

Symbiosis in an overlooked microcosm: a systematic review of the bacterial flora of mites

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(Received 12 February 2015; revised 23 March 2015; accepted 20 April 2015; first published online 25 May 2015)

SUMMARY

A dataset of bacterial diversity found in mites was compiled from 193 publications (from 1964 to January 2015). A total of 143 mite species belonging to the 3 orders (Mesostigmata, Sarcoptiformes and Trombidiformes) were recorded and found to be associated with approximately 150 bacteria species (in 85 genera, 51 families, 25 orders and 7 phyla). From the literature, the intracellular symbiont *Cardinium*, the scrub typhus agent *Orientia*, and *Wolbachia* (the most prevalent symbiont of arthropods) were the dominant mite-associated bacteria, with approximately 30 mite species infected each. Moreover, a number of bacteria of medical and veterinary importance were also reported from mites, including species from the genera *Rickettsia*, *Anaplasma*, *Bartonella*, *Francisella*, *Coxiella*, *Borrelia*, *Salmonella*, *Erysipelothrix* and *Serratia*. Significant differences in bacterial infection patterns among mite taxa were identified. These data will not only be useful for raising awareness of the potential for mites to transmit disease, but also enable a deeper understanding of the relationship of symbionts with their arthropod hosts, and may facilitate the development of intervention tools for disease vector control. This review provides a comprehensive overview of mite-associated bacteria and is a valuable reference database for future research on mites of agricultural, veterinary and/or medical importance.

Key words: Symbionts, Acari, allergy, *Rickettsiales*, *Cardinium*, microbiota.

INTRODUCTION

Mites are classified in the subclass Acari (class Arachnida) of the phylum Arthropoda. Although approximately 48 200 species have been described (Halliday *et al.* 2000), a further half-million species are believed to exist worldwide (Kettle, 1984). More so than any other arthropod group, mites are found in highly diverse habitats: terrestrial, marine, freshwater and even in the upper atmosphere due to dispersal through aerial currents (Krantz and Walter, 2009). Whereas most mite species live freely in the environment, some species have evolved to be parasitic on other animals or on plants and are therefore of great agricultural and veterinary importance, although their medical impact is generally more modest. Some species are significant destructive pests of stored food products; while others (such as house dust mites) produce faecal allergens, inducing asthma. Mites can also produce serious skin conditions by feeding on the skin of domestic animals (mange) and can cause dermatitis in humans. Finally, some species act as important vectors of pathogenic microorganisms of medical and veterinary importance (Arlian *et al.* 2003;

Brouqui and Raoult, 2006; Valiente-Moro *et al.* 2009a).

The relationship between bacteria and arthropods can be divided into 2 main aspects, which are not mutually exclusive: (1) bacteria recognized as pathogens transmitted by an arthropod vector, and (2) bacteria residing as symbionts within their arthropod host. The study of the first aspect usually concerns surveillance for emerging or re-emerging diseases and interactions between the arthropod vector, environment, wildlife, domestic animals and humans. In contrast, the second research area concerns other bacteria that may influence the physical, ecological and evolutionary traits of their arthropod host, usually without transmission of these organisms to a second host in which disease may occur. These studies are often designed to characterize and define symbiont–arthropod interactions. For example, the nutritional mutualist, *Buchnera aphidicola*, synthesizes essential amino acids for its aphid host (*Acyrtosiphon pisum*) that feeds on plant phloem, which has a very low essential amino-acid content (Gunduz and Douglas, 2009). Pea aphids also harbour defensive mutualists such as *Regiella insecticola*, which protects the host population from a natural enemy (the pathogenic fungus, *Pandora neoaphidis*) by reducing the sporulation rate in aphid cadavers, thus reducing the probability of

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pathogen transmission to other aphids (Scarborough *et al.* 2005). Other bacterial genera are capable of manipulating their hosts' reproduction: *Wolbachia*, *Cardinium*, *Spiroplasma* and *Rickettsia* induce detrimental phenotypes in their arthropod hosts such as cytoplasmic incompatibility, parthenogenesis induction, feminization and male killing (Stouthamer *et al.* 1999; Tinsley and Majerus 2006; Enigl and Schausberger, 2007; Giorgini *et al.* 2009). These findings may be utilized to enhance prospects for biological control since there is the potential to manipulate arthropod populations of agricultural, medical or veterinary importance.

Recently, the number of publications on arthropod-associated bacteria has substantially increased, particularly for the Diptera, Hemiptera and Hymenoptera (Baumann, 2005; Crotti *et al.* 2010; Martinson *et al.* 2011; Taylor *et al.* 2011; Martin *et al.* 2012; Zucchi *et al.* 2012; Skaljic *et al.* 2013). In parallel, studies on mite-bacterial relationships have also increased, but to a lesser extent compared with the insect orders above. Moreover, sources of information with respect to mites and their pathogens and symbionts are widely distributed in the literature, and the compilation of data in terms of review publications is still very limited. Accordingly, the aims of this literature review are (1) to obtain an overview of bacterial diversity in mites and its potential applications, and (2) to provide comparative data for mite-associated bacteria of agricultural, veterinary and medical importance to stimulate hypothesis-driven research.

MATERIALS AND METHODS

Literature search

This review focuses on reports of bacteria found in mites across the world. The publications were extracted by searching from 2 major scientific literature databases, PubMed (www.ncbi.nlm.nih.gov/pubmed) and Web of Knowledge (www.webofknowledge.com). Three main mite orders (Mesostigmata, Sarcoptiformes, Trombidiformes), some common names of mites (e.g. gamasid mite, dust mite, itch mite, spider mite, harvest mite, free-living mite, chigger etc.) or scientific names (e.g. *Dermanyssus*, *Dermatophagoides*, *Leptotrombidium* or *Tyrophagus*), were used in combination with the term 'bacteria' or 'bacterium' as the keywords and applied to the title field or abstracts in those databases. From the obtained literature, the number of bacterial taxa (genus and species level) was recorded for each mite species. Only the publications reporting a minimum of genus-level identifications of bacteria were included in the database for statistical analyses. Bacterial scientific names obtained from the literature were checked for taxonomic assignment following the NCBI Taxonomy Browser (<http://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi>), while for the latest mite taxonomic classifications, Krantz and Walter (2009) was consulted.

Mite classification

Taxonomically, the mites were classified into 3 orders and 14 superfamilies. In addition, for the purposes of the present investigation, mites were also grouped into 4 types based on life history (Krantz and Walter, 2009): (1) 'Vertebrate parasite' was defined as a mite species which at some lifecycle stage feeds on vertebrate animals or are confirmed as disease vectors; (2) 'Invertebrate predator' was defined as a mite species which at some lifecycle stage hunts or feeds upon other invertebrates (some of which are used as biological pest control in agricultural practice); (3) 'Plant parasite' was defined as a mite species that feeds on live plant tissues (with some species responsible for economic losses in agricultural products); and (4) 'House pest and allergen' are those mites which spoil stored foodstuffs or contain powerful allergens that induce detrimental immune responses in humans and/or animals (Table S1).

Bacterial classification

For bacteria, apart from taxonomic classification, 4 bacterial groups were categorized due to their biological characteristics. Following the scheme of Valiente-Moro *et al.* (2009b), the different categories were defined as: (1) 'Saprophyte' – examples are bacteria which have not been described as being pathogenic; (2) 'Opportunistic pathogen' – species in this category cause disease in compromised vertebrate hosts but not in healthy hosts; (3) 'Pathogen' – most species in the genus are pathogens of vertebrates; and (4) 'Symbiont' – bacteria that strictly live in association with an arthropod host.

Statistical analysis

In order to visualize the distribution of the bacteria found in each mite superfamily, a principal component analysis (PCA) was performed using R freeware (R Development Core Team, 2008) with the ade4 package (Dray and Dufour, 2007). The PCA was calculated by counting the number of bacterial genera positively reported in each mite taxa. Before starting the analysis, data from 4 mite superfamilies (Oppioidea, Rhodacaroidae, Erythraeoidea and Eviphidoidea) were removed due to only one record of bacteria each that could cause analysis bias (outliers).

To investigate the difference of the 4 biological types of mite on bacterial diversity, the species number of bacteria (species richness) in each order was recorded across the 4 mite categories. This was analysed using the non-parametric Kruskal–Wallis

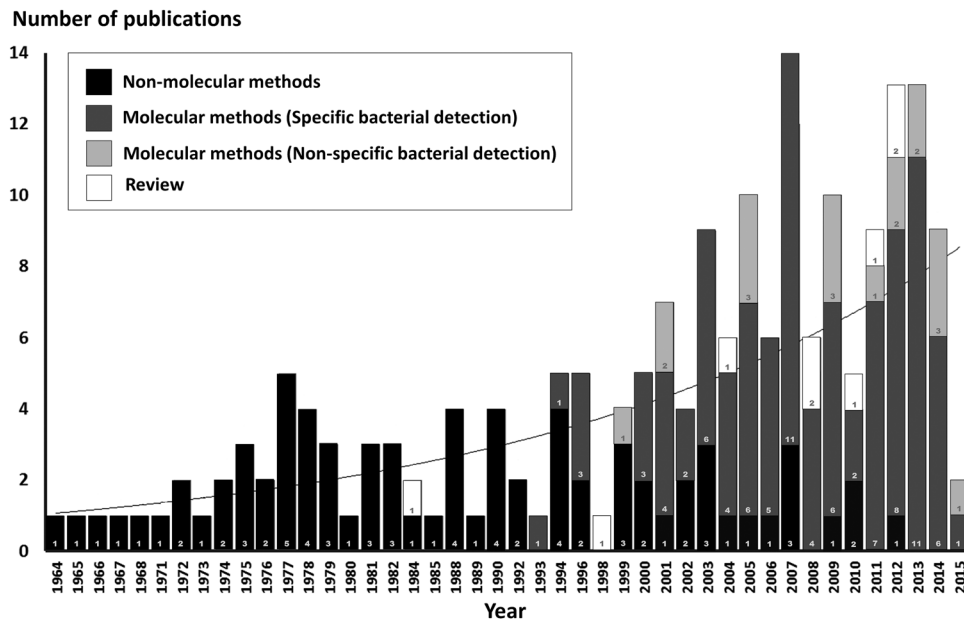


Fig. 1. The number of publications reporting mite-associated bacteria. Numbers within bars refer to a breakdown of publications by methodology. Curve represents an exponential line of best fit.

test, and multiple pairwise comparison tests were performed with SPSS version 21.0 software (IBM Corporation, Armonk, NY, USA), applying 95% confidence intervals. *P*-values were adjusted for multiple comparisons.

RESULTS & DISCUSSION

Methodological approaches to the identification of bacteria in mites

A total of 193 publications were included in this systematic review from 1964 until January 2015. The number of publications reporting mite-associated bacteria was found to increase gradually over this period (Fig. 1). However, we estimated that the total volume of literature describing mite-bacteria associations is 5 times smaller than that for ticks and 20 times smaller than that for insects (data not shown). The eligible publications covered 143 mite species belonging to 3 orders and 14 superfamilies (Table S1). The most studied mite taxon was Dermanysoidea (46 species), followed by Trombiculoidea (34 species), Tetranychoida (23 species) and Phytoseioidea (10 species).

Clearly, prior to the early 1990s (Fig. 1), analyses of bacteria in mites were restricted to non-molecular methods such as conventional bacterial cultures with biochemical characterization, inoculations of laboratory animals and serological tests. For example, *Mycoplasma* spp. were isolated from goats' ear mites, *Psoroptes cuniculi* and *Raillietia caprae*, by culturing the crushed mites in PPLO agar supplemented with pig serum, and then the bacteria were identified by biochemical characteristics (Cottew and Yeats, 1982). Similarly, the red poultry mite, *Dermanyssus gallinae*, was studied for its potential vectorial role for

Salmonella gallinarum and *Erysipelothrix rhusiopathiae* transmission in the poultry industry by culturing mite extracts in selective enrichment media, selenite broth (Zeman *et al.* 1982) and crystal-violet sodium-azide broth (Chirico *et al.* 2003), respectively. In the scrub typhus research field, a number of studies have used mouse passages to amplify *Orientia tsutsugamushi* from wild chigger mites fed on the rodents, and different strains of the bacterium were indirectly detected by various serological methods (e.g. fluorescence antibody assays, immunoperoxidase staining and complement fixation tests; Kitaoka *et al.* 1974; Roberts *et al.* 1977; Dohany *et al.* 1978; Shirai *et al.* 1982; Ree *et al.* 1992; Frances *et al.* 2001; Lerdthusnee *et al.* 2002; Phasomkusolsil *et al.* 2009). Of course, such specific methods allow the identification of the target organism only, and unculturable bacteria would not be detected.

With the advent of the molecular era, the development of specific PCR assays and conventional and next-generation sequencing techniques revealed a significantly higher microbial diversity than was previously estimated by culture-dependent approaches (Hugenholtz *et al.* 1998; Hubert *et al.* 2014; Yun *et al.* 2014). In particular, use of 16S rDNA PCR with bacterial species-specific primers has been widely used for bacterial taxonomic studies in mites (Fig. 1). Additionally, several publications used specific PCR to amplify other bacterial genes of interest. For example, the protein-coding genes: *ftsZ*, *groEL*, *wsp* and citrate synthase (*gltA*) were used in *Wolbachia* studies (Hong *et al.* 2002; Gotoh *et al.* 2005; Yu *et al.* 2011; Lu *et al.* 2012; Ros *et al.* 2012; Suh *et al.* 2014; Glowska *et al.* 2015; Zhang *et al.* 2015); outer membrane protein B gene, 17 kD antigenic gene and *gltA* were used

for *Rickettsia* spp. (Reeves *et al.* 2006, 2007; Choi *et al.* 2007; Tsui *et al.* 2007); the 16S–23S intergenic spacer (ITS) and *gltA* were used for *Bartonella* spp. (Kabeya *et al.* 2010; Kamani *et al.* 2013); *gyrB* was used for *Cardinium* (Ros *et al.* 2012; Zhu *et al.* 2012); the 5S–23S ITS was used for *Borrelia* spp. (Literak *et al.* 2008); the *epank1* gene was used for *Anaplasma phagocytophilum* (Literak *et al.* 2008); and the 56-kD type-specific antigen gene was used extensively for *O. tsutsugamushi* (Tamura *et al.* 2000; Pham *et al.* 2001; Khuntirat *et al.* 2003; Lee *et al.* 2011; Liu *et al.* 2013; Seto *et al.* 2013; Shin *et al.* 2014; Takhampunya *et al.* 2014).

An alternative approach has been the use of conserved primers to amplify 16S rRNA products in an unbiased fashion (Fig. 1), followed by cloning and sequencing of selected clones for taxonomic assignment (Hogg and Lehane, 1999, 2001; Hoy and Jeyaprakash, 2005; Hubert *et al.* 2012, 2014; Tang *et al.* 2013; Murillo *et al.* 2014). However, to the best of our knowledge, only one publication has used the Roche 454 pyrosequencing platform targeting 16S rRNA amplicons to reveal the bacterial community of a mite species (in this case, the bulb mite, *Rhizoglyphus robini*; Zindel *et al.* 2013). In a more recent study, bacterial genomic sequences from 100 species (predominantly enterobacteria) were identified during assembly of the *Dermatophagoides farinae* (dust mite) genome (Chan *et al.* 2015).

Bacterial diversity in mites

Mite species were found to be associated with 85 bacterial genera (approximately 150 identified species) belong to 7 phyla (plus 3 classes of *Proteobacteria*) and 25 orders (Table S2 and S3). *Cardinium* (in 31 mite species), *Wolbachia* (31 hosts) and *Orientia* (32 hosts) were the most prevalent bacteria; followed by *Bartonella*, *Anaplasma* and *Rickettsia*, with 16, 14 and 11 mite species reported, respectively (Fig. 2). Among the 7 bacterial phyla and the 3 classes of *Proteobacteria* (α , β and γ), *Bacteroidetes*, *Firmicutes*, *Tenericutes* and *Actinobacteria* were reported in all 3 mite orders (Fig. 3). However, *Chlamydiae* were reported only in mites from the order Mesostigmata, and *Spirochaetes* were found in the Mesostigmata and Trombidiformes, but not in the Sarcoptiformes (Fig. 3).

Symbionts can be obligatory or facultative, live inside or outside host cells, and can affect their host negatively, positively, or have no discernible phenotype. Some symbiotic bacteria may provide benefits to the host in particular environments, but can be disadvantageous under different circumstances (Hoy and Jeyaprakash, 2008). A number of bacteria were reported as potential mite symbionts in this literature survey, including *Wolbachia*, *Cardinium*, *Acaricomex*, *Spiroplasma*, *Snodgrassella*, *Serratia*, *Rickettsiella* and *Schineria*. *Wolbachia* and

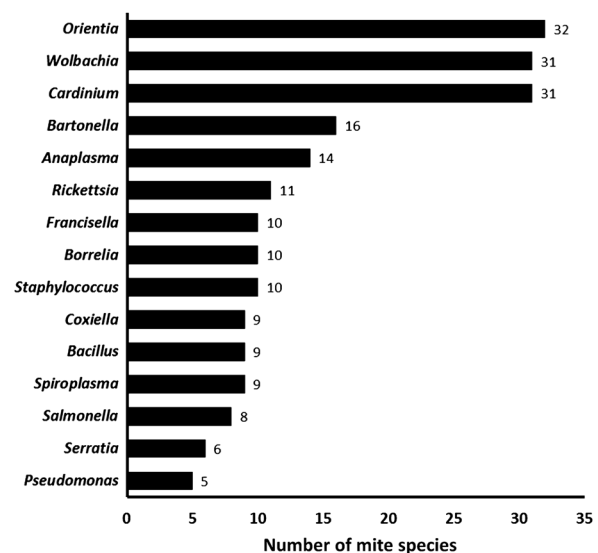


Fig. 2. The top-ranked 15 bacterial genera detected in mites.

Cardinium have been relatively well studied in terms of effects on their mite hosts, which manifest as reproductive alterations. However, the phenotypes (if any) induced by the other potential symbionts remain unknown. *Wolbachia* and *Cardinium* manipulate mite reproduction by inducing cytoplasmic incompatibility, parthenogenesis, sex-ratio distortion (e.g. male-killing and feminization), and an increase in female fecundity (Breeuwer and Jacobs, 1996; Weeks and Breeuwer, 2001; Chigira and Miura, 2005; Gotoh *et al.* 2005; Groot and Breeuwer, 2006; Gotoh *et al.* 2007; Novelli *et al.* 2008; Zhu *et al.* 2012; Zhao *et al.* 2013a; Suh *et al.* 2014; Zhang *et al.* 2015). These reproductive manipulation strategies facilitate vertical transmission through the female line and drive the spread of the symbionts into mite populations (Zhao *et al.* 2013b).

Wolbachia is the most prevalent arthropod symbiont (infecting approximately 40% of terrestrial species; Zug & Hammerstein, 2012) and is also found in some species of filarial nematodes (Ferri *et al.* 2011). In mites, although 31 species were positively reported for *Wolbachia* infection, the bacteria occurred only in 5 of 14 studied superfamilies: the Dermanyssoidea (various parasitic mites of vertebrates), Phytoseioidea (fungivorous, pollenophagous and predatory mites), Oppioidea (in an oribatid free-living mite, *Oppiella nova*), Cheyletoidea (parasitic mites of birds, but not in *Demodex* spp.), and Tetranychioidea (phytophagous mites). Interestingly, *Cardinium* was also found in 31 mite species but these were distributed across 8 superfamilies, representing a much broader host range than *Wolbachia* (Table S2). According to these findings, *Cardinium* appears to be a more important symbiont for mites than it is for other arthropods (Zug & Hammerstein, 2012).

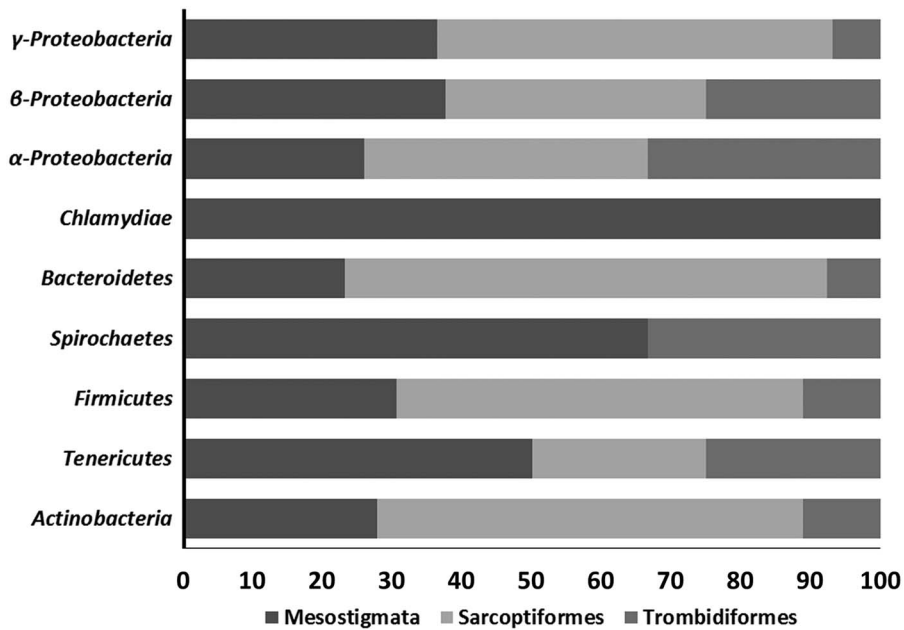


Fig. 3. Proportions (%) of the most abundant bacterial groups in the 3 principal mite orders.

Apart from these reproductive symbionts, another symbiotic bacterium, *Acaricomes phytoseiuli*, has been isolated from the predatory species, *Phytoseilus persimilis*, which is widely used for biological control of spider mites (major agricultural pests) (Pukall *et al.* 2006). Plants damaged by feeding spider mites release volatiles to attract predacious mites when hunting their prey. Schütte *et al.* (2008) reported that *A. phytoseiuli* caused *P. persimilis* to become refractory to plant volatile attraction, leading to a high tendency to miss their prey (the so-called ‘non-responding syndrome’). Moreover, infected mites developed symptoms such as body shrinkage, cessation of oviposition and even death. Accordingly, the bacterium was realized as a potential pathogen of predatory mites (Schütte and Dicke, 2008; Schütte *et al.* 2008).

Mites are often overlooked as vectors of diseases when compared with ticks or haematophagous insects, but a number of pathogenic bacteria have been reported in the vertebrate-parasitic mite superfamilies Dermanyssoidea, Acaroidea, Cheyletoidea and Trombiculoidea. In terms of veterinary importance, mites have been reported as potential vectors and reservoirs of several pathogenic bacteria of livestock. *E. rhusiopathiae*, the causative agent of erysipelas, and *S. gallinarum*, causing fowl typhoid, were reported in the poultry red mite, *D. gallinae* (Zeman *et al.* 1982; Chirico *et al.* 2003; Wales *et al.* 2010; Brännström *et al.* 2010; Valiente-Moro *et al.* 2011). These diseases rapidly spread in infected flocks with moderate to high morbidity, resulting in significant economic damage (Takahashi *et al.* 2000; Shah *et al.* 2005). With respect to mammalian livestock, *Anaplasma* spp., such as *A. phagocytophilum* (causing tick-borne fever in ruminants) were

found in various mite species of the superfamily Dermanyssoidea (Fernandez-Soto *et al.* 2001; Reeves *et al.* 2006); whereas the opportunistic pathogen *Serratia marcescens* was found in the scab mites, *Psoroptes ovis* and *P. cuniculi*, although a role for this bacterium in the pathogenesis of psoroptic mange has not been demonstrated (Mathieson and Lehane, 1996; Hogg and Lehane, 1999; Perrucci *et al.* 2005).

For human public health, the most researched mite-associated bacterium is the scrub typhus agent, *O. tsutsugamushi*. This *Rickettsia*-like bacterium has been mainly found in chiggers (the larval stage of trombiculid mites), with more than 30 species reported as hosts (Kitaoka *et al.* 1974; Shirai *et al.* 1982; Ree *et al.* 1992; Kelly *et al.* 1994; Urakami *et al.* 1999; Frances *et al.* 2001; Jensenius *et al.* 2004; Tilak *et al.* 2011; Phasomkusolsil *et al.* 2012; Seto *et al.* 2013). Thus, in contrast with *Cardinium* and *Wolbachia* (Zug and Hammerstein, 2012), *Orientia* appears to be a highly specialized symbiont of a single mite superfamily. Three genera of chiggers, *Leptotrombidium*, *Schoengastia* and *Blankaartia*, were also implicated in having a vectorial role for *Bartonella tamiae*, one of several *Bartonella* spp. that cause illness in Asian populations (Kosoy *et al.* 2008; Kabeya *et al.* 2010). Moreover, *Bartonella* spp. have been detected in other mite taxa, the Dermanyssoidea, Acaroidea, Glycyphagoidea and Cheyletoidea (Reeves *et al.* 2006; Kopecky *et al.* 2014; Murillo *et al.* 2014), suggesting that several mites could play an important role as vectors or reservoirs of human bartonellosis.

In addition to the poultry pest *D. gallinae*, members of the superfamily Dermanyssoidea that may feed on humans have been found to be infected

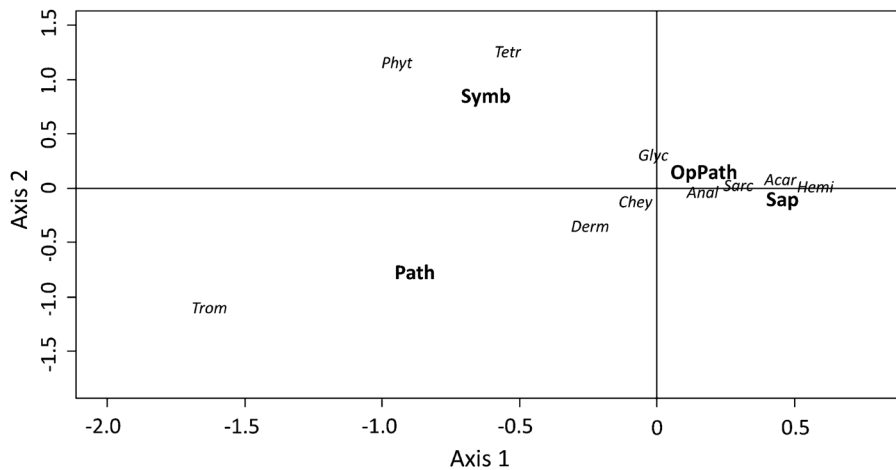


Fig. 4. Principal Component Analysis of 10 mite superfamilies (*Acar*, Acaroidea; *Anal*, Analgoidea; *Chey*, Cheyletoidea; *Derm*, Dermanyssoidea; *Glyc*, Glycyphagoidea; *Phyt*, Phytoseioidea; *Hemi*, Hemisarcoptoidea; *Sarc*, Sarcoptoidea; *Tetr*, Tetranychoida and *Trom*, Trombiculoidea) associated with the categorized bacterial groups (Sap, Saprophytes; OpPath, Opportunistic Pathogens; Path, Pathogens; Symb, Symbionts).

with pathogenic bacteria of medical importance. For example, the intracellular pathogens, *Rickettsia akari* (causing rickettsialpox) was isolated from the mouse and rat mites, *Liponyssoides sanguineus* and *Ornithonyssus bacoti* (Jensenius *et al.* 2004; Brouqui and Raoult, 2006; Reeves *et al.* 2007); *Rickettsia typhi* (causing murine typhus) was also found in *O. bacoti* (Grabarev *et al.* 2009); and *Rickettsia prowazekii* (the causative agent of epidemic typhus) was isolated from *Androlaelaps fahrenheitsi* and *Haemogamasus reidi* in addition to the main louse vector of the disease (Kettle, 1984; Jensenius *et al.* 2004; Bitam, 2012). Moreover, another intracellular pathogen, *Coxiella burnetii* (the causative agent of Q-fever) was detected in *L. sanguineus*, *O. bacoti*, *D. gallinae*, *Eulaelaps stabularis*, *Androlaelaps* spp. and *Haemogamasus* spp. (Zemskaya and Pchel'nik, 1968; Kettle, 1984; Kocianova, 1989; Reeves *et al.* 2007); the spirochete, *Borrelia burgdorferi* (a causative agent of Lyme disease) was found in *O. bacoti*, *Myonyssus gigas*, *Laelaps agilis*, *E. stabularis*, *Euryparasitus emarginatus*, *Eugamasus* sp. and *Haemogamasus* spp. (Lopatina *et al.* 1999; Netusil *et al.* 2005, 2013); and a further highly-virulent pathogenic bacterium in humans and other mammals, *Francisella tularensis* (causative agent of tularaemia), was isolated from *O. bacoti*, *Hirstionyssus* spp., *Haemogamasus* spp. and *Laelaps* spp. (Timofeeva, 1964; Petrov, 1971; Zuevskii, 1976; Lysy *et al.* 1979).

Patterns of mite-bacterial association

The PCA revealed well-separated associations between the mite taxa (10 superfamilies) and bacterial types, with the first and second dimensions explaining 96% of the total variance (Fig. 4). Trombiculoidea were reported to be strongly associated with pathogenic bacteria, whereas symbiotic

bacteria were clustered with mites from the Phytoseioidea and Tetranychoida. However, the remainder of mite taxa (Dermanyssoidea, Acaroidea, Analgoidea, Glycyphagoidea, Hemisarcoptoidea, Sarcoptoidea and Cheyletoidea) were less strongly associated with opportunistic pathogens and saprophytes. Undoubtedly, in part these data reflect important biases related to bacteria-specific studies, such as the exclusive focus on the Trombiculoidea as vectors of *O. tsutsugamushi*; or the fact that the relationship between symbiotic bacteria and mites has been better studied in the Phytoseioidea and Tetranychoida than in the other mite taxa.

Of 25 bacterial orders, only 7 taxa showed significant differences in bacterial species richness among the 4 biological mite groups: *Actinomycetales* ($\chi^2 = 24.97$, $p < 0.0001$), *Bacillales* ($\chi^2 = 30.64$, $p < 0.0001$), *Cytophagales* ($\chi^2 = 79.21$, $p < 0.0001$), *Entomoplasmatales* ($\chi^2 = 19.33$, $p < 0.0001$), *Pseudomonadales* ($\chi^2 = 24.77$, $p < 0.0001$), *Rhizobiales* ($\chi^2 = 17.69$, $p = 0.001$) and *Rickettsiales* ($\chi^2 = 21.82$, $p < 0.0001$) (Fig. 5). However, there were no significant differences in total bacterial species richness among the 4 mite groups ($\chi^2 = 5.72$, $p = 0.126$). Mites in the 'pest and allergen' group showed higher total bacterial richness than mites in the other groups (significantly so for *Actinomycetales*, *Bacillales*, *Cytophagales*, *Pseudomonadales* and *Rhizobiales*); however, *Rickettsiales* were completely absent therein (Fig. 5H). Mite species in this category are well recognized as generators of allergens and carriers of some pathogenic fungi in human stored food products (Franzolin *et al.* 1999; Hubert *et al.* 2004, 2012). Invertebrate-predator mites harboured a high number of *Entomoplasmatales* (Fig. 5E), although these were exclusively derived from the genus *Spiroplasma*. The bacteria in this genus are known as reproductive manipulators of insect

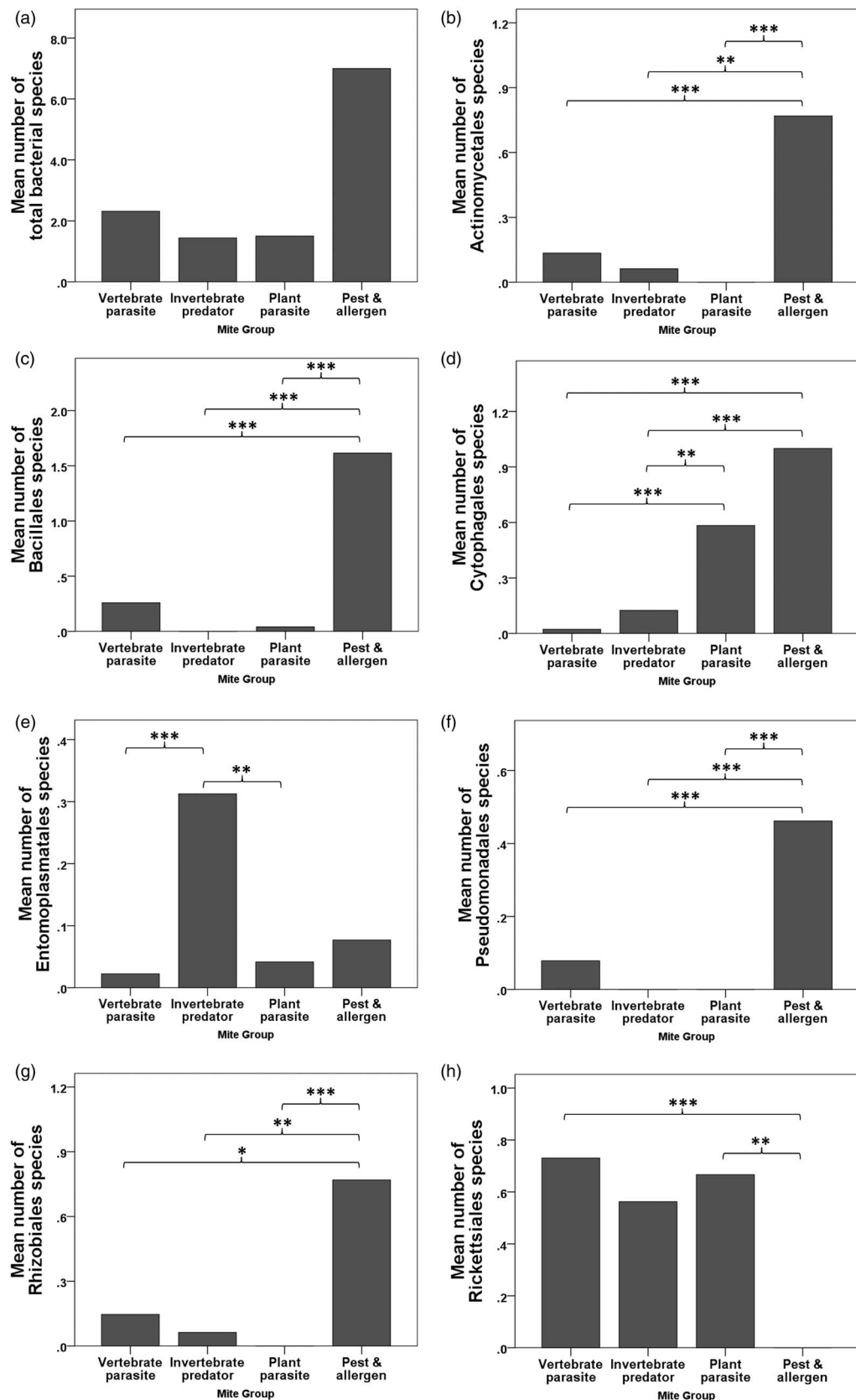


Fig. 5. Analysis of differences in bacterial species richness among mite taxa with multiple pairwise comparisons after Kruskal–Wallis test (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) for all bacterial species combined (A), *Actinomycetales* (B), *Bacillales* (C), *Cytophagales* (D), *Entomoplasmatales* (E), *Pseudomonadales* (F), *Rhizobiales* (G) and *Rickettsiales* (H).

predators and plant pests (Enigl and Schausberger, 2007; Di Blasi *et al.* 2011; Rivera *et al.* 2013), demonstrating that predacious and phytophagous mites and their plant hosts form an important habitat for maintaining *Spiroplasma* in nature.

Outcomes and perspectives

This systematic review of the literature suggests that important differences in bacterial flora may exist between mites with different lifestyles, since 'house pests and allergens' displayed a particularly diverse bacteriome enriched for several of the bacterial orders included in the analysis (with the notable exceptions of the *Entomoplasmatales* and *Rickettsiales*). A key priority for allergy research will be to determine whether these apparent associations are confirmed by further unbiased, high-throughput sequencing methods; and if so, the extent to which the bacterial flora of mite pests may modulate conditions such as atopic dermatitis (Sonesson *et al.* 2013). It would also be interesting to investigate the putative absence of *Rickettsiales* from this group of mites to reveal any potential barriers to colonization, especially as the *Rickettsiales* are clearly widespread in other mite categories.

On the basis of the mite literature published to date, very few bacterial species have become uniquely adapted to mites, with only *Orientia* spp., *R. akari* and *A. phytoseiuli* contending as mite-specific symbionts. For the former 2 species, the possibility that they are not restricted to mites with a vertebrate-parasite lifestyle should be considered. Indeed, other arthropod-transmitted human pathogens, such as *Rickettsia felis*, have been detected in non-biting arthropods (Thepparit *et al.* 2011). Our review of the literature also raises the hypothesis that *Cardinium* is so widely distributed in mites (Weeks *et al.* 2003) that it may be better adapted to this taxon [and perhaps other arachnids, Duron *et al.* (2008)] than it is to insects.

In conclusion, this review provides useful reference data of mite-associated bacteria for further research, with the intention to increase awareness of the potential for mites to transmit disease. A deeper understanding of the impact of symbionts on their arthropod hosts may also facilitate the development of intervention tools for vector and pest control, for which precedents for insects already exist (Jeffery *et al.* 2009; Iturbe-Ormaetxe *et al.* 2011). Manipulation of the bacteriome could lead to future opportunities to decrease the medical, veterinary and agricultural impact of mites, although major challenges in the handling and colonization of many species lay ahead.

SUPPLEMENTARY MATERIAL

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0031182015000530>

FINANCIAL SUPPORT

We gratefully acknowledge the Mahidol-Liverpool Chamlong Harinasuta Scholarship scheme for financial support of KC.

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