FIGURE 1. Sequencing data used in mite phylogenetic studies in 2002–2022. The y-axis shows the estimated amount of data as the number of taxa multiplied by sequence alignment length (cells in the supermatrix). For comparison with nucleotide data, amino acids data we multiplied by a factor of three. Legend shows different data types. A—Maraun *et al.* 2004, B—Domes *et al.* 2007, C—Klimov & O’Connor 2008, D—Dabert *et al.* 2010, E—Pepato *et al.* 2010, F—Schaefer *et al.* 2010, G—Pachl *et al.* 2012, H—Klimov & O’Connor 2013, I—Pepato & Klimov 2015, J—Dabert *et al.* 2016, K—Krause *et al.* 2016, L—Xue *et al.* 2016, M—Klimov *et al.* 2018, N—Pepato *et al.* 2018, O—Li & Xue 2019, P—Lozano-Fernandez *et al.* 2019, Q—Pepato *et al.* 2019, R—Arribas *et al.* 2020, S—Pachl *et al.* 2021, T—Klimov *et al.* 2022, U—Pepato *et al.* 2022

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