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RESOURCE ARTICLE

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Advancing mite phylogenomics: Designing ultraconserved elements for Acari phylogeny

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Abstract

Mites (Acari) are one of the most diverse groups of life on Earth; yet, their evolutionary relationships are poorly understood. Also, the resolution of broader arachnid phylogeny has been hindered by an underrepresentation of mite diversity in phylogenomic analyses. To further our understanding of Acari evolution, we design targeted ultraconserved genomic elements (UCEs) probes, intended for resolving the complex relationships between mite lineages and closely related arachnids. We then test our Acari UCE baits in-silico by constructing a phylogeny using 13 existing Acari genomes, as well as 6 additional taxa from a variety of genomic sources. Our Acari-specific probe kit improves the recovery of loci within mites over an existing general arachnid UCE probe set. Our initial phylogeny recovers the major mite lineages, yet finds mites to be non-monophyletic overall, with Opiliones (harvestmen) and Ricinuleidae (hooded tickspiders) rendering Parasitiformes paraphyletic.

KEYWORDS
Acari, Arachnida, mites, Opiliones, Parasitiformes, partitioning, phylogenomics, Ricinuleidae, ultraconserved elements

1 | INTRODUCTION

Acari, commonly known as mites and ticks, are an extraordinary ecologically diverse group that occupy a wide range of niches, from marine-living algae feeders, specialist ectoparasites to soil herbivores. Acari are an old lineage, and their fossil record indicates that they may have arisen in the late Silurian, with many extant superfamilies present as far back as the early Devonian (Lindquist, Krantz, & Walter, 2009), and with a burst of diversification during the late Mesozoic (Krantz & Walter, 2009).

Mites have been particularly problematic for modern systematics, with over 40,000 named species in 540 families, primarily from temperate Eurasia and North America (Lindquist et al., 2009; Walter & Proctor, 1999). Considering the paucity of data from the rest of the world, the true species diversity of mites is likely somewhere between 500,000 and 1 million (Walter & Proctor, 1999). Among the major challenges for mite systematics is the small size of most taxa, the availability of taxonomic expertise to identify them, and the complexities of their position within Arachnida (Fernández & Giribet, 2015; Giribet & Edgecombe, 2012; Giribet, Edgecombe, Wheeler, & Babbitt, 2002; Regier et al., 2010; Sharma et al., 2014; Shultz, 2007; Starrett et al., 2017; Wheeler & Hayashi, 1998).

The class Acari is traditionally comprised of two major lineages (superorders), Parasitiformes and Acariformes, that are defined primarily on the basis of shared plesiomorphic traits. Parasitiformes and Acariformes have historically been considered to be sister groups largely based on the lack of convincing evidence that they are not each other's closest relative (Lindquist et al., 2009). There have been a number of studies, however, suggesting that not only are Acari not a monophyletic group, but also that the two superorders may be somewhat distant relatives (Dabert, Witalinski, Kazmierski, Olszanowski, & Dabert, 2010; Dunlop & Alberti, 2008; Pepato, da Rocha, & Dunlop, 2010; Van der Hammen, 1989). However, problems plague the higher taxonomy, and for many orders it is unclear, based on few studies of comparative morphology, whether even their placement within the two superorders is correct (Dunlop & Alberti, 2008; Klußmann-Fricke & Wirkner, 2016; Meither & Dunlop, 2016; Shultz, 2007).

While the number of molecular phylogenetic studies on Acari is growing, the majority are based on intrafamilial relationships (Domes,

Norton, Maraun, & Scheu, 2007; Dowling & OConnor, 2010; Hendricks, Flannery, & Spicer, 2013; Klimov & OConnor, 2008; Klimov & OConnor, 2013; Murrell, Campbell, & Barker, 2001; Maraun et al. 2004; Mans, de Klerk, Pienaar, de Castro, & Latif, 2012; Pachl et al., 2012). A number of taxa-rich phylogenetic studies have addressed the evolutionary relationships within the major mite lineages Acariformes and Parasitiformes based primarily on ribosomal and mitochondrial DNA (Dabert et al., 2010; Klimov et al., 2018; Klompen, Lekveishvili, & Black, 2007; Murrell et al., 2005; Pepato & Klimov, 2015; Pepato et al., 2010). These studies present conflicting frameworks of the higher-level relationships that have yet to be tested by large-scale phylogenomic data. Some points of conflict are the monophyly of Acari and Parasitiformes, and the closest relatives to Parasitiformes and Acariformes (Garwood & Dunlop, 2014; Giribet, 2018; Pepato & Klimov, 2015).

The placement of Acari within Arachnida and their closest arachnid relatives are unclear. Various hypotheses have been proposed, including Acaramorpha sistergroup relationship between Acari and Ricinulei (hooded tickspiders). Acaramorpha, however, has not been recovered in several molecular analyses (Garwood & Dunlop, 2014; Legg, Sutton, & Edgecombe, 2013; Pepato & Klimov, 2015). Giribet (2018) described the problem, "The relationships of Pseudoscorpiones, Palpigradi, Ricinulei, Solifugae, Opiliones and the two acarine clades are however poorly understood and they conflict in virtually every published analysis of arachnid relationships." As such, the potential sister groups to either Acari or its major lineages seem wide-ranging.

Ultraconserved genomic elements (UCEs) (sensu Faircloth et al., 2012), provide a powerful approach to sequence many independent regions of the genome for phylogenetic inference. UCEs have proven useful in resolving evolutionary relationships at multiple phylogenetic scales, both shallow and deep (Blaimer et al., 2015; Faircloth, Sorenson, Santini, & Alfaro, 2013; JeŠovnik et al., 2017; Moyle et al., 2016; Van Dam et al., 2017). While UCEs have been developed across many insect and arachnid orders (Faircloth, 2017; Starrett et al., 2017), few authors have designed custom UCE probes within these orders (with the exception of ants, Branstetter, Longino, Ward, & Faircloth, 2017). Taxon-specific probes target UCE loci with more specificity and in greater numbers (Branstetter et al., 2017; Faircloth, Branstetter, White, & Brady, 2015). UCEs, like many other genomic subsampling methods, rely on oligonucleotide "bait" capture procedures (Brewer & Bond, 2013) that can be particularly useful when relying on specimens with degraded DNA (Blaimer, Lloyd, Guillory, & Brady, 2016; Van Dam et al., 2017). Given the challenges with obtaining fresh samples for taxa that are either rare or found only in logistically challenging regions of the world, such DNA capture methods are beneficial (Bi et al., 2013; McCormack, Tsai, & Faircloth, 2016). This is especially true for mites where many species have highly specific niches, for example the nasal cavities of birds (Morelli & Spicer, 2007) or the cloaca of turtles (Krantz & Walter, 2009).

An existing UCE probe set designed for arachnid phylogeny included only two mite species, both ticks (*Ixodes scapularis and Amblyomma americanum*) (Faircloth, 2017) during design. To further our understanding of Acari evolution, here we design a custom UCE probe set specific to Acari based on 13 existing mite genomes. UCE probe kits are typically designed with fewer genomes, but we included nearly all available mite genomes to enhance the probe kit's potential effectiveness across this hyperdiverse, ancient group. We then test this probe set in-silico on 2 additional mites and 3 other arachnid libraries, as well as Merostomata (horseshoe crab) in order to evaluate its effectiveness at recovering the mite phylogeny.

2 | MATERIALS AND METHODS

2.1 | Study group

We used 13 publicly available mite genomes to design a probe set specifically for Acari (Table 1). The taxa represented in the probe design included representatives of most, but not all, major divisions of mites. We then performed an in-silico test of the probes on these taxa, plus 2 additional mites, as well as the putatively related arachnids groups hooded tickspider (Order Ricinulei) and saddleback harvestman (Order Opiliones). A spider and a horseshoe crab were used as outgroups. The data for the additional taxa were in the form of 3 additional genomes (*Dermatophagoides pteronyssinus*, *Limulus polyphemus*, *Stegodyphus mimosarum*), 2 low coverage "shotgun" libraries (*Cryptocellus goodnighti*, *Mitopus morio*) and 1 UCE bait capture data set (*Neomolgus littoralis*) (Table 1).

2.2 | Identification of loci and "bait" design

Our workflow follows that of Faircloth, 2017, and we used PHYLUCE scripts (Faircloth, 2016; Faircloth et al., 2012). All programs hereafter beginning with *"phyluce"* are PYTHON programs part of the PHYLUCE package. Specifically, we used *art* (Huang, Li, Myers, & Marth, 2012) to simulate paired-end, error-free reads for each genome that we then used to align to our "base" genome. We simulated 100 bp paired end reads at 2× coverage across each genome, and these reads were then merged. We selected *Tetranychus urticae* (GenBank accession number: GCA_000239435.1) as the "base" genome because it is relatively complete and because its phylogenetic placement, according to our preliminary analyses, is neither early diverging nor recently diverging within Acari.

In order to align the genomes to the "base" and look for homologous sections, we used *stampy* (Lunter & Goodson, 2011). We set the substitution rate of 0.05 and an insert size of 400. Aligned reads were converted to the BAM format using *samtools view* function (Li et al., 2009), followed by the removal of unmapped reads. Next, the BAM files were converted to BED format using *bedtools* (Quinlan & Hall, 2010). Small gaps were then removed based on alignment position (<100) in *bedtools*.

These alignments were further filtered by removing repetitive intervals using PHYLUCE v1.6 package (Faircloth, 2016) script *"phyluce_probe_strip_masked_loci_from_set."* These filtered aligned reads were then put into an SQLite database using "*phyluce_probe_get_multi_merge_table.*" The database was then queried to identify how

TABLE 1 GenBank accession numbers for the taxa used in this study

GenBank accession	Taxon	Arachnida order	Used in UCE identification	Used in insilico test	Data format origin	Insilico test no. of filtered alignments	Number of loci in final alignment
GCA_002081605.1	*Tropilaelaps mercedesae*	Acari:Parasitiformes	x	x	Genome	811	450
GCA_000828355.1	*Sarcoptes scabiei*	Acari:Acariformes	x	x	Genome	890	584
GCA_002085665.1	*Dermatophagoides farinae*	Acari:Acariformes	x	x	Genome	655	462
GCA_000988765.1	*Achipteria coleoptrata*	Acari:Acariformes	x	x	Genome	899	565
GCA_002135145.1	*Euroglyphus maynei*	Acari:Acariformes	x	x	Genome	943	591
GCA_000988845.1	*Hypochthonius rufulus*	Acari:Acariformes	x	x	Genome	897	584
GCA_002176555.1	*Rhipicephalus microplus*	Acari:Parasitiformes	x	x	Genome	364	147
GCA_000988885.1	*Steganacarus magnus*	Acari:Acariformes	x	x	Genome	934	584
GCA_000239435.1	*Tetranychus urticae****	Acari:Acariformes	x	x	Genome	878	547
GCA_000988905.1	*Platynothrus peltifer*	Acari:Acariformes	x	x	Genome	952	591
GCA_002443255.1	*Varroa destructor*	Acari:Parasitiformes	x	x	Genome	687	366
GCA_000255335.1	*Galendromus occidentalis*	Acari: Parasitiformes	x	x	Genome	700	423
GCA_000208615.1	*Ixodes scapularis*	Acari:Parasitiformes	x	x	Genome	731	320
GCA_001901225.2	*Dermatophagoides pteronyssinus*	Acari:Acariformes		x	Genome	791	533
SRR3932788	*Neomolgus littoralis*	Acari:Acariformes		x	UCE Reads	194	73
GCA_000517525.1	†*Limulus polyphemus*	†Merostomata		x	Genome	231	86
GCA_000611955.2	†*Stegodyphus mimosarum*	†Araneae		x	Genome	410	170
SRR3879970	*Cryptocellus goodnighti*	Ricinulei		x	Shotgun Unassembled Reads	339	111
SRR3879969	*Mitopus morio*	Opiliones		x	Shotgun Unassembled Reads	412	276

Notes. The higher order taxonomic placement as well as the genus and species of the taxa are listed. The *** indicates the base taxon *Tetranychus urticae* used for conserved loci identification by aligning it to all other genomes. The outgroup *Limulus* and *Stegodyphus* are listed with a † next to its name. The data format origin indicates what type of data was initially acquired from GenBank, genome, unassembled raw reads, or UCE loci from a previous study (Faircloth, 2017). The in-silico number of filtered alignments indicates how many individual loci were captured by a particular taxon in the in-silico test before any filtering of loci was performed for phylogenetic reconstructions.

many loci were shared between taxa using "*phyluce_probe_query_multi_merge_table*." We then selected reads that were found in our base taxon plus 5 other taxa (Table 2). We chose reads found across a relatively high number of taxa because we wanted to have a broad selection of loci to choose from for future possible sub-setting. We then extracted these loci (160 bp in total) from our bed files using *"phyluce_probe_get_genome_sequences_from_bed"*.

We next focused on designing baits for these conserved regions. First, we created a set of temporary baits using *"phyluce_probe_get_tiled_probes"* at a 3× tiling density, accepting 25% masked bases and with a GC content between 30% < x < 70% of the sequence to create 2 probes per locus.

We then used *LASTZ* (Harris, 2007) to align these baits to our exemplar taxa and subsequently removed any duplicates (different baits that hit the same loci and/or multiple loci hit by the same bait) that were ≥50% identical over >50% of the loci's length using "*phyluce_probe_easy_lastz*" and "*phyluce_probe_remove_duplicate_hits_from_probes_using_lastz*" to remove the aforementioned duplicates. We then aligned these temporary *Tetranychus* baits to the other taxa at a 50% sequence identity using "*phyluce_probe_run_multiple_lastzs_sqlite.*" These non-duplicated loci were then buffered 180 bp for each locus using "*phyluce_probe_slice_sequence_from_genomes*".

To identify which of these loci were detected consistently across the different mite genomes, we used "*phyluce_probes_get_multi_fasta_table*" to produce a count of loci detected (Table 2). We selected loci that were detected in 6 of the 13 taxa. Final baits were designed using "*phyluce_probe_get_tiled_probe_from_multiple_inputs,*" followed by removal of duplicates as before. We titled these baits the "*mite-v2-master-probe-list-baits*" for clarity.

We then tested to see how closely this bait set matched against the "*all-Arachnid-baits*" of Faircloth, 2016. We compared the two sets by seeing how many baits matched at a 50% similarity over 50% of the baits length.

2.3 | In-silico *test of "bait" design*

In order to test how well the baits performed, we added another 3 genomes (from a dust mite, a spider and a horseshoe crab) as well as

2 shotgun libraries (a hooded tickspider and a saddleback harvestman) and a UCE data set (a trombiform mite *Neomolgus littoralis*), see Table 1. We trimmed shotgun libraries and the raw UCE reads with *trimgalore* (Krueger 2015) in order to remove adapters and low-quality bases. We assembled the two shotgun libraries using ABYSS 2.0 (Jackman et al., 2017), selecting an optimal khmer size with KMERGENIE (Chikhi & Medvedev, 2014). We assembled the UCE raw reads using "*phyluce_assembly_assemblo_trinity*" with TRINITY v2013–02–25 (Grabherr et al., 2011). For the data sets excluding the UCE data, we used "*phyluce_probe_run_multiple_lastzs_sqlite"* to align our probes to genomes and then extract 400 bp to either side using "*phyluce_probe_slice_sequence_from_genomes*" followed by duplicate removal using "*phyluce_assembly_match_contigs_to_probes*" with 67% minimum coverage 80% minimum match in identity. We then used "*phyluce_assembly_get_match_counts*" and "*phyluce_assembly_get_fastas_from_match_counts*" to extract the loci that matched our probes into one large fasta file. For the UCE data set, we separately used "*phyluce_assembly_match_contigs_to_probes*" and "*phyluce_assembly_get_match_counts*" to identify UCE loci that matched our probes as before. Then using "*phyluce_assembly_get_fastas_from_match_counts*," we created a fasta file for our UCE loci data set. We concatenated these two files (UCE loci identified from genomes/assembled shogun libraries and UCE capture data) into one large fasta file.

We then aligned the sequences using *muscle* (Edgar, 2004), *"phyluce_align_seqcap_align"* also removing alignments with less than or equal to 3 taxa present. Then, we trimmed internal gaps using *gblocks* (Castresana, 2000) with *"phyluce_align_get_gblocks_trimmed_alignments_from_untrimmed."* We then compiled a list of loci shared across taxa using *"phyluce_align_get_align_summary_data"* and cleaned the names of the files with "*phyluce_align_remove_locus_name_from_nexus_lines*.".

We then took these nexus files and using the R package *ips* (Heibl, 2008) removed any ragged ends with the function "*trimEnds*," having a minimum of 4 taxa present in the alignment.

TABLE 2 Number of loci shared between taxa

Shared between # of taxa	Loci shared between taxa count
Shared by 1	2,514
Shared by 2	2,474
Shared by 3	2,415
Shared by 4	2,322
Shared by 5	2,211
Shared by 6***	2,058
Shared by 7	1,856
Shared by 8	1,619
Shared by 9	1,290
Shared by 10	922
Shared by 11	551
Shared by 12	227
Shared by 13	40

The *** indicates the design that was chosen for this bait set, 2,058 loci shared between 6 of 13 taxa.

2.4 | Phylogenetic reconstructions of exemplar taxa

2.4.1 | Species tree analyses

Using R/unix scrips modified from Van Dam et al., 2017, we designated 6 character sets for each loci (the UCE central core, 160 bp, and 5 matching sets, each composed of 1/5 the remaining flanking length) (see Figure 1) and then used *partitionfinder2* (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016) to evaluate these different character sets into site rate partitions before individual gene trees were constructed. First, we created matrices by only including those alignments that are ~50% complete, with 9 or more taxa present. We then ran a partitioned maximum-likelihood (ML) analysis in RAXML 8.2.11 (Stamatakis, 2014) with 100 bootstrap replicates for each locus. A General Time Reversible +gamma (GTRGAMMA) site rate substitution model was used for each locus. Lastly, we used a modified R script from Borowiec, Lee, Chiu, & Plachetzki, 2015, to remove trees with the lowest 10% quantile of average bootstrap values. We also removed outlier loci that were potentially oversaturated, calculated as departure from a linear regression between uncorrected p-distances and inferred distances of the tips. We then constructed a species tree using ASTRAL-III (Zhang, Sayyari, & Mirarab, 2017). In addition, we also constructed a species tree with the same set of loci using SVDquartets (Chifman & Kubatko, 2015) in Paup* (Swofford, 2001). SVDquartets is expected to be more accurate than ASTRAL when there are few phylogenetically informative sites among loci, so we chose to use both of these two methods given possible biases in our loci (Molloy & Warnow, 2017).

2.4.2 | Concatenated analyses

We used this final set of alignments from above by first converting them from phylip to nexus using the R *ips* function "*write.nex*" and then concatenated the alignments using "*phyluce_align_format_nexus_files_for_raxml*." We partitioned the data set using each locus as a character set with the "greedy" search algorithm (Lanfear, Calcott, Ho, & Guindon, 2012) to select for the best partitioning strategy for the data under the GTRGAMMA site rate substitution model using the AICc metric. We then conducted 20 ML searches in RAXML 8.2.11, and used the autoMRE setting to determine a sufficient number of non-parametric bootstrap replicates. Lastly, we reconciled the bootstrap replicates with the best fitting ML tree.

3 | RESULTS

3.1 | Loci Identification and "bait" design

We identified a total of 1,832 conserved loci and 32,922 baits for the final bait design. The average number of taxa represented in each bait set per-loci is 9 (*SE* 0.04, 95% CI 8.89–9.07) of the 13 taxa. The mean number of loci targeted per taxon is 1,266 (*SE* 92.61, 95% CI 1,081–1,451). For details for specific taxa see Table 3.

When we compare the "*mite-v2-master-probe-list-baits*" against the "*all-Arachnid-baits*" (Faircloth, 2017), we found that 477 loci matched at a 50% identity over 50% coverage between bait sets. If we increased the metrics of similarity to 80% identity over 80% coverage, 303 duplicated loci where found. Lastly, if we looked for 100% matches over the full probe length, we only found 2 loci.

3.2 | In-silico *test of bait design*

We initially filtered loci to include those represented by greater than 3 taxa which resulted in 1,437 loci. This subset was further filtered to only include alignments that had 9 or more taxa present (47%), representing 713 loci. These loci have a mean length of 302.58 bp, a mean number of taxa per locus of 11.71 (Figure 2), and a mean number of 135.39 phylogenetically informative sites (Figure 3). Loci length was highly correlated with the number of phylogenetically informative sites *p*-value: <2.2e–16, see Figure 4. Removing the lowest 10% quantile of average bootstrap support trees and potentially over saturated outlier loci resulted in retaining 643 loci. This final data set was then used for phylogenetic reconstructions.

3.3 | Phylogenetic reconstructions of exemplar taxa

3.3.1 | Concatenated analyses

Our concatenated analysis returns a non-monophyletic Acari. A monophyletic Acariformes is recovered as well as its major subdivisions, Trombidiformes and Sarcoptiformes. Sister group to Acariformes is a paraphyletic Parasitiformes, with the non-mite groups, saddlebacked harvestman (Opiliones) and hooded tickspider (Ricinulei), placed inside Parasitiformes. Ricinulei is placed as sister to ticks (Ioxdida) and Opiliones as sister to (Ricinulei +ticks), with the remaining Parasitiformes, Mesgostigmata, sister to Opiliones + (Ricinulei +ticks). These relationships are relatively well supported, excluding the placement of the harvestman and hooded tickspider (Figure 5).

3.3.2 | Species tree analyses

The results from the Partitionfinder analysis of our initial six character sets, (the UCE central core: 160 bp, and 5 matching sets, each composed of 1/5 the remaining flanking length) identified 466 loci with a single partition, 222 with 2 partitions and 25 with 3 partitions, there were 0 loci of greater than 3 partitions.

Our ASTRAL species tree analysis recovered a monophyletic Acari, though support along the backbone of the trees is lacking (Figure 6). The ASTRAL tree recovers essentially a polytomy between two major monophyletic clades of mites, Parasitiformes and Acariformes, and the single Opiliones represented. Ricinulei is included in a basal polytomy with Araneae and the horseshoe crab *Limulus*. The SVDquartets tree has a similar topology within the ingroup as the ASTRAL tree, but varies in the relationships between the mites' close relatives and recovers a paraphyletic Parasitiformes, with ticks as the closest relative to the remaining mites. Another primary difference between the Astral topology and that of the concatenated and SVDquartets tree is that in the Astral tree, Trombidiformes is non-monophyletic, with the spider mite placed as the sister group to Astigmata.

4 | DISCUSSION

Here, we present a novel toolkit to facilitate future, comprehensive phylogenomic studies of Acari. Our initial test of this toolkit provides the first phylogenomic estimation of Acari and succeeds in recovering major mite lineages (Figure 5). Our analyses here do not aim to resolve mite phylogeny with sufficient taxon sampling, but instead, demonstrate the potential of our Acari probe kit for generating sufficient data for resolving major outstanding questions regarding the relationships among mites.

Our phylogenetic analyses, based on few exemplar taxa, do not recover a monophyletic Acari. Both our concatenated and species tree analyses indicate that closely related non-mite arachnids may render the mites non-monophyletic. Previous molecular analyses

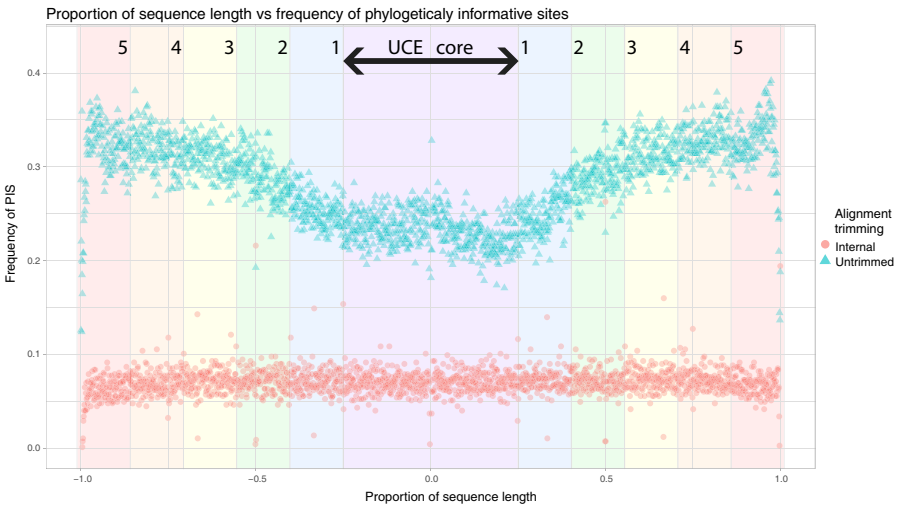

FIGURE 1 Frequency of phylogenetically informative sites (PIS) versus proportion of sequence length. Values represent phylogenetically informative sites (from final data alignments after G-blocks internal trimming, or raw untrimmed alignments). Background colours represent the 6 character sets used to partition site rate substitution. Phylogenetically informative sites were calculated with the *pis* function in the R library ips [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Distribution of the number of probes per taxon, followed by the number of loci targeted per taxon

Taxon	Number of probes	Number of loci
Tropilaelaps mercedesae	2,294	1,147
Sarcoptes scabiei	3,005	1,503
Dermatophagoides farinae	2,189	1,095
Achipteria coleoptrata	3,071	1,536
Euroglyphus maynei	2,906	1,453
Hypochthonius rufulus	3,116	1,558
Rhipicephalus microplus	962	481
Steganacarus magnus	3,033	1,517
*Tetranychus urticae****	3,150	1,575
Platynothrus peltifer	3,064	1,532
Varroa destructor	2,002	1,001
Galendromus occidentalis	2,271	1,136
Ixodes scapularis	1,859	930
Total unique	32,922	1,832

The base taxon *Tetranychus urticae* is indicated with ***.

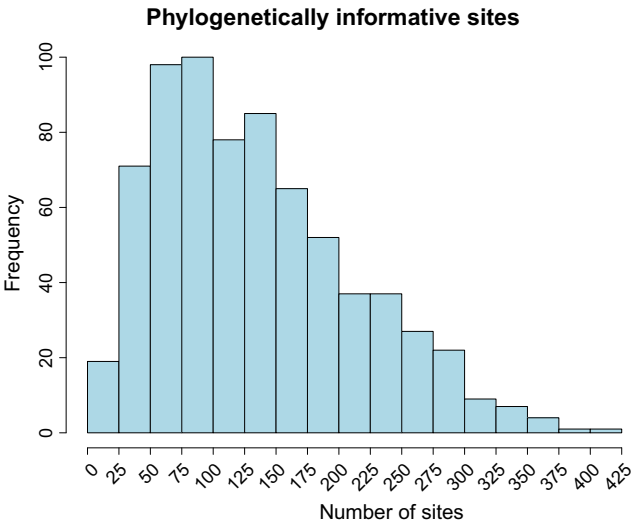

FIGURE 3 Frequency of phylogenetically informative sites from the final data matrices. Calculated with the *pis* function in the R library ips [Colour figure can be viewed at wileyonlinelibrary.com]

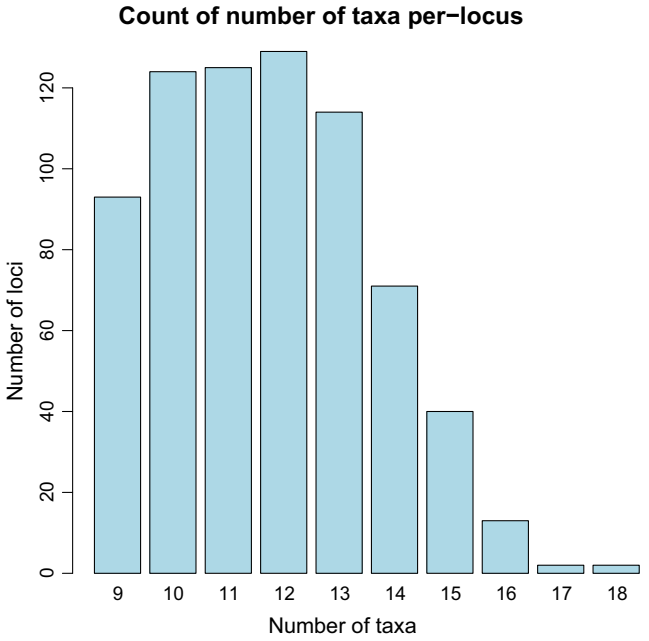

FIGURE 2 Number of taxa in each alignment. Frequency of loci found per number of taxa in each alignment along *Y*-axis. Counts based on final 50% complete matrix used to reconstruct initial gene trees [Colour figure can be viewed at wileyonlinelibrary.com]

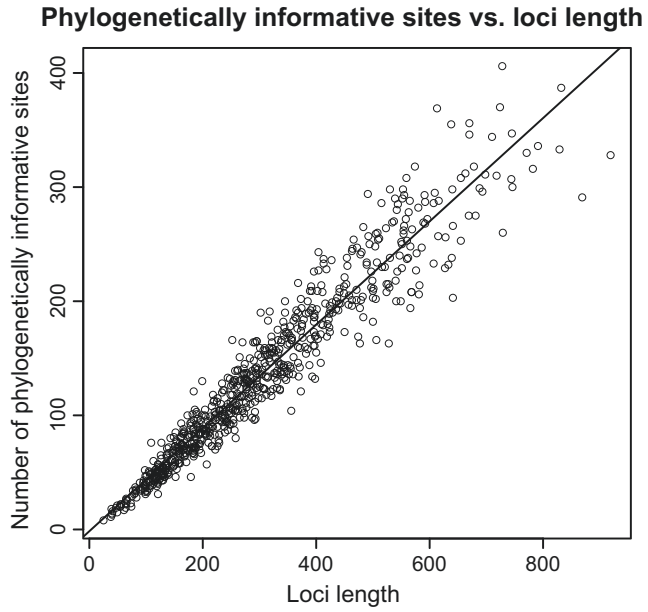

FIGURE 4 Linear regression between the number of phylogenetically informative sites and locus length. Phylogenetically informative sites calculated with the *pis* function in the R library ips

have also recovered a non-monophyletic Acari (Dabert et al., 2010, Pepato et al., 2010, Pepato & Klimov, 2015). Here, Opiliones alone, or Opiliones and Ricinulei together exhibit affinity with Parasitiformes (Figures 5 and 6). Ricinulei has long been considered a close Acari relative (Weygoldt & Paulus, 1979), but we find a novel placement of Opiliones, possibly resulting from our limited taxon sampling of closely related arachnids. Our study did not include previously proposed Acari relatives such as Solifugae and Pseudoscorpiones. Though our placement of Opiliones may be spurious, a previous rDNA phylogenetic study could not exclude the placement of Opiliones as sister group to Acari (Pepato et al., 2010).

We consistently recover a monophyletic Acariformes, yet a non-monophyletic Parasitiformes. Even when non-mites are excluded, Parasitiformes may be paraphyletic with respect to the remaining mites (Figure 6). Future work needs to include adequate sampling of closely related non-tetrapulmonate arachnid outgroups as well as dense sampling within "Parasitiformes" to resolve these outstanding questions in the acarine tree of life.

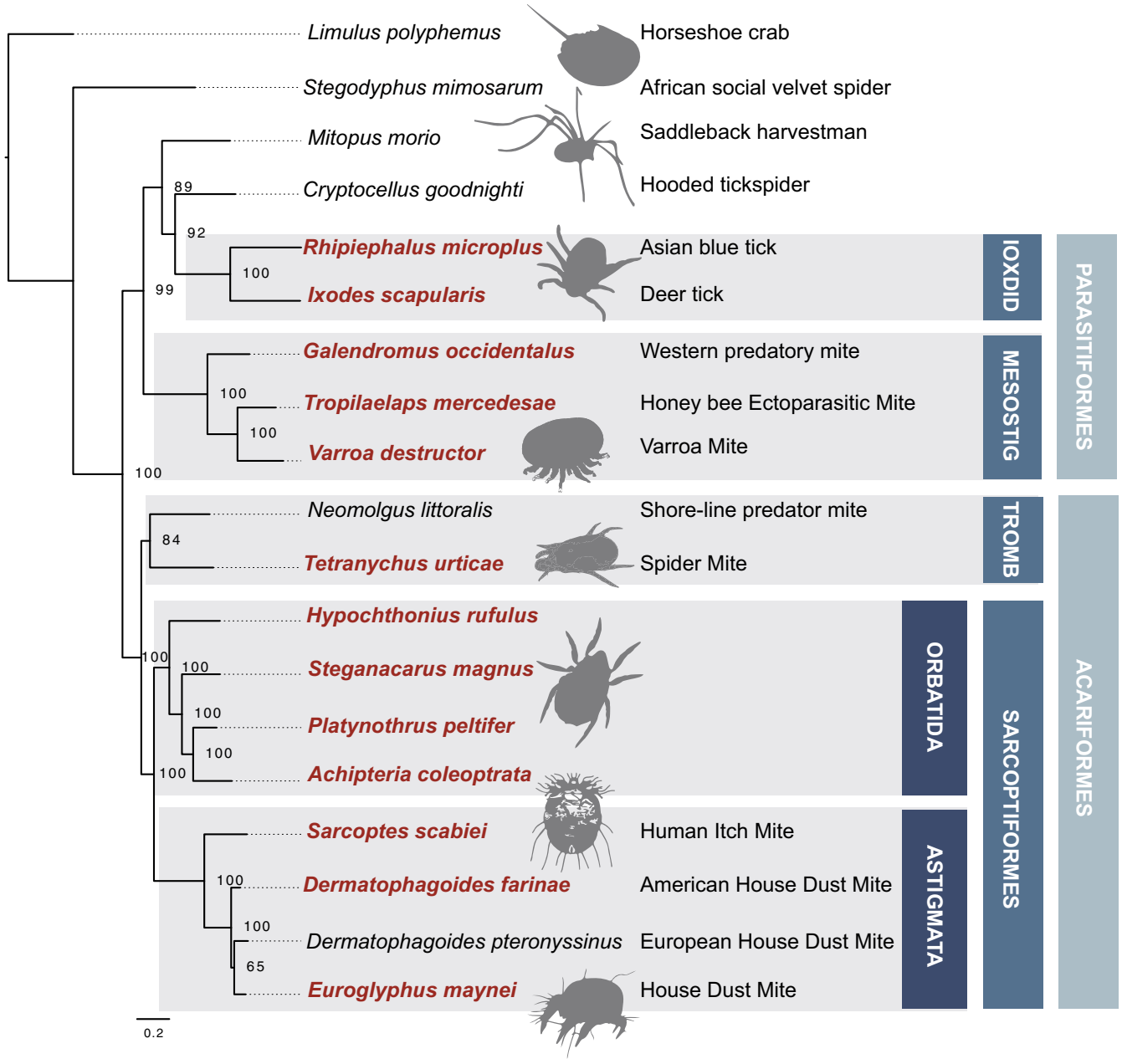

FIGURE 5 RAXML phylogenetic reconstruction from concatenation of 643 loci. Values at nodes indicate bootstrap support. Tip labels in bold were taxa used in probe design. Vertical boxes with text represent higher taxonomic classification [Colour figure can be viewed at wileyonlinelibrary.com]

Our concatenated topology is generally well-supported; yet, the taxa with the fewest number of loci tend to have lower bootstrap support and unstable placement. Taxa represented by fewer loci, including Ricinulei, Opiliones and the trombidiform mite *Neoglomus*, are represented by data that were not captured from high-quality genomes, but instead from unassembled shotgun sequencing reads, or in the case of *Neoglomus* from a previously captured arachnid UCE data set. The pre-existing sequences that were used for capture in these cases insufficiently represented the genomes of these taxa (Table 1) in terms of phylogenetic loci recovery. We expect that loci recovery from these taxa would be higher based on new extractions with more sequencing data. However, considering that only 170 *Neoglomus* loci were recovered from the arachnid UCE data set of Starrett et al., 2017, indicates effectiveness of the mite baits.

Our bait design purposefully selected loci to be less highly conserved (uniformly present), occurring in just 6 of the 13 taxa used for bait design. We relied on this less conserved design, first, because we were uncertain of how genome completeness could give a false indication of locus absence in a taxon. Secondly, we expected that this more inclusive probe design may allow for the capture of more loci within particular groups, for example Acariformes, as opposed to being primarily designed to capture loci found across both

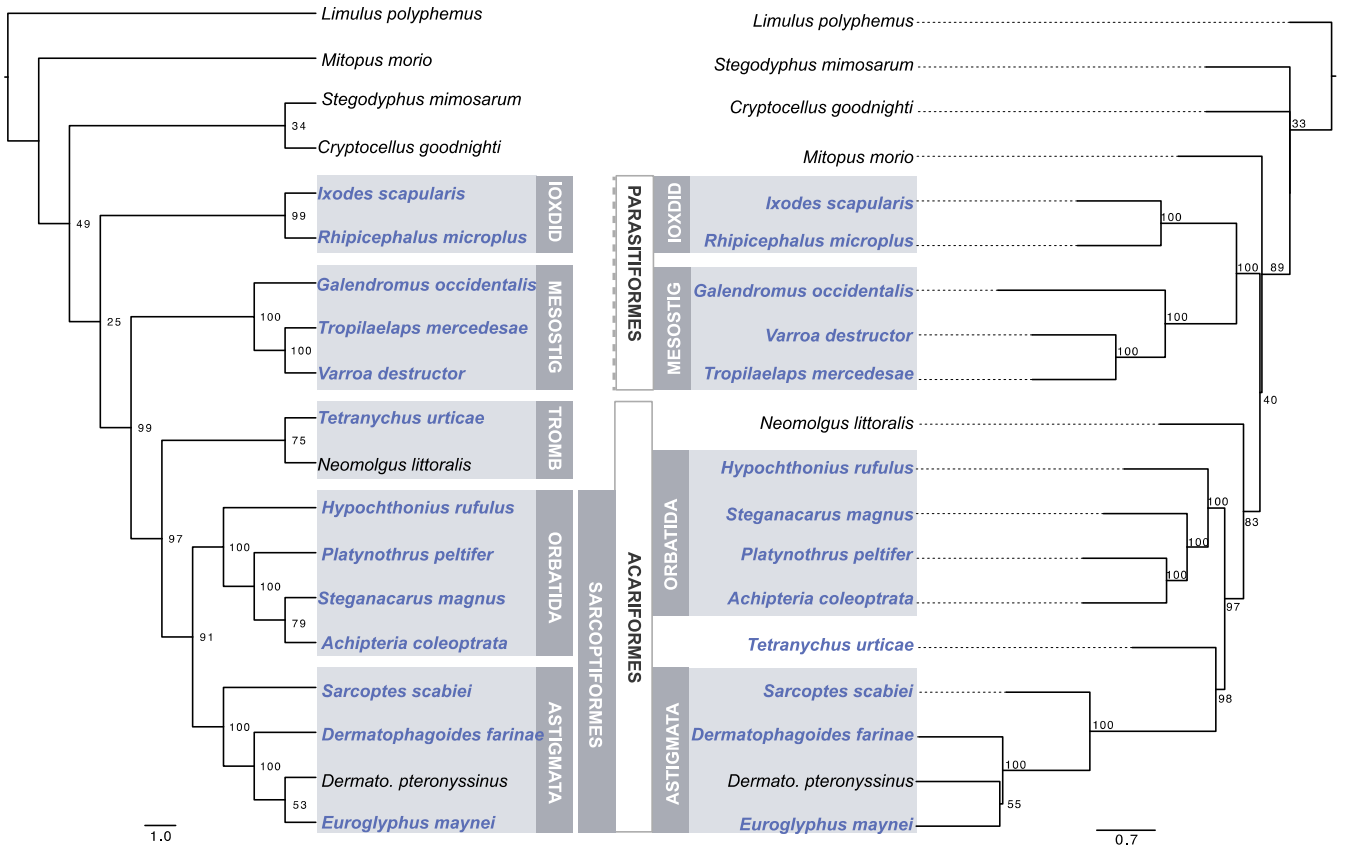

FIGURE 6 LEFT: SVDquartets species tree. Node values indicate bootstrap support values. RIGHT: ASTRAL species tree, input trees derived from RAXML gene trees. Values at nodes indicate bootstrap support. Vertical boxes with text represent higher taxonomic classification. The dashed line bordering Parasitiformes indicates paraphyly. Tip labels in bold are taxa that were used in probe design [Colour figure can be viewed at wileyonlinelibrary.com]

Acariformes and Parasitiformes. Ultimately, our design was conservative enough to capture, in-silico, hundreds of loci from not only putatively close mite relatives, like hooded tickspiders (Ricinulei), but also groups more distantly related to Acari, like a spider, horseshoe crab and in particular, saddleback harvestman (Opiliones). This relatively high level of locus recovery from Opiliones may be due either to the completeness of the Opiliones genome we relied on, or represent the actual phylogenetic affinity between Acari and Opiliones. In the previous arachnid UCE study (Starrett et al., 2017), they recovered on average 359.4 loci for Opiliones. For our one exemplar Opiliones (*Mitopus_morio*), we recovered 412 loci, which was greater than the highest number of loci, 406, recovered by Starrett et al., 2017. These results suggest that although our bait set was designed for Acari, it performs as well as the Faircloth, 2017 "*all-Arachnid-baits*" for Opiliones.

To understand the relationship of the superorders of Acari to one another, as well as their relationships to other arachnid orders, it is clear that a more thorough taxon sampling of Acari and Arachnida is required. No molecular analyses to date, including ours, have included all relevant mite and arachnid taxa to conclusively test mite monophyly. Acari may hold the key to understanding early arachnid evolution, which has remained unresolved even in the genomic era (Fernández & Giribet, 2015; Giribet & Edgecombe, 2012; Giribet et al., 2002; Mans et al., 2012; Pepato & Klimov, 2015; Regier et al., 2010; Sharma et al., 2014; Shultz, 2007; Starrett et al., 2017; Wheeler & Hayashi, 1998). We hope that by contributing this novel probe set, our understanding of the relationships among Acari, and indeed, arachnid phylogeny as a whole, can progress.

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AUTHOR CONTRIBUTIONS

M.H.V.D., M.T., G.S. and L.E. designed the research. M.H.V.D. performed the research and analysed the data. M.H.V.D. wrote the first draft of the manuscript, with all authors contributing to final version. M.H.V.D. and M.T. made the figures.

DATA ACCESSIBILITY

mite-uce-probe-set Dryad link: http://datadryad.org/review?doi=doi:10.5061/dryad.2168568. mite-uce-probe-set Dryad link https://doi.org/10.5061/dryad.2168568.

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