HHS Public Access

Author manuscript

Ticks Tick Borne Dis. Author manuscript; available in PMC 2024 March 06.

Published in final edited form as:

Ticks Tick Borne Dis. 2022 November ; 13(6): 102020. doi:10.1016/j.ttbdis.2022.102020.

A new species of tick, Ixodes (Ixodes) mojavensis (Acari: Ixodidae), from the Amargosa Valley of California

Laura H. Backus[a], **Janet E. Foley**[a], **Guy B. Hobbs**[b], **Ying Bai**[c], **Lorenza Beati**[b,*]

[a]Department of Medicine and Epidemiology, School of Veterinary Medicine, University of California, Davis, CA 95616, United States

[b]U.S. National Tick Collection, Institute for Coastal Plain Science, Georgia Southern University, 69 Georgia Avenue, Statesboro, GA 30460, United States

[c]Division of Vector-Borne Diseases, Centers for Disease Control and Prevention, Bacterial Diseases Branch, Fort Collins, CO 80521, United States

Abstract

Ixodes (Ixodes) mojavensis, n. sp. (Acari: Ixodidae), is described from all parasitic stages collected from the endangered vole Microtus californicus scirpensis Bailey, 1900 (Rodentia: Cricetidae), Mus musculus L. 1758 (Rodentia: Muridae), and Reithrodontomys megalotis (Baird; 1857) (Rodentia: Cricetidae) in the Amargosa Valley of California. When first collected in 2014, this tick was tentatively identified as Ixodes minor Neumann, 1902 because the nucleotide similarity between its 16S rDNA sequence and a homologous GenBank sequence from an I. minor from the eastern U.S. was 99.51%. Nevertheless, adults of I. mojavensis differ morphologically from I. minor by hypostomal dentition, absence of a spur on palpal segment I, and punctation patterns; nymphs by the shapes of basis capituli, auriculae, cervical grooves and external files of hypostomal denticles; and larvae by the length of idiosomal setae and hypostomal dentition. DNA sequencing of fragments of 4 different genes, 12S rDNA, 16S rDNA, cytochrome c oxidase subunit I (COI), and intergenic transcribed spacer 2 (ITS2) of I. mojavensis and of closely related species of Ixodes shows that the mitochondrial gene sequences of the new tick species are almost identical to the I. minor homologous genes. Phylogenetically, the two species do not cluster in mutually exclusive monophyletic clades. However, ITS2 sequences of I. mojavensis and I. minor diverge deeply (≥ 5.74% maximum likelihood divergence) and are as different as homologous genes from other recognized species. The discrepancy between the two sets of genes is suggestive of past mitochondrial introgression or incomplete mitochondrial lineage sorting.

Keywords

Ixodes mojavensis; Ixodes minor; Ixodes dentatus; New species; United States

*Corresponding author. lorenzabeati@georgiasouthern.edu (L. Beati).

CRediT author statement

Laura Backus: Conceptualization, Methodology, Data Curation, Writing-Original draft. **Janet Foley:** Conceptualization, Investigation, Writing- Review and Editing, Funding acquisition, Resources. **Ying Bai:** Data Curation, Methodology, Writing-Review & Editing. **Guy Hobbs:** Data Curation, Writing**. Lorenza Beati:** Supervision, Conceptualization, Project administration, Methodology, Data Curation, Writing-Original draft preparation, Review and Editing, Funding acquisition, Resources.

1. Introduction

DNA sequencing and molecular genotyping methods have allowed for expanded understanding of tick identity and phylogenetic relationships in ways that were impossible using morphology or cross breeding experiments alone. Nevertheless, genotyping, especially of just one or a few genes, may not be adequate to describe differences between species and phylogenetic relationships.

Ixodes (Acari: Ixodidae) ticks that were first collected from the Amargosa vole *Microtus californicus scirpensis* Bailey, 1900 (Foley et al., 2014; Ott-Conn et al., 2014; Poulsen et al., 2015) were tentatively identified as *Ixodes minor* Neumann, 1902 based on the comparison of their 16S rRNA and calreticulin gene sequences with homologous sequences in GenBank. The Amargosa vole is a federally endangered species (Klinger et al., 2015; US Fish and Wildlife Service, 1997) residing only in the Amargosa Valley of Inyo County in southern California. The vole is a burrow dwelling rodent limited to the riparian marsh habitat formed by springs along the Amargosa River, an isolated region that is otherwise surrounded by desert. Ticks were collected multiple times between 2011 and 2018 when voles were trapped for routine population health monitoring and population genetics studies. The tick species identified tentatively as *I. minor* was the predominant tick species on the voles which were sometimes also parasitized by immatures of *Dermacentor variabilis* (Say, 1821) (Paulsen et al., 2015), specimens now reidentified as *Dermacentor similis* Lado, Glon and Klompen, 2021 (López-Pérez et al., 2022). It was also collected sporadically from the house mouse, *Mus musculus* L. 1758, the western harvest mouse, *Reithrodontomys megalotis* (Baird, 1857), and from the nearby Owens Valley vole, *M. c. vallicola* Bailey, 1898 (Foley et al., 2014; Ott-Conn et al., 2014; Poulsen et al., 2015).

The 16S rRNA gene sequence was 99.51% identical (Foley et al., 2014) to a sequence (AF549841) from a colony of *I. minor* established from ticks collected in Georgia twenty years ago (Xu et al., 2003), and thus tentatively considered to be conspecific. However, identification based exclusively on percentage of base differences generated by BLAST can be misleading. The calreticulin gene differed from homologous genes of *I. minor* by 8%, but the extent of intraspecific variability in this gene has yet to be fully evaluated and the taxonomic meaning of such a finding is hard to appreciate. In addition, some morphological differences were noted between *I. minor* and the tick from the vole (Foley et al., 2014; Poulsen et al., 2015), warranting further investigation.

The collected samples included all parasitic stages of this tick and further morphological examination corroborated earlier observations indicating that it differs markedly from *I. minor* and, also, from all presently known *Ixodes* species. In this study, we provide descriptions of all stages of the new tick species. In addition, to further characterize and classify it, we analyze its molecular relationships with closely related taxa.

2. Materials and methods

2.1. Sample

A total of 26 female, 5 male, 7 nymphal, and 21 larval ticks, not used for pathogen detection during the 2014–2018 surveys, was examined and used for these descriptions. The map in Fig. 1 illustrates the location of collection sites. All ticks were collected from *M. c. scirpensis*, with the exception of 5 larvae from *M. musculus*, two nymphs from *M. c. vallicola*, and 2 females from *R. megalotis* (Table 1).

2.2. Morphological examination

Ticks were cleaned with household detergent in water (1: 9) and examined with a Nikon SMZ25 stereomicroscope (Nikon Instruments; Inc. Melville; NY), which was also used to take measurements (in millimeters for adults and nymphs and micrometers for larvae, given as range followed by mean and standard deviation in parentheses). Scanning electron microscope images were taken with a JEOL JSM-6610LV (JEOL USA, Inc.; Peabody, MA). Macroscopic images of adults, nymphs, and slide mounted larvae were generated with a BK Plus Lab System (Visionary Digital; Los Angeles, CA). The stacking images of the larvae were used to create hand drawn composite illustrations, as most larval ticks were damaged to the point that good SEM or macroscopic images of intact whole specimens could not be obtained.

2.3. Molecular characterization

DNA was extracted from 8 specimens of the new tick species (4 adults, 1 nymph, and 3 larvae) (Table 2). The exoskeletons of all ticks used for extractions were kept as voucher specimens by following previously described methods (Beati and Keirans, 2001; Beati et al., 2012). When possible, four different gene fragments (12S rDNA, 16S rDNA, COI, and ITS2) were amplified and sequenced for each tick (Beati and Keirans, 2001; Beati et al., 2012; Folmer et al., 1994; Mangold et al., 1998). In addition, the same genes were amplified and sequenced from available closely related species of *Ixodes* for comparison purpose. Also, 18S rDNA and 28S rDNA (Klompen et al., 2000) sequences were obtained from samples of the new tick species. Sequences were manually aligned with Mesquite 3.6 (Maddison and Maddison, 2018). Each data set was analyzed by maximum parsimony (MP) and maximum likelihood (ML) with PAUP (Swofford, 2000) and by Bayesian inference analysis (BA) using MrBayes 3.2.4 (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2011). Branch support was assessed by bootstrap analysis (1000 replicates) with PAUP for MP and ML. MP heuristic searches were performed by branch-swapping using the tree bisection-reconnection (TBR) algorithm. Maximum likelihood distances were calculated after the nucleotide substitution model best fitting the data was selected by JModeltest v.2.1.7 (Darriba et al., 2012). The best model was used to calculate pairwise distances by using PAUP. Two runs with four chains each were run simultaneously for BA analyses (1,000, 000 generations). Trees were sampled every 100 iterations. Trees saved before the average standard deviation of split fragments converged to a value < 0.01 were discarded from the final sample. When necessary, the number of generations was increased so that the number of discarded samples would not exceed 25% of the total sampled trees. The 50%

majority-rule consensus tree of the remaining trees was inferred, and posterior probabilities recorded for each branch.

3. Results

3.1. Description

Ixodes* (*Ixodes*) *mojavensis Backus & Beati**, new species** (Figs. 2, 6A and B)

The name *Ixodes mojavensis* has been registered with ZooBank according to the International Commission of Zoological Nomenclature. LSID: urn:lsid:zoobank.org:act:F71B8BD4-CEEA-4F47-AF02-D7B808BA 1BF7.

Note: all examined specimens were partially engorged and, therefore, body length and width will be overestimated in females, nymphs, and larvae.

Female (Figs. 2A–F, 6A and B)

Material analyzed (U.S. National Tick Collection USNMENT accession number; followed by the UC Davis [UCD] laboratory collection number): USNMENT00981933 UCD5706; USNMENT00981927 UCD5588; USNMENT00981850 UCD5571; USNMENT00981851 UCD5555; USNMENT00981854 UCD5591; USNMENT00981855 UCD5704; USNMENT00981788 UCD5840; USNMENT00981789 UCD5843; USNMENT00981929 UCD5611; USNMENT00981852 UCD 5570; USNMENT00981853 UCD5572; USNMENT00981848 UCD5724; USNMENT00981856 UCD5708 = HOLOTYPE; USNMENT00981785 UCD5698 (Table 1)

Body (Figs. 2A and B, 6A and B): oval, reddish-brown; body length from palpal apices to posterior margin 1.63 to 5.48 (3.54 ± 1.03); body width 0.83 to 2.78 (1.80 ± 0.52); idiosoma with homogeneously distributed, dense setation (Figs. 2A, 6B), setae whitish of moderate length 0.05–0.10 (0.07 ± 0.01); marginal groove lining idiosoma and reaching scutum edge at its widest point (Fig. 2A). **Scutum:** Oval, longer (from tip of scapulae to posterior margin) 0.93 to 1.30 (1.13 ± 0.10) than wide 0.75 to 1.04 (0.91 ± 0.08), length: width ratio 0.3, with few sparse whitish setae 0.01–0.11 (0.06 ± 0.03) mostly along anterolateral edges and anterior central field; scapulae pointed; lateral carinae present and slightly elevated; cervical grooves starting behind cornua as deep short triangular pits; extending into shallow but visible, somewhat shagreened cervical fields, first converging and then diverging posteriorly reaching about two thirds of scutal length, not reaching scutal margin; punctuation fine and shallow slightly deeper along anterolateral edge (Figs. 2A, 6B). **Capitulum:** length from tip of cornua to tip of hypostome 0.63 to 0.81 (0.73 ± 0.06); basis capituli (Fig. 2C) length from tip of cornua to cheliceral insertion 0.26 to 0.36 (0.30 ± 0.03); width 0.39 to 0.49 (0.43 ± 0.03), triangular-shaped, chaeliceral insertion marked by transversal line; cornua present, small, length 0.03 to 0.05 (0.04 ± 0.01), triangular shaped with a somewhat truncated tip; porose areas large, width 0.11 to 0.15 (0.12 ± 0.01), length 0.07 to 0.12 (0.10 ± 0.01), subtriangular, placed in distinct depressions, separated by v-shaped shallow groove, distance between areas 0.07 to 0.1 (0.08 ± 0.01) and outlined externally by ridge. Palps elongate; palpal article I small, length 0.03 to 0.08 (0.05 ± 0.01),

width 0.06 to 0.09 (0.08 ± 0.01), dorsal or ventral projections absent; palpal article II length 0.28 to 0.35 (0.32 ± 0.03), width 0.12 to 0.16 (0.14 ± 0.01), widest point close to suture with palpal article III; palpal article III length 0.20 to 0.26 (0.23 ± 0.02), width 0.11 to 0.15 (0.13 ± 0.01). Ventrally, basis capituli (Fig. 2D): auriculae present, length 0.03 to 0.05 (0.04 ± 0.01), pointed, posteriorly directed; transverse suture visible; posterior part of the basis capituli not constricted; posterior margin rounded; hypostome elongated (Fig. 2D), length from insertion to rounded apex 0.36 to 0.53 (0.42 ± 0.06), dentition 4:4 near crown, 3:3 down to hypostomal mid-length; then 2:2. **Venter** (Fig. 2B–D): Anal grove anterior to anus and reaching posterior margin of body at perpendicular angles; anal valves with 3 pairs of setae; genital aperture situated between coxa IV; genital groove reaching posterior margin. Body with homogeneously distributed fine whitish setae 0.02–0.07 (0.04 ± 0.02); absent along genital groove (Figs. 2B, 6A). **Legs:** trochanters with no spurs; syncoxa present on coxa I and II; coxa I with 2 pointed spurs, internal twice as long as external, barely reaching anterior edge of coxa II; coxa II with short, triangular shaped external spur joined to inconspicuous internal spur by syncoxa; coxa III-IV with short, rounded external spur extending medially into sclerotized ridge (Figs. 2B, 6A). Tarsus I length 0.40 to 0.63 (0.51 ± 0.07) (Fig. 2F); metatarsus I length 0.26 to 0.36 (0.31 ± 0.02); tarsus IV length 0.32 to 0.54 (0.44 ± 0.08); metatarsus IV length 0.29 to 0.48 (0.36 ± 0.06). Spiracular plates (Fig. 2E) subcircular, longitudinal length 0. 21 to 0.30 (0.27 ± 0.03), transversal length 0.24 to 0.33 (0.30 ± 0.03).

Male (Figs. 3A–F, 6C and D):

Material analyzed: USNMENT00981855 UCD5705; USN-MENT00981785 UCD5699 (mating). USNMENT00981815 UCD5672 = ALLOTYPE; USNMENT00981925 UCD5569; USNMENT00981934 UCD5715.

Body (Figs. 3A–C, 6C and D): Dark brown, oval, length 1.82 to 2.09 (1.96 ± 0.12) from palpal apices to posterior margin; width 0.96 to 0.1.06 (1.01 ± 0.04). **Conscutum:** marginal groove reaching level of coxa II; setation sparse, fine, of moderate length 0.03–0.09 (0.07 ± 0.02), denser along lateral marginal fold; cervical grooves fine and shallow first slightly converging, then diverging in anterior third of conscutum; 3–4 lateral shallow but visible depressions at mid-length; punctuation large, shallow in median field, deeper along marginal groove; finer anterolaterally, in posterior forth of the conscutum and on marginal fold; posterior marginal fold creased; scapulae with blunt point (Figs. 3A, 6D). **Capitulum**: length from tip of cornua to tip of hypostome 0.46 to 0.55 (0.50 ± 0.06); dorsal basis capituli (Fig. 3D) length from tip of cornua to cheliceral insertion 0.2 to 0.28 (0.23 ± 0.04), roughly triangular shaped, narrowed posteriorly, extending smoothly into hypostome, width 0.21 to 0.32 (0.27 ± 0.05), punctate, with triangular, pointed cornua, cornua length 0.02 to 0.04 (0.03 ± 0.01); edge separating cornua straight. Ventrally (Fig. 3F), basis subtriangular with transversal rounded ridge joining triangular-shaped postero-laterally directed auriculae, auriculae length 0.02–0.05 (0.03 ± 0.02); palps inserted in antero-lateral extension of basis capituli. Hypostome slightly shorter than palps 0.22 to 0.27 (0.25 ± 0.03), notched apically; lateral denticles as posterolaterally directed sharp large triangles (on 1 or sometimes 2 files, and 4 rows), separated by crenulated ridges (7–8 recognizable rows). Palps clublike; palp I with no spurs, length 0.03 to 0.05 (0.04 ± 0.01), width 0.05 to 0.06 (0.004 ± 0.0); palp II

length 0.11 to 0.15 (0.13 ± 0.02), width 0.11 to 0.15 (0.13 ± 0.02); palp III length 0.11 to 0.14 (0.13 ± 0.01), width 0.11 to 0.15 (0.13 ± 0.02). **Venter** (Fig. 3B and C): Anal groove anterior to anus; converging slightly towards posterior margin of body; fine whitish setae 0.03–0.08 (0.06 ± 0.01) densely and uniformly distributed; genital plate notched posteriorly; punctation large and shallow in median and genital plates, finer and deeper elsewhere, in particular around spiracular plates; genital aperture at level of posterior margin of coxa III, anal valves with 3 pairs of setae. Spiracular plates oval (not illustrated), elongated, longitudinal length 0.23 to 0.25 (0.24 ± 0.01), width 0.18 to 0.19 (0.19 ± 0.01, only two measurements). **Legs:** spurs absent from trochanters; coxa I and II with syncoxa and with two spurs; internal and external spurs on coxa I and II short ending in rounded points almost equal in length; external spur on coxa III short, round more conspicuous than internal spur; external spur of coxa IV short and round extending medially into sclerotized ridge (Figs. 3B and C, 6C). Tarsus I (Fig. 2F) length 0.25 to 0.41l (0.37 ± 0.07) (Fig. 3F); metatarsus I length 0.1 to 0.2 (0.15 ± 0.04); tarsus IV length 0.25 to 0.29 (0.27 ± 0.03; only 2 measurements); metatarsus IV length 0.16 to 0.23 (0.19 ± 0.05; only 2 measurements).

Nymph **(**Figs. 4A–G, 6E and F):

Material analyzed: USNMENT00981926 UCD5581, USN-MENT00981826 UCD5596; USNMENT00981928 UCD5597; USN-MENT00981825 UCD5584; USNMENT00981847 UCD5696; USNMENT00981817 UCD5678; USNMENT00981827 UCD5626; USN-MENT00981818 UCD5694; USNMENT00981819 UCD5686; USNMENT00981787 UCD5888.

Body (Figs. 4A and B, E, 6E and F): Outline overall oval, length from palpal apices to posterior margin 1.26 to 2.21 (1.81 ± 0.34); width 0.83 to 1.44 (1.15 ± 0.22); widest at level of coxa IV; Soma homogeneously setate; setae 0.04 to 0.06 (0.05 ± 0.01). **Scutum** (Fig. 4A): Oval-shaped, length 0.54 to 0.85 (0.63 ± 0.10), width 0.48 to 0.8 (0.57 ± 0.10) with scattered fine and shallow punctation and scattered short fine setae 0.01–0.02 (0.02 ± 0.01); lateral carinae moderately elevated (variable between specimens); cervical groove well defined, first converging and then diverging, reaching posterolateral margins of scutum, cervical field shallow. **Capitulum** (Fig. 4C and D): Length from tip of cornua to tip of hypostome 0.63 to 0.81 (0.73 ± 0.06); basis capituli length from from tip of cornua to insertion of chelicerae 0.13 to 0.17 (0.15 ± 0.02), width 0.21 to 0.35 (0.25 ± 0.04), dorsally subtriangular extending smoothly into the chelicerae with triangular, pointed, posteriorly directed cornua length 0.02 to 0.04 (0.03 ± 0.01); line joining cornua straight; chaelicheral insertion marked by transversal line; palpi elongate; suture between articles II and III distinct; palpal article one with ventral roundish plate, length 0.03 to 0.05 (0.04 ± 0.01), width 0.04 to 0.06 (0.05 ± 0.01); palp II length 0.15 to 0.23 (0.17 ± 0.03); width 0.06 to 0.11 (0.08 ± 0.02); palp III 0.12 to 0.20 (0.14 ± 0.03); width 0.07 to 0.11 (0.08 ± 0.01). Ventrally, basis with well-defined posteriorly directed triangular auriculae (length 0.03 to 0.05; 0.04 ± 0.01), constricted posterior to auriculae with no visible suture line, posterior margin rounded; hypostome lanceolate, apically rounded, length 0.22 to 0.37 (0.28 ± 0.05); dental formula 3:3 over the 6–7 apical rows, then 2:2 (3–4 additional rows) to the insertion of the hypostome, lateral files with much larger pointed triangular denticles than median ones. **Venter** (Figs. 4B and E, 6F): Body setate, setae scattered uniformly but absent from

discernible future genital groove, length 0.04–0.06 (0.05 ± 0.01), longer between coxa I; anal groove curving around anus and joining posterior margin at a perpendicular angle; spiracular plates (Fig. 4F) subcircular length 0.11 to 0.13 (0.12 ± 0.01), width 0.12 to 0.16 (0.14 ± 0.01). **Legs**. Trochanters lacking spurs. Coxa I-II with 2 spurs, spurs in coxa I of similar length, rounded at apex; internal spurs shorter than external in coxa II-III decreasing in size; external spurs triangular and rounded; coxa IV with single short triangular, rounded, external spur, shorter than external spur in coxa III. Tarsus I (Fig. 4G) length 0.26 to 0.42 (0.32 ± 0.05); metatarsus I length 0.09 to 0.17 (0.12 ± 0.03; 3 specimens), tarsus IV length 0.23 to 0.26 (0.24 ± 0.02); metatarsus IV length 0.14 to 0.15 (0.15 ± 0.01; 3 specimens).

Larvae (Fig. 5A–F)

Material examined: USNMENT00981827 UCD5741; USN-MENT00981829 UCD5633; USNMENT00981830 UCD5740; USN-MENT00981831 UCD5745; USNMENT00981832 UCD5634; USNMENT00981833 UCD5632; USNMENT00981834 UCD5647; USN-MENT00981845 UCD5873; USNMENT00981846 UCD5874, UCD5875, UCD5876, UCD5877, and UCD5878. Terminology for larval chaetotaxy follows Clifford and Anastos (1960), and Clifford et al., (1961, 1973).

Body: (Fig. 5A): subcircular, length from tip of scapulae to posterior edge from 750.01 to 1377.78 (961.61 ± 190.25), widest near midlength 506.67 to 700.02 (626.93 ± 96.04). Sensilla sagittiformia (large wax glands) absent. Dorsal setae 10–12 pairs; 4 central dorsal setae, CD1 from 0.026 to 0.032 (0.029 ± 0.002), CD2 0.024 to 0.036 (0.030 ± 0.005); 7–8 marginal dorsal pairs, MD1 0.034 to 0.045 (0.040 ± 0.04), MD7 or MD8 0.032 to 0.037 (0.035 ± 0.002); 1 pair of supplementary setae 0.021 to 0.027 (0.025 ± 0.003). **Scutum** (Fig: 5A): length 433.33 to 457.78 (450.41 ± 8.64), breadth 487.67 to 514.29 (503.13 ± 8.57), outline broadly oval with posterolateral margins slightly concave; cervical grooves distinct but shallow, first converging then diverging posteriorly, almost reaching scutal margins (not visible in mounted specimens); 5 pairs of setae, SC1 0.013 to 0.020 (0.016 ±0.003), SC2 0.018 to 0.028 (0.022 ± 0.005), SC3 0.011 to 0.024 (0.018 ± 0.05), SC4 0.18 to 0.027 (0.022 ± 0.004), SC5 0.014 to 0.027 (0.021 ± 0.006). **Capitulum** (Fig. 5B, D): dorsal length from palpal apices to tip of cornua from 229.63 to 249.37 (237.84 ± 7.37), length from cheliceral insertion to tip of cornua from 82.22 to 89.78 (86.01 ± 2.45), width of basis capituli from 127.14 to 136.67 (133.07 ± 2.85). Basis capituli with straight posterior margin; lateral margins notched under insertion of palpal article I, cornua pointed and posterolaterally directed as extensions of slightly raised ridges, width at tips of cornua not exceeding width of tips of scapulae. Basis capituli ventrally constricted posterior to blunt posteriorly directed auriculae, posterior margin straight. Post-hypostomal setae 2 pairs, PH1 0.006 to 0.016 (0.010 ± 0.005), PH2 0.006 to 0.013 (0.009 ± 0.002). Palps elongated 154.29 to 171.46 (162.18 ± 4.88) with 4 sensilla, Palp I 21.43 to 27.78 (25.15 ±2.05) long by 25.71 to 30.00 (28.13 ±1.48) broad; palp II (85.71 to 98.57 (91.90 ± 4.10) long by 35.36 to 41.43 (38.43 ±1.80) broad, palp III 40.00 to 50.34 (45.12 ± 3.13) long by 37.33 to 42.86 (40.33 ±1.55) broad; setae absent from article I, 3 ventral and 8 dorsal setae on segment II and II combined, suture between segments II and III barely visible ventrally, absent dorsally; article IV with approximately 9 setae. Hypostome length 147.41 to 159.59 (151.82 ± 8.33), arising from anterior median extension of basis capituli, toothed portion covering approx. ¾

of hypostomal length; dental formula below crown 3:3 in first 2–3 rows, then 2:2; file 1 with ca. 9–10 denticles, file 2 with ca. 8–9 denticles, file 3 with ca. 2–3 denticles. **Venter** (Fig. 5D): Ventral setae: 13 pairs plus 1 pair on anal valves; 3 pairs of sternals, ST1 0.022 to 0.038 (0.032 ± 0.006), ST2 0.020 to 0.035 (0.030 ± 0.005), ST 3 0.013 to 0.035 (0.024 ± 0.007); 2 pairs of preanals PA1 0.016 to 0.020 (0.019 ± 0.002), PA2 0.016 to 0.023 (0020 ± 0.004); 4 pairs of premarginals 0.015 to 0.027 (0.019 ± 0.003), 4 pairs of marginal ventrals MV1 0.020 to 0.025 (0.024 ± 0.002) and MV4 0.023 to 0.027 (0.025 ± 0.002). **Legs** (Fig. 5C, E, F): Coxa I with broad triangular internal spur rounded at tip, narrower pointed, triangular, external spur; coxa II with internal rounded ridge-like thickening and narrow triangular rounded external spur; coxa III with no internal and inconspicuous external squarish ridge somewhat representing external spur; coxal setae 3 on coxa I, 2 on coxa II, 2–3 on coxa III. Tarsus I (Fig. 5E) length 135.71 to 178.57 (153.87 ± 10.91), Haller's organ as in Fig. 5F with 5 setae in anterior pit, 4 pre-halleral and 4 posthalleral setae; tarsus IV from 136.78 to 187.51 (160.17 ± 17.39).

Type Data: Holotype female from *M. c. scirpensis*, Amargosa Valley, CA, United States of America (35.8610 °N, −116.2421 °W), collected on May 12, 2016 by Austin Roy. Deposited in the U.S. National Tick Collection (USNMENT00981856). Allotype male from *M. c. scirpensis*, Amargosa Valley, CA, United States of America (35.8742 °N, −116.2337 °W) on February 20, 2017 by Austin Roy. Deposited in the U.S. National Tick Collection (USNMENT00981815). Paratype adults, nymphs, and larvae as listed in Table 1.

3.2. Species relationships

As is demonstrated by the molecular analyses (see below), *I. mojavensis* is closely related to taxa that feed on both rodents and birds. Because host associations have yet to be fully explored for *I. mojavensis*, the possibility of it being carried by birds along the flyway from Central America to the Great Basin cannot be dismissed. Therefore, at least for adults, species relationships are described for North and Central American species of the subgenus *Ixodes* (Augustson, 1939; Bermudez at al., 2018; Cooley, 1944, 1945; Cooley and Kohls, 1938, 1942, 1943, 1945; Guzmán-Cornejo and Robbins, 2010; Keirans and Clifford, 1978; Keirans and Eckerlin, 2005; Kohls, 1953, 1956; Kohls and Clifford, 1962, 1964, 1966). For the immature stages, comparisons are limited to species of the U.S (Clifford et al., 1961; Durden and Keirans, 1996a; Keirans et al., 1996; Kleinjan and Lane, 2008; Kohls and Clifford, 1964; Oliver et al., 1987; Smith and Gouck, 1947).

Females: *I. mojavensis* females differ from *I. minor* (Neumann, 1902; Smith and Gouck, 1947; Keirans and Clifford, 1978) by auriculae not curving medially, absence of spines on palpal article I; porose area well defined, surrounded by a visible ridge and delimited medially by a fine longitudinal groove. Also, the number of denticle rows are 3 (inner file), 6 (median file), 10–11 (2 external files) rather than 5, 7, 10 and the scutum is almost lacking punctuation, while the scutum of *I. minor* has deep and large punctations in its posterior half. *I. mojavensis* and *Ixodes muris* Bishopp and Smith, 1937, both have posteriorly projecting auriculae, but these are proportionally shorter in *I. mojavensis*; porose areas are not as shallow as in *I. muris*; hypostome with 4 and not 3 files of denticles and with less rows (10 vs. 15), hypostome rounded apically and not pointed (Bishopp

and Smith, 1937; Cooley and Kohls, 1945; Keirans and Clifford, 1978). When compared with *Ixodes dentatus* Marx, 1899, *I. mojavensis* has fewer hypostomal denticle files (4 vs. 5), inconspicuous scutal punctation, and palpal article I without ventral spur (Cooley and Kohls, 1945; Keirans and Clifford, 1978; Neumann, 1899, Smith, 1940). In addition, more succinctly, *I. mojavensis* can be differentiated from the other North and Central American members of the subgenus *Ixodes* Latreille, 1795 (Clifford et al., 1973) by the following characters: very long and wide external spur on coxa I (*Ixodes loricatus* Neumann, 1899 and *Ixodes luciae* Sénevet, 1940*);* auriculae absent, ridge-like, or rounded (*Ixodes affinis* Neumann, 1899, *Ixodes guatemalensis*Kohls, 1956, *Ixodes jellisoni* Cooley and Kohls, 1938, *I. loricatus, I. luciae, Ixodes pacificus* Cooley and Kohls, 1943, *Ixodes rubidus* Neumann, 1901, *Ixodes scapularis* Say, 1821, *Ixodes tamaulipas* Kohls and Clifford, 1966, *Ixodes tancitarius* Cooley and Kohls, 1942, *Ixodes tapirus* Kohls, 1956, and *Ixodes tecpanensis* Kohls, 1956); auriculae either like laterally extending hooks (*Ixodes dentatus* Marx, 1899), or curved (*Ixodes bequaerti* Cooley and Kohls, 1945, *Ixodes boliviensis* Neuamnn, 1904, *Ixodes cuernavacensis* Kohls and Clifford, 1966, *Ixodes eadsi* Kohls and Clifford, 1964, *Ixodes mexicanus* Cooley and Kohls, 1942, *Ixodes pomerantzi* Kohls, 1956, *Ixodes sinaloa* Kohls and Clifford, 1966, *Ixodes spinipalpis* Hadwen and Nuttall, 1916, *Ixodes tovari* Cooley, 1945, *Ixodes venezuelensis* Kohls, 1953). The absence of spur or pointed processes on palpal article I will differentiate *I. mojavensis* from *Ixodes bocatorensis* Apanaskevitch and Bermudez, 2017, *I. dentatus, I. jellisoni, I. pacificus, I. pomerantzi, Ixodes peromysci* Augustson, 1939, *I. spinipalpis, Ixodes tiptoni* Kohls and Clifford, 1962, and *I. tovari*.

Males*: I. mojavensis*, unlike *I. minor* (Keirans and Clifford, 1978; Neumann, 1902; Smith and Gouck, 1947), has a straight posterior margin of the basis capituli, blunter auriculae without a sharp point, missing ventral spur on palp I. The pseudoscutum is visible, but not concave, nor heavily punctate; dorsal setation is scant and scattered, punctuation in posterior half of scutum is of moderate size and shallow; the pregenital plate is notched posteriorly, and the median plate is flat posteriorly, not pointed; the punctuation on the median plate is denser (over 70–90 vs. 50–60), shallower and finer; ventral setation is finer. When compared with *I. muris* (Bishopp and Smith, 1937; Keirans and Clifford, 1978), the scutum of *I. mojavensis* is less punctate in the anterior half (over the conscutum which is visible in both species, convex in *I. muris* but not in *I. mojavensis*), the auriculae are more visible and well-defined and cornua are present, the ventral median plate is flat posteriorly rather than pointed, and the spiracular plates are distinctly elongated (subcircular in *I. muris*). The males of *I. dentatus* (Cooley and Kohls, 1945; Keirans and Clifford, 1978; Smith, 1940) can be differentiated from *I. mojavensis* by the larger scutal punctations, denser and deeper and by the presence of a very long internal spur on coxa I reaching over mid length of coxa II, by the absence of an apical notch on the hypostome, by more rows of hypostomal denticles (about 11 vs. 8) and the proximal denticle rows not terminating with an external large posteriorly directed tooth as in *I. mojavensis*. Distinct pointed cornua distinguish *I. mojavensis* from *I. affinis, I. bocatorensis, I. boliviensis, I. eadsi, I. guatemalensis, I. pacificus, I. scapularis*, and *I. tapirus*. As for females, the males of *I. loricatus* and *I. luciae* have long external spurs on coxa I, while *I. mojavensis* has two subequal short spurs. The hypostome of *I. dentatus* is rounded with diagonally arranged crenulations each with 4 denticles and not notched with larger external denticles like *I. mojavensis*. The hypostome

of *I. pomerantzi* is also not notched. Scutal punctations are shallower than in *I. spinipalpis, I. eadsi*, and *I. affinis*. The male of *I. jellisoni*, and *I. spinipalpis* are characterized by a spur on palpal article I which is absent in *I. mojavensis. I. peromysci* can be differentiated from *I. mojavensis* by finer and homogeneous punctation and denser setation on conscutum. *I. tovari* has a very elongate and lanceolate hypostome, very unlike the short, notched hypostome of *I. mojavensis*.

Nymphs: The nymph of *I. mojavensis* differs from *I. minor* by the shape of the basis capituli which does not extend posterolaterally, by having shorter, less massive auriculae, and less conspicuous cervical grooves; also, unlike in *I. minor*, the external files of hypostomal denticles in *I. mojavensis* are much larger than the internal ones. The nymph of *I. dentatus* differs from *I. mojavensis* by an almost round scutum with deep punctations in its posterior portion, by a posterolaterally extending dorsal basis capituli, and hypostomal dentition 4:4. The nymph of *I. muris* is characterized by wider auriculae, wider cornua, longer scutal setae, by the absence of internal spurs on coxa II and III, and by a pointed hypostome. The presence of well-defined, rather than round and, or inconspicuous auriculae differentiates *I. mojavensis* from *I. affinis, I. jellisoni, I. peromysci, I. pacificus*, and *I. spinipalpis*, and the absence of curved auriculae from *I. eadsi*. Unlike in *I. mojavensis* which has fairly straight external edges, the basis capituli of *I. tovari* extends poster-olaterally; *I. tovari* also has longer, pointed external spurs on coxa I-IV. *I. scapularis* differs from *I. mojavensis* by a sinuous, rather than straight posterior margin of the basis capituli, and by the absence of internal spurs on coxa II-III.

Larvae. *I. dentatus, I. jellisoni, I. muris, I. scapularis, I. pacificus*, and *I. tovari* have more than 2 pairs of central dorsal setae. *I. peromysci* lacks supplementary setae. Unlike *I. mojavensis, I. affinis* has a well-defined, pointed external spur on coxa III. *I. mojavensis* and *I. minor* larvae are difficult to differentiate; nevertheless, the idiosomal setae in *I. minor* are markedly longer (Md1 mean 0.073 vs. 0.040; Md7 average 0.057 vs. 0.035) and the hypostomal files carry more denticles than *I. mojavensis. I. dentatus* has weak inconspicuous auriculae, while auriculae in *I. mojavensis* are well-defined. The basis *capituli* of *I. spinipalpis* is distinctly broader than long behind the hypostome and widening into posterolaterally extending sharp cornua and the auriculae are notched. *Ixodes eadsi* has auriculae that are triangular, pointed and better defined than *I. mojavensis*.

Distribution and hosts: *I. mojavensis* is reported so far only from the Amargosa and the Owens Valley of California where it was collected mainly from *M. c. scirpensis*. Less often it has been collected from *M. c. vallicola, M. musculus*, and *R. megalotis*.

3.3. Molecular analyses

Sequences generated for this study were submitted to GenBank (Table 2). Accession numbers are in parentheses: *12S rDNA* (MT840315–MT840331 and MT898578–MT898587); *16S rDNA* (MT840295–MT840309); *COI* (MT906024–MT906040); *ITS2* (MT880311–MT880332); *28S rDNA* (MT897884–MT897893); *18S rDNA* (MT860474–MT860481).

3.3.1. Mitochondrial gene sequences—By using BLAST (Altschul et al., 1990) in GenBank, 12S rDNA gene sequences of *I. mojavensis* shared 98.76% nucleotide similarity with an unidentified tick collected on migratory birds in Texas (Cohen et al., 2015) and 95.60% with a sequence from *I. minor* from Costa Rica (KF702338). The 16S rDNA sequences of *I. mojavensis* were 99.50% identical to a sequence of *I. minor* from the eastern U.S. (AF549841) and 97.76% to those of *I. minor* from Costa Rica (KF702348- KF702350). The COI sequences of *I. mojavensis* were 95.03% identical to an *I. dentatus* from Canada (KX360409).

Phylogenetic reconstructions showed that the species belonging to subgenus *Ixodes* were always found within a strongly supported group (Clade A in Figs. 7A and B, 8A). Within this clade, however, the basal organization of lineages was not consistently the same and was characterized by an overall weak support. When several sequences of a single species were available, they consistently clustered together. Nevertheless, the phylogenetic analyses revealed that *I. mojavensis* sequences were always embedded within an *I. minor* (U.S.) - *I. mojavensis* mono-phyletic clade (Figs. 7A and B, 8A, Clade B - with posterior probability support of 0.89 for 16S rDNA and 1.00 for 12S rDNA and COI). While the *I. mojavensis* sequences (when different from each other) always clustered in supported lineages, the remaining *I. minor* branches did not segregate monophyletically. Basal to this clade were lineages of *I. minor* from Central America which did not group with the *I. minor* of the U.S. When the tree species (*I. mojavensis, I. minor*, and *I. dentatus*) were included in the analyses, they always clustered in a well-supported group with 1.00, 0.97, and 1.00 posterior probability support for 12S rDNA, 16S rDNA, and COI respectively. After applying the best-fitting models identified with JModelTest (Darriba et al., 2012), distances within *I. mojavensis* (0–0.29%, 0%, 0–0.33%, for 12S rDNA, 16S rDNA, and COI, respectively) were always slightly lower that distances between *I. mojavensis* and *I. minor* (U.S.) (0.59–1.17%, 0.28–0.56%, and 1.67–2.00%, for 12S rDNA, 16S rDNA, and COI, respectively). When sequences were available, distances between *I. minor* (U.S.) and *I. minor* (Central America) were higher (3.53–3.82% and 1.46–2.43% for 12S rDNA and 16S rDNA, respectively) but comparable to distances between clade B and *I. dentatus* (2.66 −3.54% for 12S rDNA). Distances between the three taxa and the remaining recognized species were higher than 8.33%, 4.10%, and 9.52% for 12S rDNA, 16S rDNA, and COI, respectively.

3.3.2. Nuclear gene sequences—The number of species used in the ITS2 analyses had to be reduced to members of the subgenus *Ixodes* (mitochondrial Clade A), because sequences from more distantly related taxa could not be aligned with confidence. *I. mojavensis, I. minor* and *I. dentatus* clustered in a strongly supported Clade B (1.00 posterior probability) (Fig. 8B). Within this group, *I. minor* and *I. mojavensis* were found in a well-supported lineage (0.99 posterior probability). In this case, however, the two species segregated in deeply split mutually exclusive monophyletic clades. Within the available sequences of subgenus *Ixodes*, the intraspecific distances varied from 0 to 0.16% in *I. mojavensis*, from 0.16 to 0.80% within *I. minor* (U.S. only), from 0.32 to 2.42% within *I. dentatus*, and 0.85 to 1.72% in *I. scapularis*. The closest relatives, *I. minor* and *I. dentatus*, differed from *I. mojavensis* by 5.74–6.39% and 6.58–7.61%, respectively. These values were

similar to distances between *I. dentatus* and *I. minor* (5.90–6.93%). Interspecific distances between more distantly related taxa varied from 8.60 to 12.92%. The conserved nuclear gene sequences (28S rDNA and 18S rDNA) were phylogenetically uninformative within subgenus *Ixodes* but were, nonetheless, deposited in GenBank.

4. Discussion

In 2014, studies on the endangered Amargosa vole and its ectoparasites (Foley et al., 2014; Ott-Conn et al., 2014) revealed the occurrence of what was then considered to be *I. minor* in the western U.S. The identification was performed by comparing 287 bp fragment of 16S rDNA gene sequence of the Amargosa ticks with GenBank accessions through BLAST (Foley et al., 2014). The occurrence of *I. minor* in an area of such extreme aridity was, however, puzzling. *I. minor* is known to prefer rather humid climates that characterizes the eastern U.S. and Central America. It was hypothesized that the tick might have reached the Mojave Desert from either the eastern U.S. by anthropogenic dispersal of the common house mouse or from Central America on migratory birds. *Ixodes minor* has frequently been reported on birds both in the eastern U.S. and Central America (Cohen et al., 2015 [as genotype MI13–006]); Keirans and Clifford, 1978; Ogrzewalska et al., 2015) and the Amargosa Valley is a known important avian migratory flyway leading to the Great Basin. While certainly similar to *I. minor*, particularly in its immature stages, the tick had sufficient phenotypic peculiarities (Poulsen et al., 2015) to be tentatively named the "Mojave morphotype" of *I. minor*. Nevertheless, this finding warranted a more thorough morphological examination and molecular analysis.

Based on morphology, *I. mojavensis* is a new *Ixodes* tick species, with an important number of fixed phenotypic characters differentiating it from its closest morphological relatives, *I. minor, I. dentatus* and *I. muris*. Its distribution in the United States appears to be limited, so far, to the Amargosa and Owens Valleys where it parasitizes small rodents. This new addition brings the total number of *Ixodes* species of the U.S. to 34 and of California to 19 (Durden and Keirans, 1996a; Keirans and Clifford, 1978; Kleinjan and Lane, 2008). These findings identify California, with its contrasting landscape and distinctive ecosystems, as a hot-spot for tick biodiversity.

Molecular analyses, based on the ITS2 nuclear gene, demonstrate that *I. mojavensis* is a strongly supported monophyletic lineage, close to its sister taxon, *I. minor*, which also clusters in a monophyletic clade. Their closest relative is *I. dentatus*. Other species belonging to subgenus *Ixodes* are more distantly related. Intraspecific distance values are always significantly smaller (0–2.42%) than interspecific distances (5.74–12.92%). Molecular analyses, based on mitochondrial gene sequences, consistently cluster *I. mojavensis, I. minor*, and *I. dentatus* in a strongly supported clade (with support slightly weaker in the 16S rDNA reconstruction, Fig. 7B). *Ixodes mojavensis* and *I. minor* never group into mutually exclusive mitochondrial monophyletic lineages. Discrepancies between nuclear and mitochondrial reconstructions have been reported in other studies and were usually ascribed to past hybridization events (Araya-Anchetta et al., 2013; Kovalev et al., 2015, 2016; Patterson et al., 2017; Rees et al., 2003). Experimental hybridization between different tick species have been reported as far back as in 1972 (Oliver et al., 1972). In

our case, this would require *I. minor* and *I. mojavensis* to have experienced secondary contact after they speciated. While it is possible to imagine *I. minor* from Central America sporadically reaching the Amargosa Valley while carried on birds, *I. minor* from the eastern U.S. would be unlikely to have easily reached western longitudes, because avian flyways more commonly follow a north-south direction. Migratory birds have been shown to enter the U.S. while carrying *I. minor* (called MI13–006 in GenBank, Figs. 7A and 8B) (Cohen et al., 2015). There is no doubt, however, that *I. minor* would hardly survive or establish itself in the Mojave Desert. The hypothesis of hybridization occurring after speciation is, therefore, not very probable, although based on our data it cannot be totally dismissed. Our molecular results, however, confirm that *I. minor* and *I. mojavensis* share a common ancestor in all our reconstructions. A more compelling hypothesis would involve a wide-spread species that underwent speciation while its mitochondrial genome experienced incomplete lineage sorting (persistence of a common ancestral set of genes in otherwise diverging lineages). *Ixodes mojavensis* could have speciated when climatic conditions changed in the region East of the Sierra Nevada in the early Holocene (approx. after 12, 000 ya). After the Last Glacial Maximum (approx. 20,000–25,000 ya), the retreat of glaciers reduced the water runoff into the Owens, Mojave, and Amargosa River systems of eastern California and the concomitant increase in temperature contributed to the progressive aridification of an area which had previously been characterized by a vast network of lakes and rivers (Orme and Orme, 2008). If adapted to rather humid conditions, the ancestral lineage of *I. mojavensis*, like its main host (Klinger et al., 2015), might have been trapped along the shores of the remaining and very reduced river drainages. Human activities have further contributed to the desertification of this area, thus endangering the survival not only of the Amargosa vole, but also of its parasites. Nevertheless, on account of *I. mojavensis* being able to feed on more common hosts, such as *M. musculus*, it is unlikely that it would qualify as an endangered tick species (Durden and Keirans, 1996b; Mihalca et al., 2011).

The 12S and 16S rDNA sequences of *I. minor* from Central America (Fig. 7A and B) did not cluster with the eastern *I. minor*, while sequence MI13–006 did. MI13–006 was imported to Texas by a migratory bird from Central America (Cohen et al., 2015). Our work clearly proves that analyses of mitochondrial genes alone can be misleading, nevertheless, this indicates that the taxonomic status of *I. minor* needs to be reassessed by comparing all the stages of the Central American (type locality in Guatemala, in Neumann [1902]) and the eastern North American populations, formerly called *I. bishoppi* (Smith and Gouck, 1947). The synonymy of *I. bishoppi* with *I. minor* was based on comparisons of little and/or damaged material and the reasons for dismissing *I. bishoppi* as a valid species were never clearly stated (Neumann, 1902; Keirans and Clifford, 1978; Kohls, 1953; Smith and Gouck, 1947). For instance, males of *I. bishoppi* have auriculae while males of *I. minor* do not. Also, palp articles II and III are equal in length in *I. bishoppi*, while they are of different length in *I. minor*. Recent studies showed that ticks that were thought to have a wide distribution area from South America, through Central and North America are in fact different species. The taxonomic status of some of them, particularly of the most recently diverging lineages, is still under scrutiny (Lado et al., 2016, 2018; Saracho-Bottero et al., 2019, 2021).

As for disease relationships, *I. mojavensis* has been found infected with a spirochetal strain close to *Borrelia carolinensis* (Foley et al., 2014). The spirochete is not known to be pathogenic to humans or animals but interestingly it has also been detected in *I. minor* from South Carolina (Rudenko et al., 2011a). The evolutionary and geographic relationship between this species and others of the *Borrelia burgdorferi* sensu lato group are not well enough understood (Rudenko et al., 2011b) at this time to hypothesize that the common ancestor of the two tick species was carrying this *Borrelia*. Based on what is known at this time about the geographic distribution and host associations of *I. mojavensis*, it is unlikely to play a significant role as a vector of medical or veterinary importance. However, more work is needed to determine its role in enzootic pathogen maintenance. The importance of using multiple identification tools is highlighted here, and that multiple modalities — morphologic, genetic and ecological — should be utilized when determining species identity.

Acknowledgments

We are grateful for the multitude of members of the Foley Lab and Amargosa Vole Team without whom this work would not have been possible. This work was partially funded through the Pacific Southwest Regional Center of Excellence for Vector-Borne Diseases, funded by the U.S. Centers for Disease Control and Prevention (Cooperative Agreement 1U01CK000516). The National Ecological Observatory Network is a program sponsored by the National Science Foundation and operated under cooperative agreement by Battelle. This material uses specimens and/or samples collected as part of the NEON Program. Some outgroup samples were also obtained through the efforts of the Lyme Disease Consortium, funded by NSF grant EF0914390 to L.B. We also wish to thank the anonymous reviewer whose contribution has enhanced this manuscript.

References

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ, 1990. Basic local alignment search tool. J. Mol. Biol 215, 403–410. [PubMed: 2231712]

Araya-Anchetta A, Scoles GA, Giles J, Busch JD, Wagner DM, 2013. Hybridization in natural sympatric populations of *Dermacentor* ticks in northwestern North America. Ecol. Evol 3, 714–724. [PubMed: 23531531]

Augustson GF, 1939. A new Ixodes (Acarina: Ixodidae). Bull. South Calif. Acad. Sci 38, 141–147.

Beati L, Keirans JE, 2001. Analysis of the systematic relationships among ticks of the genera Rhipicephalus and Boophilus (Acari: Ixodidae) based on mitochondrial 12S ribosomal DNA gene sequences and morphological characters. J. Parasitol 87, 32–48. [PubMed: 11227901]

Beati L, Patel J, Lucas-Williams H, Adakal H, Kanduma EG, Tembo-Mwase E, Krecek R, Mertins JW, Alfred JT, Kelly S, Kelly P, 2012. Phylogeography and demographic history of Amblyomma variegatum (Fabricius) (Acari: Ixodidae), the tropical bont tick. Vector Borne Zoonotic Dis. 12, 514–525. [PubMed: 22448720]

Bermúdez S, Apanaskevich D, Domínguez L, 2018. Garrapatas Ixodidae de Panamá 129. ISBN 978-9962-699-25-5.

Bishopp FC, Smith CN, 1937. A new species of *Ixodes* from Massachussetts. Proc. Entomol. Soc. Wash 39, 133–138.

Clifford CM, Anastos G, 1960. The use of chaetotaxy in the identification of larval ticks (Acarina: Ixodidae). J. Parasitol 46, 567–578. [PubMed: 13694092]

Clifford CM, Anastos G, Elbl A, 1961. The larval ixodid ticks of the eastern United States. Misc. Publ. Entomol. Soc. Am 2, 213–237.

Clifford CM, Sonenshine DE, Keirans JE, Kohls GM, 1973. Systematics of the subfamily Ixodinae (Acarina: Ixodidae). 1. The subgenera of Ixodes. Ann. Entomol. Soc. Am 66, 489–500.

Cohen EB, Auckland LD, Marra PP, Hamer SA, 2015. Avian migrants facilitate invasions of Neotropical ticks and tick-borne pathogens into the United States. Appl. Environ. Microbiol 81, 8366–8378. [PubMed: 26431964]

Cooley RA, 1944. Ixodes neotomae, a new species from California (Acarina: Ixodidae). Pan-Pac. Entomol 20, 7–12.

Cooley RA, 1945. Ixodes tovari, a new species from Mexico (Ixodidae). Pan-Pac. Entomol 21, 144–148.

Cooley RA, Kohls GM, 1938. Two new species of ticks (Ixodes) from California (Acarina: Ixodidae). Public Health Rep. Wash 53, 1616–1621.

Cooley RA, Kohls GM, 1942. Ixodes mexicanus n. sp. e Ixodes tancitarius n. sp. dos nuevas garrapatas mexicanas (Acarina: Ixodidae). Rev. Soc. Mex. Hist. Nat 3, 149–154.

Cooley RA, Kohls GM, 1943. *Ixodes californicus* Banks, 1904, *Ixodes pacificus* n. sp., and *Ixodes conepati* n.sp. Pan-Pac. Entomol 19, 139–147.

Cooley RA, Kohls GM, 1945. The genus *Ixodes* in North America. Natl. Inst. Health Bull 184, 246.

Darriba D, Taboada GL, Doallo R, Posada D, 2012. jModelTest 2: more models, new heuristics and parallel computing. Nat. Methods 9, 772.

Durden LA, Keirans JE, 1996a. Nymphs of the Genus Ixodes of the United States: Taxonomy, Identification Key, Distribution, Hosts, and Medical/Veterinary Importance. Thomas Say Publications in Entomology-Monographs; Entomological Society of America, Lanham, MD, p. 95.

Durden LA, Keirans JE, 1996b. Host-parasite co-extinction and the plight of tick conservation. Am. Entomol 42, 87–91.

Foley J, Ott-Conn C, Worth J, Poulsen A, Clifford D, 2014. An *Ixodes minor* and *Borrelia carolinensis* enzootic cycle involving a critically endangered Mojave Desert rodent. Ecol. Evol 4, 576–581. [PubMed: 25035799]

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R, 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotechnol 3, 294–299. [PubMed: 7881515]

Guzmán-Cornejo C, Robbins RG, 2010. The genus Ixodes (Acari: Ixodidae) in Mexico: adult identification keys, diagnoses, hosts, and distribution. Rev. Mex. Biodiv 81, 289–298.

Huelsenbeck JP, Ronquist F, 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755. [PubMed: 11524383]

Keirans JE, Brown RN, Lane RS, 1996. Ixodes (Ixodes) jellisoni and I. (I.) neotomae (Acari: Ixodidae): descriptions of the immature stages from California. J. Med. Entomol 33, 319–327. [PubMed: 8667376]

Keirans JE, Clifford CM, 1978. The genus *Ixodes* in the United States: a scanning electron microscope study and key to the adults. J. Med. Entomol Suppl. 2, 149.

Keirans JE, Eckerlin RP, 2005. Description of the male and redescription of the female of Ixodes (Ixodes) guatemalensis and description of the male, nymph and larva of Ixodes (Afrixodes) moreli and redescription of the female (Acari: Ixodida: Ixodidae). Int. J. Acarol 31, 259–268.

Kleinjan JE, Lane RS, 2008. Larval key to the genera of Ixodidae (Acari) and species of Ixodes (Latreille) ticks established in California. Pan-Pac. Entomol 84, 121–142. [PubMed: 20027236]

Klinger R, Cleaver M, Anderson S, Maier P, Clark J, 2015. Implications of scale-independent habitat specialization on persistence of a rare small mammal. Glob. Ecol. Conserv 3, 100–114.

Klompen JSH, Black WC, Keirans JE, Norris DE, 2000. Systematics and biogeography of hard ticks, a total evidence approach. Cladistics 16, 79–102. [PubMed: 34902921]

Kohls GM, 1953. Ixodes venezuelensis, a new species of tick from Venezuela, with notes on Ixodes minor Neumann, 1902 (Acarina: Ixodidae). J. Parasitol 39, 1–4. [PubMed: 13035576]

Kohls GM, 1956. Eight new species of Ixodes from Central and South America (Acarina: Ixodidae). J. Parasitol 42, 636–649. [PubMed: 13398869]

Kohls GM, Clifford CM, 1962. Ixodes tiptoni, a new species of tick from Panama (Acarina-Ixodidae). J. Parasitol 48, 182–184. [PubMed: 14457835]

Kohls GM, Clifford CM, 1964. Ixodes eadsi, a new species of tick from rodents in southern Texas (Acarina: Ixodidae). J. Parasitol 50, 466–470. [PubMed: 14169545]

Kohls GM, Clifford CM, 1966. Three new species of Ixodes from Mexico and description of the male of I. auritulus auritulus Neumann, I. conepati Cooley & Kohls, and I. lasallei Mendez & Ortiz (Acarina: Ixodidae). J. Parasitol 52, 810–820. [PubMed: 5969128]

Kovalev SY, Mikhaylischeva MS, Mukhacheva TA, 2015. Natural hybridization of the ticks *Ixodes persulcatus* and *Ixodes pavlovskyi* in their sympatric populations in Western Siberia. Infect. Genet. Evol 32, 388–395. [PubMed: 25858121]

Kovalev SY, Golovljova IV, Mukhacheva TA, 2016. Natural hybridization between *Ixodes ricinus* and *Ixodes persulcatus* ticks evidenced by molecular genetics methods. Ticks Tick Borne Dis. 7, 113–118. [PubMed: 26460161]

Lado P, Nava S, Labruna MB, Szabó MPJ, Durden L, Bermúdez SE, Montagna M, Sánchez Quiros AC, Beati L, 2016. Amblyomma parvum Aragão, 1908 (Acari: Ixodidae): phylogeography and systematics considerations. Ticks Tick Borne Dis. 7, 817–827. [PubMed: 27062445]

Lado P, Nava S, Mendoza-Uribe L, Caceres AG, Delgado-de la Mora J, Licona-Enriquez JD, Delgado-de la Mora D, Labruna MB, Durden LA, Allerdice MEJ, Paddock CD, Szabó MPJ, Venzal JM, Guglielmone AA, Beati L, 2018. The Amblyomma maculatum Koch, 1844 (Acari: Ixodidae) group of ticks: phenotypic plasticity or incipient speciation? Parasite Vectors 11, 1–22.

López-Pérez AM, Pesapane R, Clifford DL, Backus L, Foley P, Voll A, Silva RB, Foley J, 2022. Host species and environment drivers of ectoparasite community of rodents in a Mojave Desert wetlands. PLoS One 17 (6), e0269160. [PubMed: 35653332]

Maddison WP, Maddison DR, 2018. Mesquite: A Modular System for Evolutionary Analysis. Version 3.51. http://www.mesquiteproject.org.

Mangold AJ, Bargues MD, Mas Coma S, 1998. Mitochondrial 16S rDNA sequences and phylogenetic relationships of species of Rhipicephalus and other tick genera among Metastriata. (Acari: Ixodidae). Parasitol. Res 84, 478–484. [PubMed: 9660138]

Mihalca AD, Gherman CM, Cozma V, 2011. Coendangered hard-ticks: threatened or threatening? Parasite Vectors 4, 71.

Neumann LG, 1899. Ŕevision de la famille des Ixodidés. Mém. Soc. Zool. Fr 12, 107–294.

Neumann LG, 1902. Notes sur les Ixodidés. Arch. Parasitol 6, 109–128.

Ogrzewalska M, Literák I, Capek M, Sychra O, Álvarez Calderón V, Calvo Rodríguez B, Prudencio C, Martins TF, Labruna MB, 2015. Bacteria of the genus Rickettsia in ticks (Acari: Ixodidae) collected from birds in Costa Rica. Ticks Tick Borne Dis 6, 478–482. [PubMed: 25869035]

Oliver JH, Keirans JE, Lavender DR, Hutcheson HJ, 1987. Ixodes affinis Neumann (Acari : Ixodidae) : new host and distribution records, description of immatures, seasonal activities in Georgia, and Laboratory rearing. J. Parasitol 73, 646–652. [PubMed: 3598811]

Oliver JH, Wilkinson PR, Kohls GM, 1972. Observations on hybridization on three species of North American *Dermacentor* ticks. J. Parasitol 58, 380–384. [PubMed: 5022874]

Orme AR, Orme AJ, 2008. Late Pleistocene shorelines of Owens Lake, California, and their hydroclimatic and tectonic implications. In: Late Cenozoic drainage history of the southwestern Great Basin and lower Colorado River Region: Geologic and biotic perspectives. In: Reheis MC, Hershler R, Miller DM (Eds.), Late Pleistocene shorelines of Owens Lake, California, and their hydroclimatic and tectonic implications. In: Late Cenozoic drainage history of the southwestern Great Basin and lower Colorado River Region: Geologic and biotic perspectives. Geol. Soc. Am Special Paper 439, 207–225.

Ott-Conn C, Clifford T, Branston T, Klinger R, Foley J, 2014. Pathogen infection and exposure, and ectoparasites of the federally endangered Amargosa vole (Microtus californicus scirpiensis), California, USA. J. Wildl. Dis 50, 767–776. [PubMed: 25121407]

Patterson JW, Duncan AM, McIntyre KC, Lloyd VK, 2017. Evidence for genetic hybridization between *Ixodes scapularis* and *Ixodes cookei*. Can. J. Zool 95, 527–537.

Poulsen A, Conroy C, Foley P, Ott-Conn C, Roy A, Brown R, Foley J, 2015. Ectoparasites of *Microtus californicus* and possible emergence of an exotic *Ixodes* species tick in California. J. Med. Entomol 52, 1060–1066. [PubMed: 26336217]

Rees DJ, Dioli M, Kirkendall LR, 2003. Molecules and morphology: evidence for cryptic hybridization in African Hyalomma (Acari: Ixodidae). Mol. Phylogen. Evol 27, 131–142.

Ronquist F, Huelsenbeck J, Teslenkoet M, 2011. MrBayes Version 3.2 Manual: Tutorials and Model Summaries. http://mrbayes.sourceforge.net/manual.php.

Rudenko N, Golovchenko M, Grubhoffer L, Oliver JH, 2011a. *Borrelia carolinensis* sp. nov., a novel species of the *Borrelia burgdorferi* sensu lato complex isolated from rodents and a tick from the south-eastern USA. Int. J. Syst. Evol. Microbiol 61, 381–383. [PubMed: 20305062]

Rudenko N, Golovchenko M, Grubhoffer L, Oliver JH, 2011b. Updates on *Borrelia burgdorferi* sensu lato complex with respect to public health. Ticks Tick Borne Dis 2, 123–128. [PubMed: 21890064]

Saracho-Bottero MN, Beati L, Venzal JM, Guardia L, Thompson CS, Mangold AJ, Guglielmone AA, Nava S, 2021. Ixodes silvanus n. sp. (Acari: Ixodidae), a new member of the subgenus Trichotoixodes Reznik, 1961 from northwestern Argentina. Ticks Tick Borne Dis. 12, 101572. [PubMed: 33068841]

Saracho-Bottero MN, Venzal JM, Tarragona EL, Thompson CS, Mangold AJ, Beati L, Guglielmone AA, Nava S, 2019. The Ixodes ricinus complex (Acari : Ixodidae) in the Southern Cone of America : Ixodes pararicinus, Ixodes aragaoi, and Ixodes sp. cf. I. affinis. Parasitol. Res 119, 43–54. [PubMed: 31782013]

Smith CN, 1940. The male, nymph, and larva of Ixodes dentatus Marx (Acarina : Ixodidae). Proc. Entomol. Soc. Wash 42, 16–20.

Smith CN, Gouck HK, 1947. Ixodes bishoppi, a new species from Georgia (Acarina : Ixodidae). Ann. Entomol. Soc. Am 40, 75–81.

Swofford DL, 2000. PAUP*: Phylogenetic Analysis Using Parsimony (and Other Methods) 4.0 Beta. Sinauer Associates, Sunderland, MA.

U.S. Fish and Wildlife Service, 1997. Amargosa vole (Microtus Californicus Scirpensis) Recovery Plan, 43. U.S. Department of the Interior - Fish and Wildlife Service; Region 1, Portland; Oregon, p. 53.

Xu G, Fang QQ, Keirans JE, Durden LA, 2003. Molecular phylogenetic analyses indicate that the *Ixodes ricinus* complex is a paraphyletic group. J. Parasitol 89, 452–457. [PubMed: 12880241]

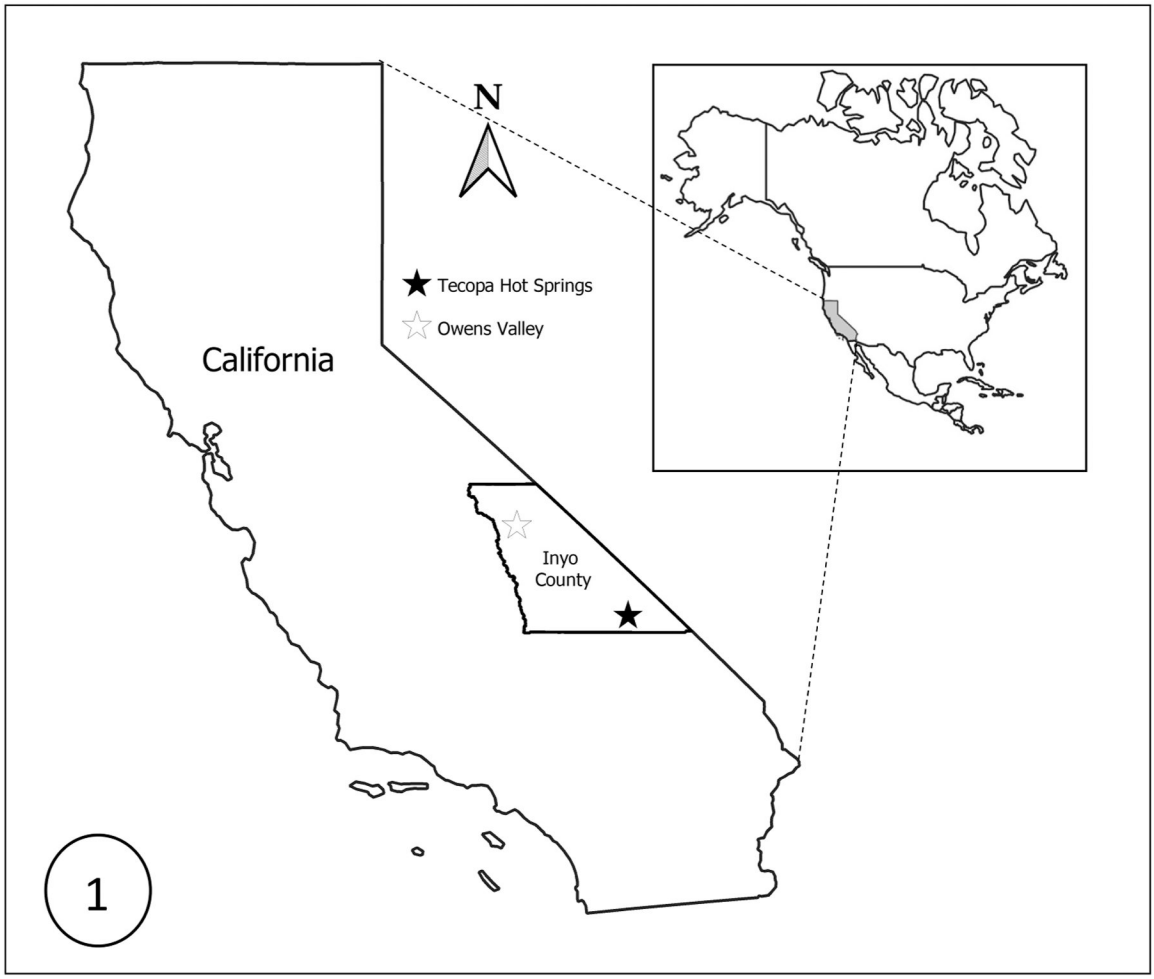

Fig. 1.

Map showing location of collection of *Ixodes mojavensis* sites in Inyo County, California, USA.

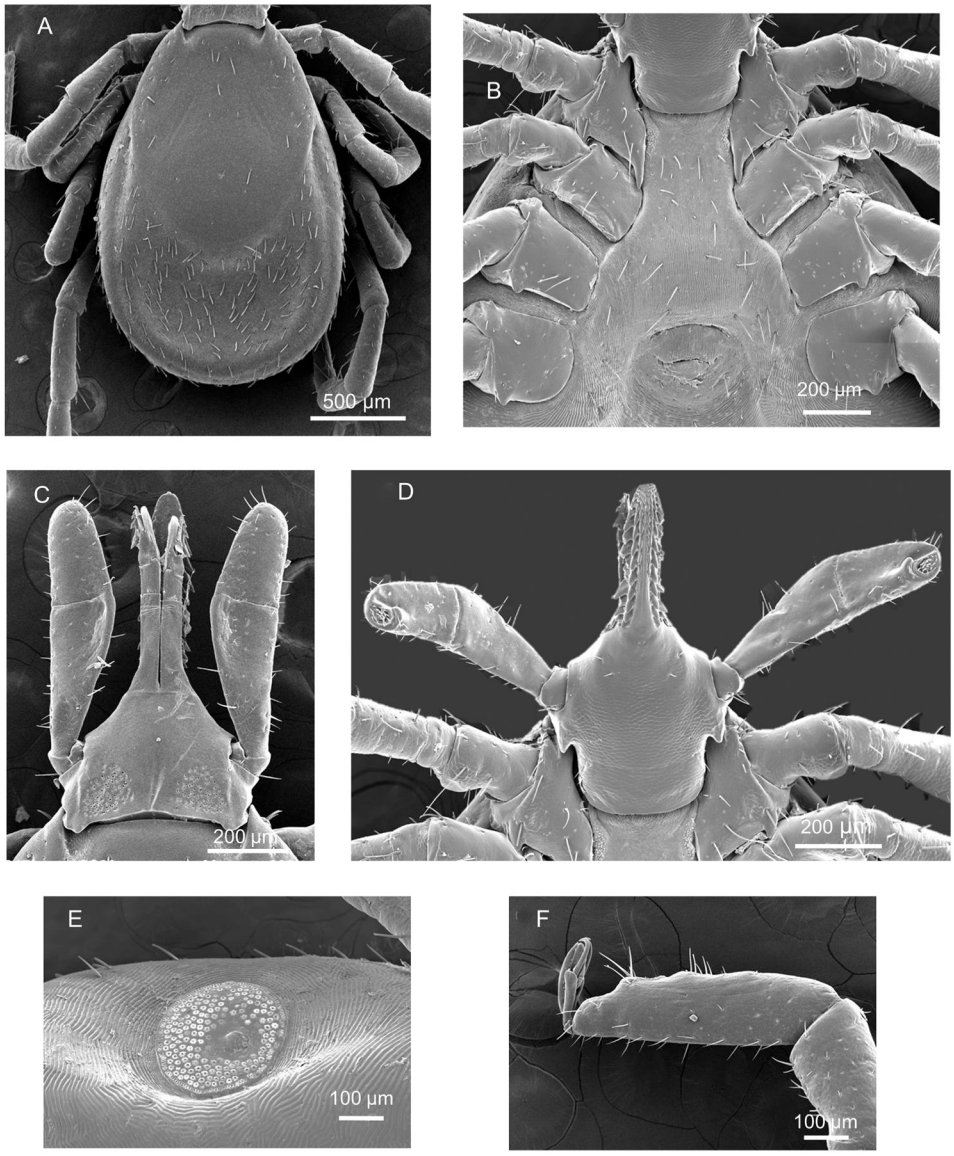

Fig 2.

Scanning electron images of adult female *Ixodes mojavensis*. A: Dorsal idiosoma; B: Coxae and genital aperture; C: Dorsal basis capituli; D: Ventral basis capituli; E: Spiracular plate; F: Tarsus.

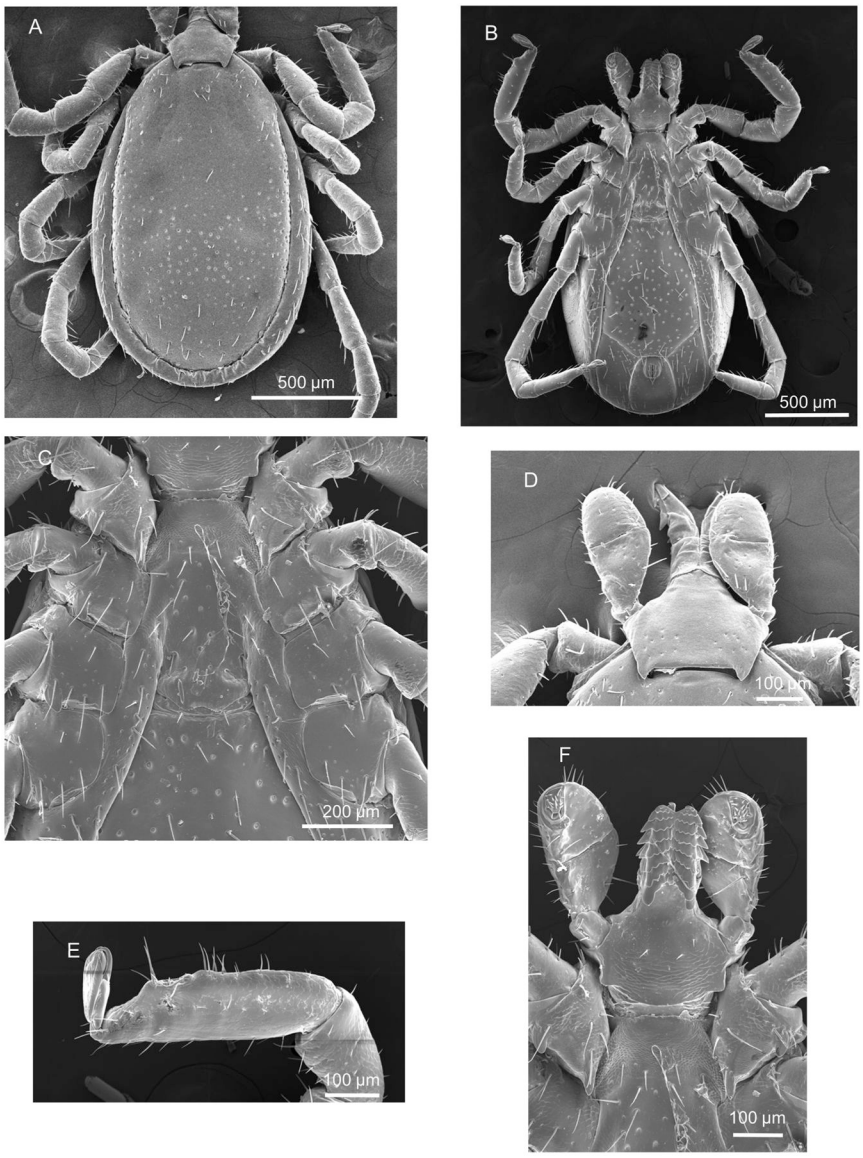

Fig. 3.

Scanning electron microscopy images of adult male *Ixodes mojavensis*. A: Dorsal view; B: Ventral view; C: Coxae and genital aperature; D: Dorsal basis capituli; E: Tarsus; F: Ventral basis capituli.

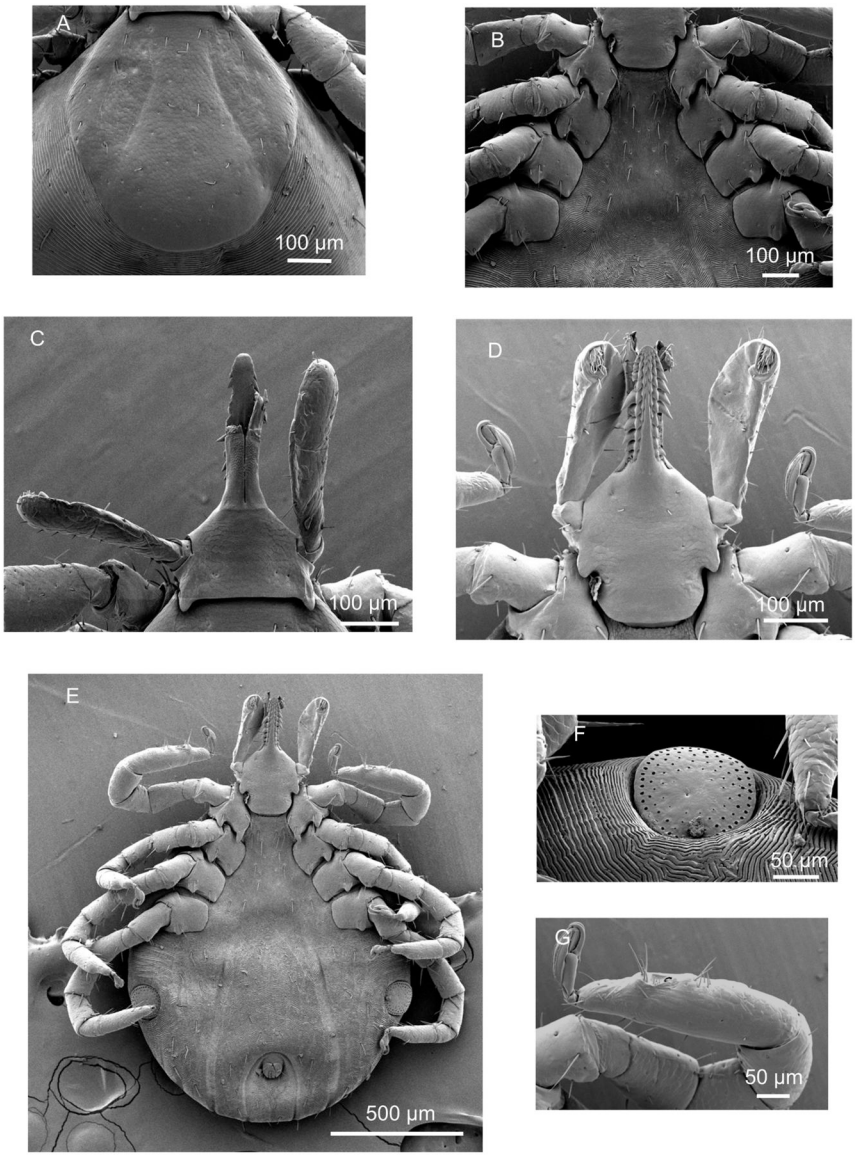

Fig. 4.

Scanning electron microsopy images of nymphal *Ixodes mojavensis*. A: Scutum; B: Coxae; C: Dorsal basis capituli and palps; D: Ventral basis capituli, hypostome, and palps; E: Ventral idiosoma; F: Spiracular plate; G: Tarsus.

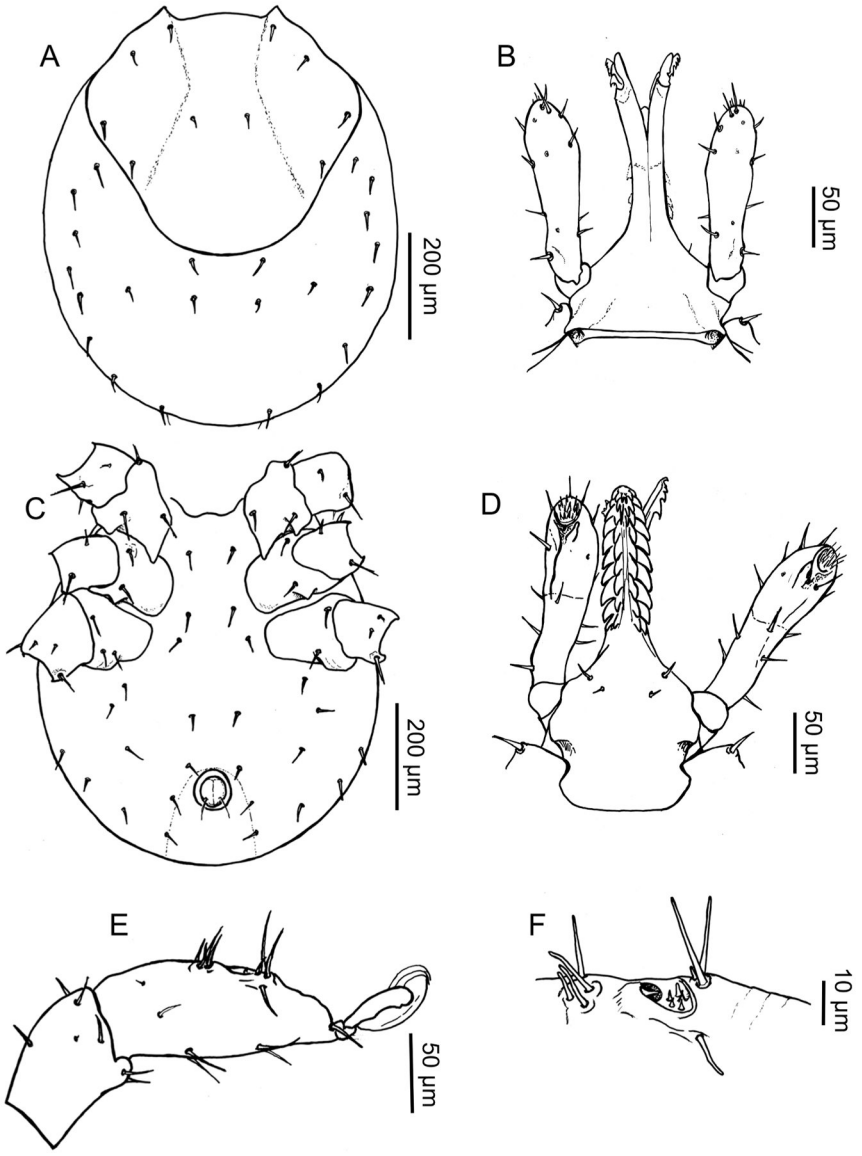

Fig. 5.

Drawings of *Ixodes mojavensis* paratype larvae. A: Dorsal idiosoma; B: Dorsal capitulum; C: Ventral idiosoma and coxae; D: Ventral capitulum; E: Tarsus; F: Haller's Organ. Measurements in micrometers.

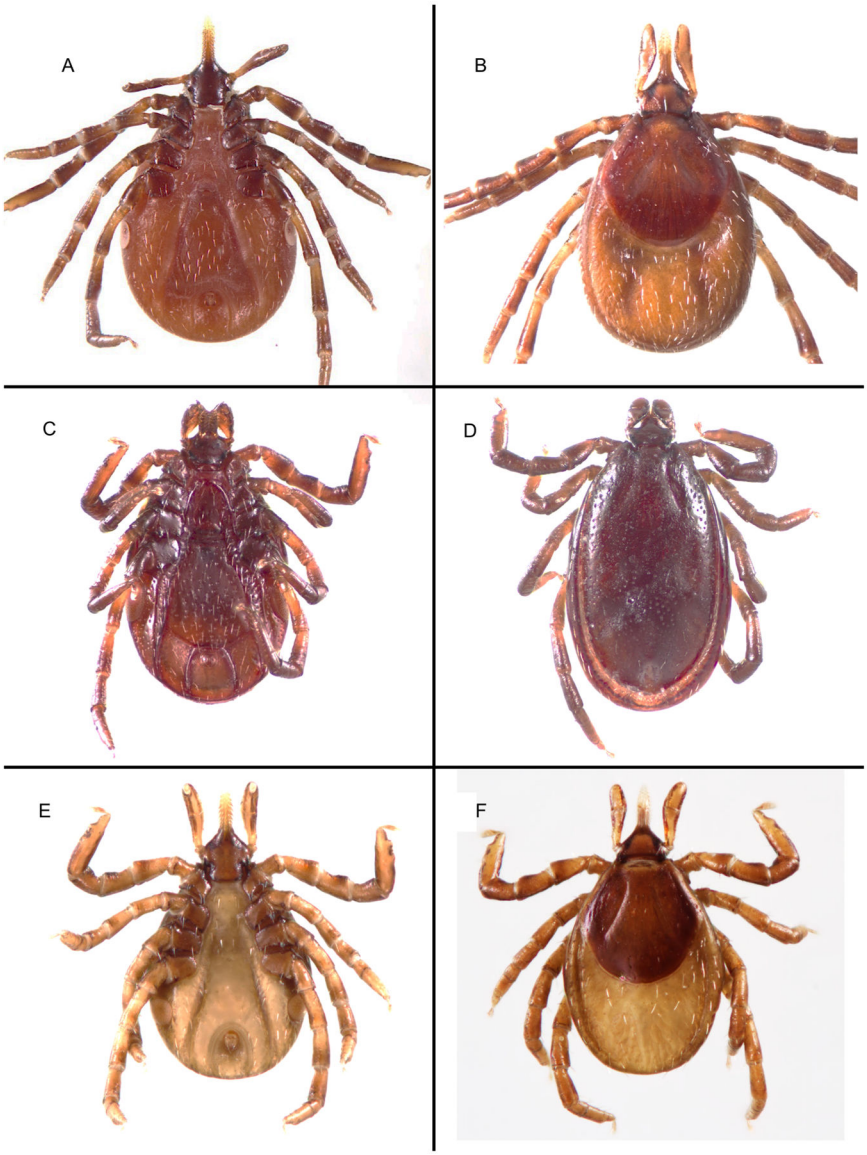

Fig. 6.

Macroscopic images of *Ixodes mojavensis*. Adult female paratype ventral view (A) and dorsal view (B). Adult male paratype ventral view (C) and dorsal view (D). Nymph paratype ventral view (E) and dorsal view (F).

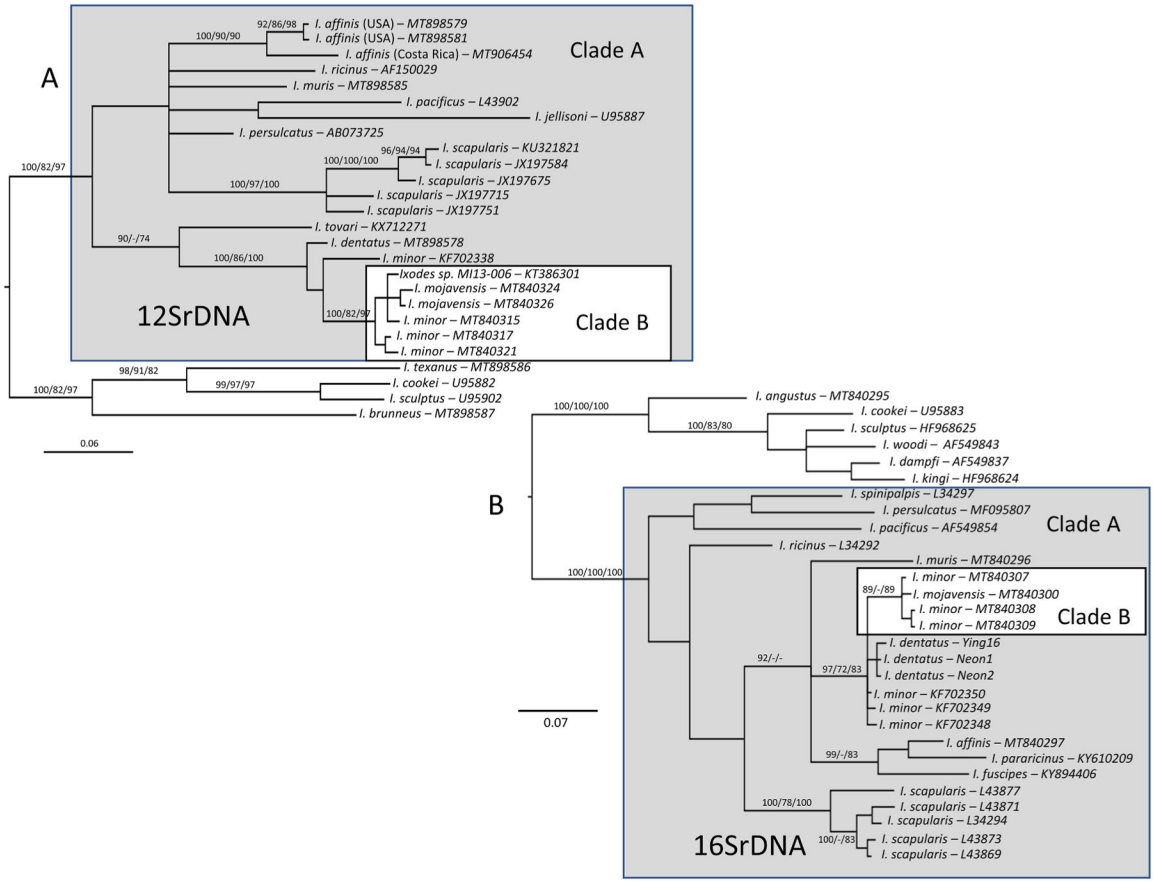

Fig. 7.

Phylogenetic reconstruction based on maximum parsimony, maximum likelihood, and Bayesian inference analysis using alignment of gene fragments of 12S rDNA (A) and 16S rDNA (B).

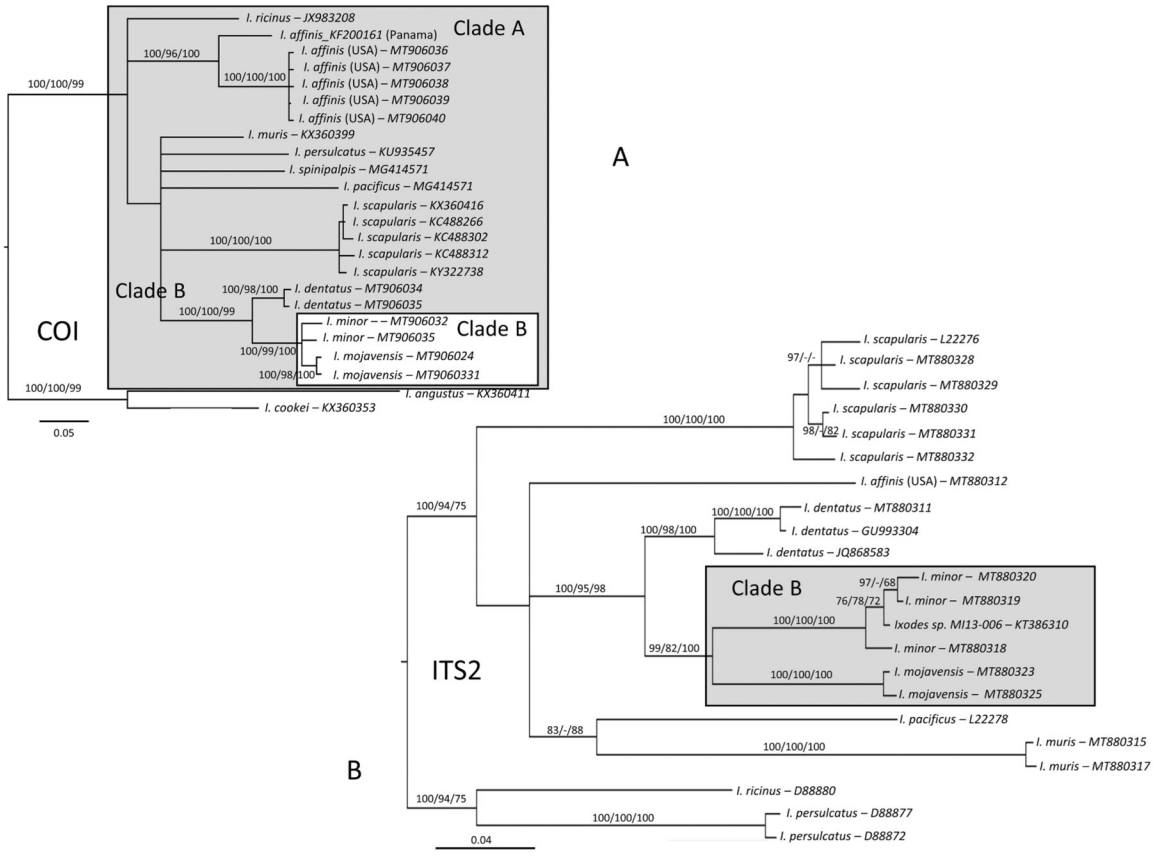

Fig. 8.

Phylogenetic reconstruction based on maximum parsimony, maximum likelihood, and Bayesian inference analysis using alignment of gene fragments of COI (A) and ITS2 (B).

Table 1

List of *I. mojavensis* ticks used in this study.

UCD ID #	USNMENT	Species	Stage/Sex	Host	Collection Date
5571 **	USNMENT00981850	*I. mojavensis*	A/F	MISC	1-Jul-16
5555 **	USNMENT00981851	*I. mojavensis*	A/F	MISC	1-Jul-16
5569 **	USNMENT00981925	*I. mojavensis*	A/M	MISC	1-Jul-16
5570 **	USNMENT00981852	*I. mojavensis*	A/F	MISC	1-Jul-16
5572 **	USNMENT00981853	*I. mojavensis*	A/F	MISC	1-Jul-16
5575 **	USNMENT00981835	*I. mojavensis*	A/F	MISC	1-Jul-16
5581 **	USNMENT00981926	*I. mojavensis*	N	MISC	1-Jul-16
5584 **	USNMENT00981825	*I. mojavensis*	N	MISC	29-Sep-16
5588 **	USNMENT00981927	*I. mojavensis*	A/F	MISC	24-Mar-16
5591 **	USNMENT00981854	*I. mojavensis*	A/F	MISC	26-Mar-16
5596 **	USNMENT00981826	*I. mojavensis*	N	MISC	25-Mar-16
5597 **	USNMENT00981928	*I. mojavensis*	N	MISC	25-Mar-16
5611 **	USNMENT00981929	*I. mojavensis*	A/F	MISC	10-Apr-16
5626 **	USNMENT00981827	*I. mojavensis*	N	MISC	8-Nov-15
5627 **	USNMENT00981836	*I. mojavensis*	L	MISC	8-Nov-15
5629 **	USNMENT00981838	*I. mojavensis*	L	MISC	7-Nov-15
5632 **	USNMENT00981833	*I. mojavensis*	L	MISC	5-Nov-15
5633 **	USNMENT00981829	*I. mojavensis*	L	MISC	7-Nov-15
5634 **	USNMENT00981832	*I. mojavensis*	L	MISC	7-Nov-15
5642 **	USNMENT00981837	*I. mojavensis*	L	MISC	7-Nov-15
5647 **	USNMENT00981834	*I. mojavensis*	L	MISC	6-Nov-15
5649 **	USNMENT00981932	*I. mojavensis*	L	MISC	6-Nov-15
5652 **	USNMENT00981839	*I. mojavensis*	A/F	REME	1-Jun-17
5672 **	USNMENT00981815	*I. mojavensis*	A/M	MISC	20-Feb-17

UCD ID #	USNMENT	Species	Stage/Sex	Host	Collection Date
5878 **	USNMENT00981846	*I. mojavensis*	L	MISC	4-Jan-18
5888 **	USNMENT00981787	*I. mojavensis*	N	MISC	5-Jun-18
5840 **	USNMENT00981788	*I. mojavensis*	A/F	MISC	4-Apr-18
5843 **	USNMENT00981789	*I. mojavensis*	A/F	MISC	4-Apr-18

A, adult; F, female; M, male; N, nymph; L, larva; MISC, *M. c. scirpensis*; MIVA, *M. c. vallicola*; REME, *R. megalotis*; MUMU, *M. musculus*. UCD ID: original accession number at University of California Davis, CA; USNMENT: numbers for permanent accession at the U.S. National Tick Collection, Georgia Southern University, GA. Origin:

** Tecopa Hot Springs, Inyo County, CA, USA;

~~ Owens Valley, Inyo County, CA, USA.

Table 2

list of samples used for molecular analyses, their accession codes (when accessioned), collection information, and GenBank accession numbers for the different genes.

						GenBank Accession Numbers					
Species	**Code**	**USNMENT ID**	**Location**	**Collection Date**	**Host**	**12S**	**16S**	**18S**	**COI**	**ITS2**	**28S**
Ixodes minor	RML121407	USNMENT1483612	Bulloch Co., GA, USA	13-Apr-1994	*Peromyscus gossypinus*	MT840315					
Ixodes minor	RML120050	USNMENT865892_B	Wedger Plantation, Charleston Co., SC, USA	19-Feb-1991	"Rat"	MT840316	MT840308		MT906032		
Ixodes minor	RML120050	USNMENT865892_C	Wedger Plantation, Charleston Co., SC, USA	20-Feb-1991	"Rat"	MT840321					
Ixodes minor	RML120050	USNMENT865892_D	Wedger Plantation, Charleston Co., SC, USA	21-Feb-1991	"Rat"	MT840322					
Ixodes minor	RML120050	USNMENT865892A	Wedger Plantation, Charleston Co., SC, USA	22-Feb-1991	"Rat"	MT840323					
Ixodes minor	RML122314	USNMENT1483620	Hobcaw Barony, Georgetown Co., SC, USA	12-Jul-1995	*Neotoma floridana*	MT840317	MT840307		MT906033	MT880319	
Ixodes minor	RML123025	USNMENT865897C	Statesboro, Bulloch Co., GA, USA	8-Aug-2000	Laboratory colony	MT840318		MT860478		MT880320	
Ixodes minor	RML123025	USNMENT565897A	Statesboro, Bulloch Co., GA, USA	9-Aug-2000	Laboratory colony	MT840319					
Ixodes minor	RML123025	USNMENT565897B	Statesboro, Bulloch Co., GA, USA	10-Aug-2000	Laboratory colony	MT840320	MT840309				
Ixodes mojavensis	5767	USNMENT00981858	Tecopa Hot Springs, Inyo Co., CA, USA	6-Jul-2017	*Microtus californicus scirpensis*	MT840324	MT840302/ MT860475		MT906031	MT880321	MT897893
Ixodes mojavensis	5575	USNMENT00981835	Tecopa Hot Springs, Inyo Co., CA, USA	1-Jul-2016	*Microtus californicus scirpensis*	MT840325	MT840300	MT860476	MT906028	MT880324	MT897885

Species	Code	USNMENT ID	Location	Collection Date	Host	GenBank Accession Numbers					
						12S	16S	18S	COI	ITS2	28S
Ixodes mojavensis	5649	USNMENT00981932	Tecopa Hot Springs, Inyo Co., CA, USA	6-Nov-2015	*Microtus californicus scirpensis*	MT840326	MT840306	MT860474	MT906026		MT897884
Ixodes mojavensis	5652	USNMENT00981839	Tecopa Hot Springs, Inyo Co., CA, USA	1-Jun-2017	*Microtus californicus scirpensis*	MT840327	MT840299		MT906029	MT880326	MT897889
Ixodes mojavensis	5673	USNMENT00981816	Tecopa Hot Springs, Inyo Co., CA, USA	20-Feb-2017	*Microtus californicus scirpensis*	MT840328	MT840305		MT906027	MT880323	
Ixodes mojavensis	5688	USNMENT00981931	Tecopa Hot Springs, Inyo Co., CA, USA	23-Sep-2015	*Microtus californicus scirpensis*	MT840329	MT840304		MT906030	MT880327	MT897890
Ixodes mojavensis	5746	USNMENT00981930	Tecopa Hot Springs, Inyo Co., CA, USA	8-Oct-2014	*Microtus californicus scirpensis*	MT840330	MT840303		MT906025	MT880325	MT897892
Ixodes mojavensis	5768	USNMENT00981786	Tecopa Hot Springs, Inyo Co., CA, USA	8-Aug-2016	*Microtus californicus scirpensis*	MT840331	MT840301	MT860477	MT906024	MT880322	MT897891
Ixodes angustus		USNMENT981452	No Data				MT840295				
Ixodes muris		USNMENT1361452	Treehaven, Lincoln Co., WI, USA	8-Sep-2017	Vegetation	MT898585	MT840296			MT880316	
Ixodes muris		USNMENT1482746	Steigerwaldt Land Services, Lincoln Co., WI, USA	30-Aug-2018	Vegetation			MT860479		MT880315	
Ixodes affinis		USNMENT981451	Statesboro, Bulloch Co., GA, USA	2018	Vegetation		MT840297				
Ixodes affinis		USNMENT981450	Statesboro, Bulloch Co., GA, USA	2018	Vegetation		MT840298				
Ixodes affinis	Dan6		Statesboro, Bulloch Co., GA, USA	2018	Vegetation	MT898580		MT860480	MT906039		
Ixodes affinis	Dan7		Statesboro, Bulloch Co., GA, USA	2018	Vegetation			MT860481		MT880314	
Ixodes affinis	LAD508_2		St. Catherine's Island, Liberty Co., GA, USA	17-Mar-1993	*Peromyscus gossypinus*	MT898582				MT880312	

Species	Code	USNMENT ID	Location	Collection Date	Host	GenBank Accession Numbers					
						12S	16S	18S	COI	ITS2	28S
Ixodes affinis	LAD508_3		St. Catherine's Island, Liberty Co., GA, USA	17-Mar-1993	*Peromyscus gossypinus*				MT906037		
Ixodes affinis	LAD508_4		St. Catherine's Island, Liberty Co., GA, USA	17-Mar-1993	*Peromyscus gossypinus*	MT898579			MT906036	MT880313	
Ixodes affinis	LAD508_1		St. Catherine's Island, Liberty Co., GA, USA	17-Mar-1993	*Peromyscus gossypinus*	MT898581			MT906040		
Ixodes affinis	LAD529		St. Catherine's Island, Liberty Co., GA, USA	27-Apr-1993	*Peromyscus gossypinus*				MT906038		
Ixodes affinis	LAD528_2		St. Catherine's Island, Liberty Co., GA, USA	27-Apr-1993	*Peromyscus gossypinus*	MT898583					
Ixodes affinis	LAD525		St. Catherine's Island, Liberty Co., GA, USA	27-Apr-1993	*Peromyscus gossypinus*	MT898584					
Ixodes affinis	RML122838		Costa Rica			MT906454					
Ixodes dentatus		USNMENT0098073	No Data			MT898578				MT880311	
Ixodes dentatus	Nymph 1	USNMENT1512111	The University of Kansas Field Station, Jefferson Co., KS, USA	13-May-2019	Vegetation				MT906034		
Ixodes dentatus	Nymph2	USNMENT1512111	The University of Kansas Field Station, Jefferson Co., KS, USA	14-May-2019	Vegetation				MT906035		
Ixodes scapularis	AL7181_5_W3		Oakmulgee Talladega Natl. Forest, AL, USA		Vegetation					MT880328	
Ixodes scapularis	2012_044_1		Guana River, FL, USA	00-000-2012	Vegetation					MT880329	
Ixodes scapularis	GA0011_4_W1		Statesboro, Bulloch Co., GA, USA	00-000-2011	Vegetation					MT880330	
Ixodes scapularis	GA0011_4_W2		Statesboro, Bulloch Co., GA, USA	00-000-2011	Vegetation					MT880331	

Species	Code	USNMENT ID	Location	Collection Date	Host	GenBank Accession Numbers					
						12S	16S	18S	COI	ITS2	28S
Ixodes scapularis	AL7181_5_W1		Oakmulgee Talladega Natl. Forest, AL, USA	27-Jan-2011	*Odocoileus virginianus*					MT880332	
Ixodes texanus	1008_8		Savannah River Site, SC, USA	28-Sep-2011	*Procyon lotor*	MT898586					
Ixodes brunneus	RML122470		Holly Springs, Marshall Co., MS, USA	6-Mar-1997	*Vegetation*	MT898587					

Ticks Tick Borne Dis. Author manuscript; available in PMC 2024 March 06.