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

KITTIPONG CHAISIRI1,2, JOHN W. MCGARRY3, SERGE MORAND4 and BENJAMIN L. MAKEPEACE1*

1 Institute of Infection and Global Health, University of Liverpool, 146 Brownlow Hill, Liverpool L3 5RF, UK
2 Department of Helminthology, Faculty of Tropical Medicine, Mahidol University, Bangkok 10400, Thailand
3 School of Veterinary Science, University of Liverpool, 401 Great Newton Street, Liverpool L3 5RP, UK
4 CNRS CIRAD AGIRs, Centre d’Infectiologie Christophe Mérieux du Laos, Vientiane, Lao PDR

(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 (Acyrthosiphon pisi) 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...
Bacterial flora of mites

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, parthenogenetic inuction, 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 pod-associated bacteria has substantially increased, medical or veterinary importance. The latest mite taxonomic classification, 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 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.

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, Trombidiiformes), 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. Dermaanyssus, 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.

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, Rhodacaroidea, Erythraeoida 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
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 Dermanyssoidea (46 species), followed by Trombiculoidea (34 species), Tetranychoidea (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; Głowaska et al. 2015; Zhang et al. 2015); outer membrane protein B gene, 17 kDa 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. (Literatek et al. 2008); the epank1 gene was used for *Anaplasma phagocytophilum* (Literatek 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; Takkampunya 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. 2014). In a more recent study, bacterial genomic sequences from 100 species (predominantly enterobacteria) were identified during assembly of the *Dermatophagooides 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*, *Acaricomes*, *Spiroplasma*, *Smogdgrassella*, *Serratia*, *Rickettsiella* and *Schinneria*. *Wolbachia* and *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 Dermaphysoidea (various parasitic mites of vertebrates), Phytoseioidea (fungivorous, pollinophagous and predatory mites), Oppiidae (in an orbibatid free-living mite, *Oppiella nova*), Cheyletidea (parasitic mites of birds, but not in *Demodex* spp.), and Tetramychoidea (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).
Apart from these reproductive symbionts, another symbiotic bacterium, *Acaricomes phytoseiuli*, has been isolated from the predatory species, *Phytoseiulus 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 Trombiculoidae. 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...
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* (Jenseni 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 fahrenholzi* 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. (Zemskaya and Pchelnika, 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,* *Euryprausis emarginatus, Eugamasus* sp. and *Haemogamasus* spp. (Lotapina 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 tularemia), was isolated from *O. bacoti, Hirstonyssus* 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-separate associations between the mite taxa (10 superfamilies) and bacterial types, with the first and second dimensions explaining 96% of the total variance (Fig. 4). Trombiculoida were reported to be strongly associated with pathogenic bacteria, whereas symbiotic bacteria were clustered with mites from the Phytoseioida and Tetranychoida. However, the remainder of mite taxa (Dermeszioidea, Acaroidea, Analgoidea, Glycyphagoidea, Hemisarcoptoidea, Sarcoptoeidea and Tetranychoida and Trombiculoida) associated with the categorized bacterial groups (Sap, Saprophytes; OpPath, Opportunistic Pathogens; Path, Pathogens; Symb, Symbionts).

![Fig. 4. Principal Component Analysis of 10 mite superfamilies (Acar, Acaroidea; Anal, Analgoidea; Chey, Cheyletoidea; Derm, Dermeszioidea; Glyc, Glycyphagoidea; Phyt, Phytoseioida; Hemi, Hemisarcoptoidea; Sarc, Sarcoptoeidea; Tetr, Tetranychoida and Trom, Trombiculoida) associated with the categorized bacterial groups (Sap, Saprophytes; OpPath, Opportunistic Pathogens; Path, Pathogens; Symb, Symbionts).](https://www.cambridge.org/core/doi/10.1017/S0031182015000530)
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. phytoseiulid containing 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 (Theparit 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.

REFERENCES


