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A morphological and phylogenetic analysis of *Ornithodoros marinkellei* (Acari: Argasidae), with additional notes on habitat and host usage

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Abstract
Ornithodoros marinkellei was described from larvae collected on *Pteronotus* spp. bats in Colombia and Panama. More recently, this tick was reported in the Brazilian Amazon. Because some morphometric differences were observed between *O. marinkellei* larvae from Colombia and Brazil, it was proposed that further investigations were needed to assess whether the differences could be attributed to intra- or inter-specific polymorphism. Herein, we collected *O. marinkellei* specimens in the type locality of Colombia, in Brazil, and in a new locality in Nicaragua, expanding the distribution of the species to Nicaragua. Morphometric analysis of larvae and adults, corroborated by a principal component analysis (PCA), indicated that the Brazilian specimens were larger than specimens from Colombia and Nicaragua. Phylogenetic analysis inferred from the mitochondrial 16S rRNA gene showed ticks from Colombia and Nicaragua more genetically related than any of them with ticks from Brazil, although ticks from the three countries grouped in a clade sister to a major clade containing sequences of various Neotropical *Ornithodoros* species. We concluded that ticks identified as *O. marinkellei* from Colombia, Nicaragua, and Brazil represent the same taxon, and that the genetic and morphological differences between them are likely to have a geographical bias. We redescribed the nymph of *O. marinkellei*, which has a vestigial hypostome, probably incompatible with blood feeding. We also report human infestation by *O. marinkellei* adults. As all reports of *O. marinkellei* adults have been from hot caves (temperature > 35 °C), this abiotic condition could be a limiting factor for the occurrence of this tick species.

Keywords Ticks · Bats · *Pteronotus* · Human parasitism · Hot cave

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Introduction

The argasid tick *Ornithodoros marinkellei* Kohls, Clifford and Jones was described from larvae collected on bats of the genus *Pteronotus* in Colombia and Panama (Kohls et al. 1969). Based on larval morphological characters, this tick species was included to the subgenus *Subparmatus* Clifford, Kohls and Sonenshine (Kohls et al. 1969). The geographical distribution of *O. marinkellei* was expanded with larval records on *Pteronotus psilotis* [=*Pteronotus personatus psilotis* (Dobson)] in Venezuela (Jones et al. 1972), and on omitted hosts in Guiana (Guglielmone et al. 2003) and Brazil (Venzal et al. 2006). More recently, Labruna et al. (2011) redescribed the larva of *O. marinkellei* based on specimens collected on *Pteronotus* bats from a hot cave in Rondônia state, western Brazilian Amazon. In this same cave, the authors collected adult males and females, which were described for the first time. In addition, some of the engorged larvae collected from bats were allowed to molt to nymphs inside tubes that were left inside the cave; three nymphs molted from these larva and were used for the description of the nymphal stage of *O. marinkellei*; however, the external morphology of these nymphs was extensively damaged, resulting in a partial description without illustration (Labruna et al. 2011). Additional records of *O. marinkellei* were adult ticks from a cave in Pará state, eastern Brazilian Amazon (Henrique-Simões et al. 2012), and larvae on *Pteronotus gymnonotus* Natterer from the Caatinga, a semiarid biome of northeastern Brazil (Luz et al. 2016).

In the larval redescription of *O. marinkellei*, Labruna et al. (2011) called the attention to few morphological differences between the Brazilian specimens and the type specimens from Colombia, which indicated that the Colombian specimens were smaller than the Brazilian specimens. The authors stated that further investigations were needed to assess whether these differences could be attributed to intraspecific polymorphism or to the occurrence of a *O. marinkellei* species complex. For the present study, we collected new specimens of *O. marinkellei* in the type locality of Colombia, and in a new locality in Nicaragua, expanding the distribution of the species to this later country. Besides morphological comparisons of larvae and adults from these two countries with specimens from Brazil, we performed a molecular analysis including 16S rDNA sequences of *O. marinkellei* ticks from Colombia, Nicaragua and Brazil, and redescribed the nymphal stage. Finally, additional comments on host and habitat usage are also included.

Materials and methods

Collection of ticks

In 11 December 2010, we visited the type locality of *O. marinkellei,* the San Fernando de Bocachica Fort (10°19′10″N, 75°34′54″W, elevation 5 m) in Cartagena, Bolivar Department, Colombia. This Fort is precisely the type locality of *O. marinkellei,* as confirmed to us in 2010 by Prof. C.J Marinkelle, who collected the type specimens in 1966. Ticks were collected on the walls of the fort tunnels, which were inhabited by thousands of *Pteronotus* bats. During tick collection around 10:00 h, the tunnel entrance had a temperature of 30 °C, and 73% relative humidity (RH). Inside the tunnel, where the ticks were collected, temperature varied from 37.5 to 39.4 °C with 100% RH, and the atmosphere was noisome and rich in nitrogen compounds.

In 31 May 2012, we visited a cave (12°55′50″N, 86°46′47″W, elevation 75 m) in a locality called Rincón García, Villanueva Municipality, Chinandega Department, Nicaragua. The cave used to be a gold mine until ≈40 years before. Ticks were collected on the walls of the cave, which were inhabited by thousands of *Pteronotus* bats. During tick collection around 9:30 h, the cave entrance had a temperature of 31.6 °C. Inside the cave, where the ticks were collected, temperature was around 36 °C. RH was not measured, but the atmosphere was noisome and rich in nitrogen compounds.

Ticks collected in the two above caves were placed in plastic vials containing 100% ethanol, and brought to the laboratory for analyses. In addition, in both caves a few bats were captured and examined for the presence of ticks, which were collected and also preserved in ethanol. In March 2011, we collected new adult specimens of *O. marinkellei* from the same cave of the adult specimens described by Labruna et al. (2011) in Brazil; these new adult specimens were also placed in plastic vials containing 100% ethanol, and brought to the laboratory for analyses.

Morphological analyses

Ticks collected from the caves were separated as males, females and nymphs, and were identified as *O. marinkellei* following the descriptions provided by Labruna et al. (2011). These ticks were measured (length and width of the idiosoma) under a stereomicroscope (Discovery V12, Carl Zeiss, Göttingen, Germany) with the Hardware ZEN Pro 2012 (Carl Zeiss), and the values were compared to the measurements of the adult and nymphal specimens from Brazil, previously reported by Labruna et al. (2011). All values are given in millimeters.

Larvae collected from bats, after been identified as *O. marinkellei* according to Kohls et al. (1969) and Labruna et al. (2011), were mounted in Hoyer's medium to make semipermanent slides and examined by light microscopy for morphometry. Larval measurements were also compared to the values reported for the *O. marinkellei* larvae that were collected in Brazil by Labruna et al. (2011). A principal component analysis (PCA) based on a Pearson's correlation matrix was applied on 43 morphometric variables for larvae from Brazil (Labruna et al. 2011), Colombia, and Nicaragua to elucidate relationships among the three tick populations. Raw measurements were log(x + 1)-transformed to standardize variances and improve normality.

Molecular and phylogenetic analyses

Adult specimens of the *O. marinkellei* ticks from Colombia and Nicaragua were individually submitted to DNA extraction by the guanidine isothiocyanate-phenol technique (Sangioni et al. 2005), and tested by polymerase chain reaction (PCR) targeting a fragment of ≈460 bp of the mitochondrial 16S rRNA gene, as described (Mangold et al. 1998). PCR products of the expected size were purified and sequenced using an ABI automated sequencer (Applied Biosystems/Thermo Fisher Scientific, model ABI 3500 Genetic Analyzer, Foster City, CA, USA) with the same primers used in the PCR. Generated sequences were compared to each other and submitted to BLAST analyses (www.ncbi.nlm.nih.gov/blast) to infer closest similarities available in GenBank. Consensus sequences of *O. marinkellei* from Colombia and Nicaragua were aligned with other sequences of argasid ticks from GenBank, including three haplotypes of *O. marinkellei* from Brazil (HM582438,

HM582439, KX781700). Sequences were aligned with the program Clustal X (Thompson et al. 1997), and manually adjusted using GeneDoc (Nicholas et al. 1997). With this alignment two phylogenetic analyses were performed. A maximum parsimony tree was constructed in PAUP v4.0b1 (Swofford 2002), with 500 bootstrap replicates, random stepwise addition starting trees (with random addition sequences) and TBR branch swapping. A Bayesian analysis was performed using MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001) with four independent Markov chain runs for 1,000,000 metropolis-coupled MCMC generations, sampling a tree every 100th generation. The first 25% of the trees represented burn-in, and the remaining trees were used to calculate Bayesian posterior probability. Sequences of *Ixodes holocyclus* Neumann and *Ixodes uriae* White were used as outgroups (accessions numbers of all sequences are shown in the phylogenetic tree).

Results

A total of 41 males and 20 females of *O. marinkellei* were collected in the walls of the cave tunnels in Colombia. Among these ticks, 3 specimens (2 males and 1 female) were apparently engorged, contrasting to the remaining ticks that had a flatter appearance. While collecting ticks in the cave tunnels, 2 males and 2 females attached to one of us (JMV) (Fig. 1); these ticks were allowed to feed, which took between 10 and

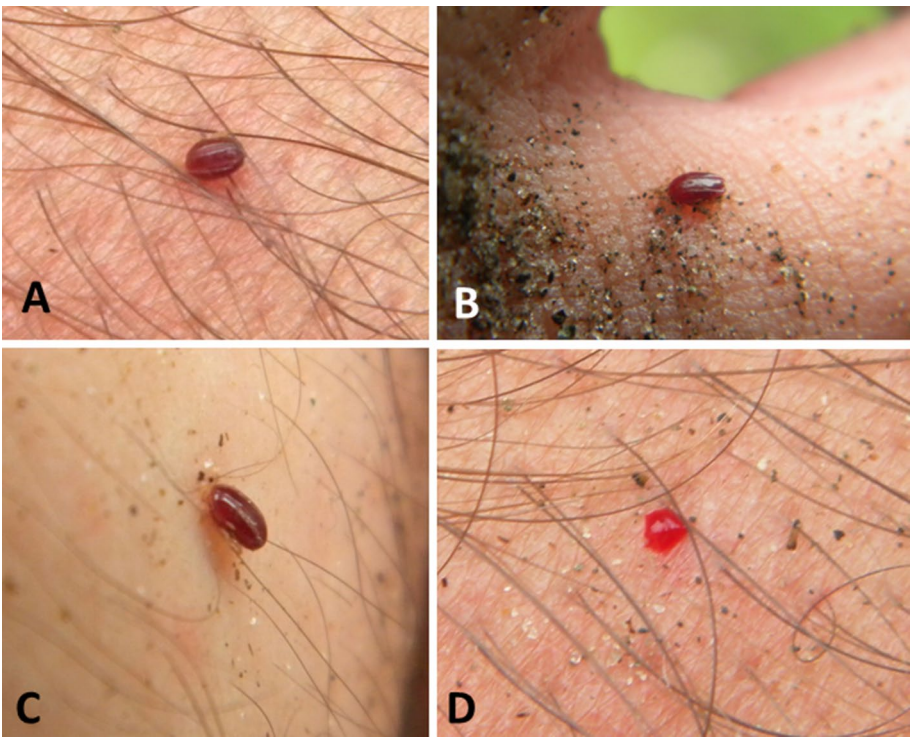

Fig. 1 *Ornithodoros marinkellei* adults feeding on the arm (**a**), finger (**b**), and abdomen (**c**) of a human. **d** Bleeding at the tick feeding site immediately after tick detachment

20 min to become as engorged as the above 3 specimens that were found engorged in the cave. No nymphs were found; however, 11 engorged larvae of *O. marinkellei* were collected on the guano. In Nicaragua, 8 males, 2 females, and 1 nymph were collected in the cave walls. In Brazil, 2 males and 4 females were collected in March 2011. Adult ticks from Colombia, Nicaragua, and Brazil were measured (apparently engorged ticks were not measured), and compared to the measurements reported for the Brazilian adults described by Labruna et al. (2011). Overall, adults from Brazil were larger than those from Colombia and Nicaragua, as shown in Table 1.

A total of 11 larvae of *O. marinkellei* were collected from 7 bats of the species *Pteronotus personatus* (Wagner) in Colombia, whereas 7 larvae of the same tick species were collected from 3 *P. gymnonotus* in Nicaragua. From these larvae, 10 from Colombia and 3 from Nicaragua (the ones with unbroken mouthparts) were slide-mounted and measured. All 43 morphometric variables (Table S1) were from non-expansive, hard cuticle; therefore they could be used for comparisons between larval specimens regardless of the engorgement state. These variables were used for morphological analysis through PCA, which included measurements of 10 *O. marinkellei* larvae from Brazil, previously reported by Labruna et al. (2011). PCA based on morphometric characters of larvae showed a clear differentiation between *O. marinkellei* ticks from Colombia and Nicaragua and those from Brazil (Fig. 2). The difference is observed in the first component axis of the PCA (Fig. 2), which explains the 49.4% of the total variance, and it is almost fully loaded with the following characters: length of dorsal plate, length of basis capituli, palpal length, and hypostome length.

Partial sequences (416 to 426 bp) of the mitochondrial 16S rRNA gene were generated for 2 adult ticks (1 male and 1 female) from each population of Colombia and Nicaragua. In each of the two populations, the 2 adult ticks yielded an identical 16S rRNA haplotype; however, the haplotype from Colombia differed by a single nucleotide substitution from the Nicaraguan haplotype. By BLAST analysis, the Colombian and Nicaraguan haplotypes were 94-95% identical to three haplotypes of *O. marinkellei* from Brazil (HM582438, HM582439, KX781700), to which they differed by 22–25 nucleotide substitutions. In the phylogenetic analysis inferred from mitochondrial 16S rRNA partial sequences of argasid ticks, the 5 available haplotypes of *O. marinkellei* grouped in a single clade under 100% bootstrap support; however, the clade separated the 3 sequences of Brazil from the ones from Colombia and Nicaragua (Fig. 3). This *O. marinkellei* clade was sister to a major clade containing sequences of various *Ornithodoros* species from the Neotropical region; the only exception was *Ornithodoros sawaii* Kitaoka and Suzuki.

Tick specimens collected in this study have been deposited in the tick collections 'Coleção Nacional de Carrapatos Danilo Gonçalves Saraiva' (CNC) of the Faculty of Veterinary Medicine, University of São Paulo, Brazil (CNC), and Department of Veterinary Parasitology, Faculty of Veterinary, Salto, Uruguay (DPVURU), under the accession numbers CNC-1752, 1760, 1761, 1907, 3702-3704 and DPVURU-775, 883-896, 897-899. The two mitochondrial 16S rRNA haplotypes of *O. marinkellei* generated in this study have been submitted to GenBank under the accession numbers MH743139 (Colombia) and MH743140 (Nicaragua).

The single nymph collected in Nicaragua was undamaged, and for this reason, it was used for redescription of this stage of *O. marinkellei*.

Table 1 Mean (± SD; range in parentheses) length and width (mm) of the idiosoma of adult specimens of *Ornithodoros marinkellei* from three countries

Country	Males			Females		
	N	Length	Width	N	Length	Width
Colombia	10	2.24 ± 0.12 (2.04–2.40)	1.25 ± 0.06 (1.18–1.36)	10	2.41 ± 0.06 (2.33–2.50)	1.35 ± 0.06 (1.25–1.43)
Nicaragua	8	2.26 ± 0.10 (2.12–2.44)	1.17 ± 0.07 (1.06–1.28)	2	2.29 ± 0.06 (2.33–2.45)	1.34 ± 0.08 (1.28–1.39)
Brazil[a]	3	2.44 ± 0.04 (2.40–2.47)	1.35 ± 0.03 (1.32–1.37)	5	2.53 ± 0.06 (2.42–2.57)	1.40 ± 0.04 (1.35–1.45)
Brazil[b]	2	2.53 ± 0.20 (2.40–2.67)	1.37 ± 0.00 (1.37–1.37)	4	2.60 ± 0.04 (2.55–2.64)	1.48 ± 0.05 (1.43–1.55)

N number of specimens

[a]Values reported by Labruna et al. (2011) for the description of adults of *O. marinkellei*

[b]New specimens collected in the present study, from the same cave reported by Labruna et al. (2011)

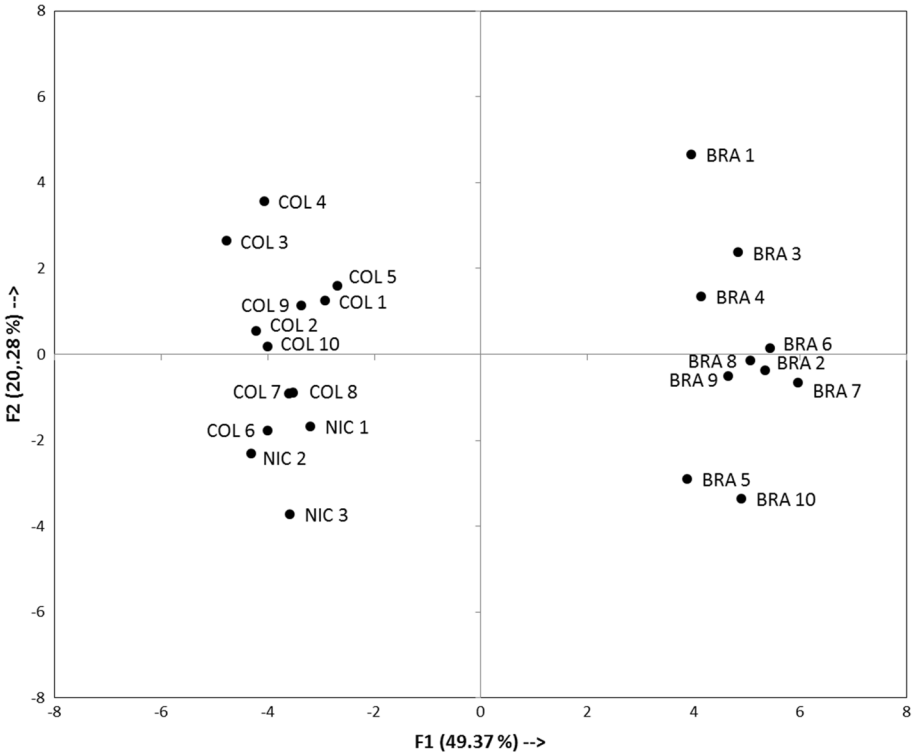

Fig. 2 Principal components analysis of the body and setal measurements of the larvae of *Ornithodoros marinkellei* using the features detailed in Table S1. Each point constitutes the position of each measured specimen on the reduced space. *BRA* Brazil, *NIC* Nicaragua, *COL* Colombia

Redescription of the nymph of *Ornithodoros marinkellei* Kohls, Clifford and Jones, 1969 (Fig. 4)

Dorsal

Outline elliptical, broadest at level of spiracular plates. Length from anterior to posterior body margin 2.340, breadth 1.216. Entire idiosoma micromammillated, with numerous integumental ridge-like or tubercle-like elevations. Two long and parallel deep grooves extending from anterior to near posterior margin.

Lateral

Micromammillated. Deep lateral groove extending from anterior end of idiosoma to level of anus. Spiracular plates located above lateral groove at level of coxa IV, elliptical (length 0.140, width 0.093); dorsal margin visible from above, with numerous small goblets; macula located on medio-ventral margin.

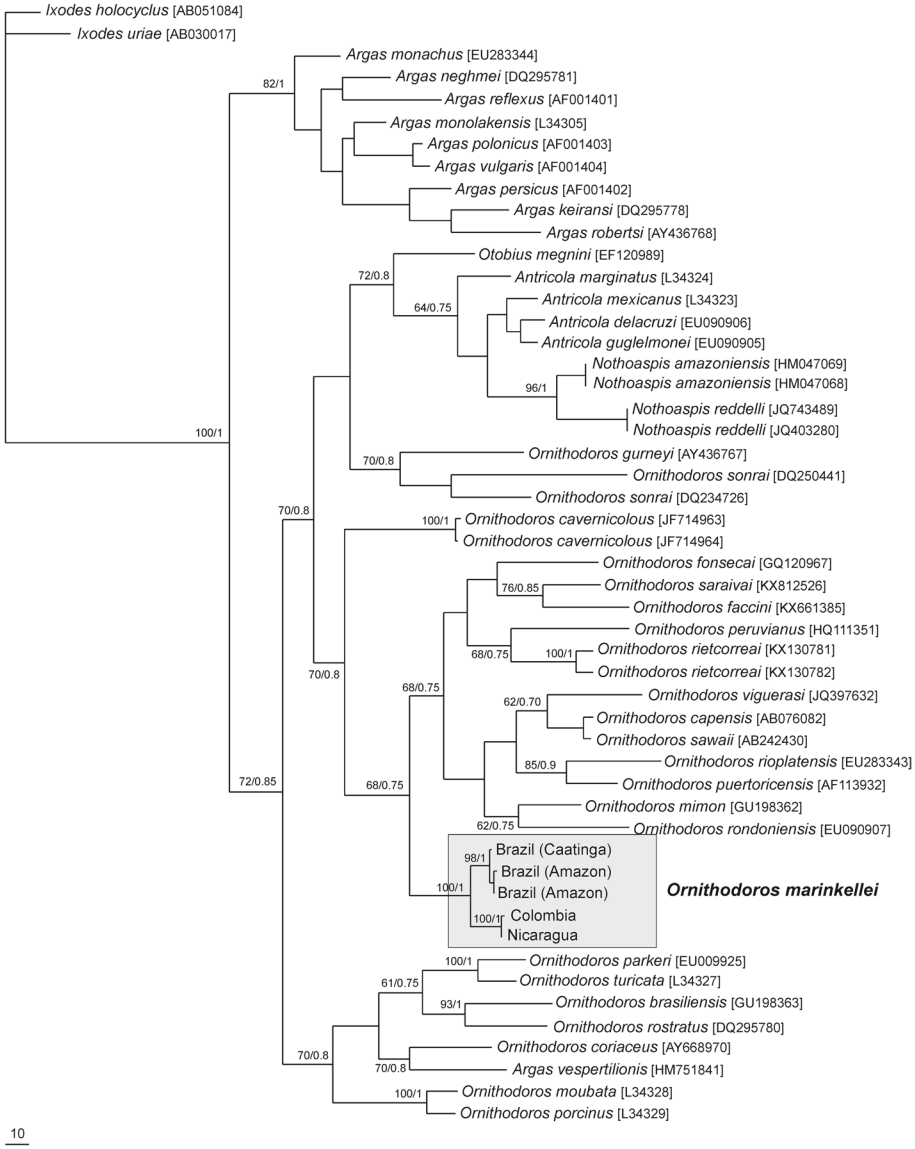

Fig. 3 Bayesian inference phylogenetic tree with Maximum parsimony (MP) support values inferred from 16S rDNA partial sequences of *Ornithodoros marinkellei* and other argasid tick species. *Ixodes uriae* and *I. holocyclus* were used as the outgroup. Numbers at nodes are support values derived from bootstrap (1000 replicates for MP/posterior probabilities for Bayesian inference analysis). Numbers in brackets are GenBank accession numbers. The *O. marinkellei* sequences include 2 haplotypes generated in the present study (from Colombia and from Nicaragua), and 3 haplotypes from Brazil available in GenBank: 1 from the Caatinga biome (KX781700), and 2 from the Amazon biome (HM582438, HM582439)

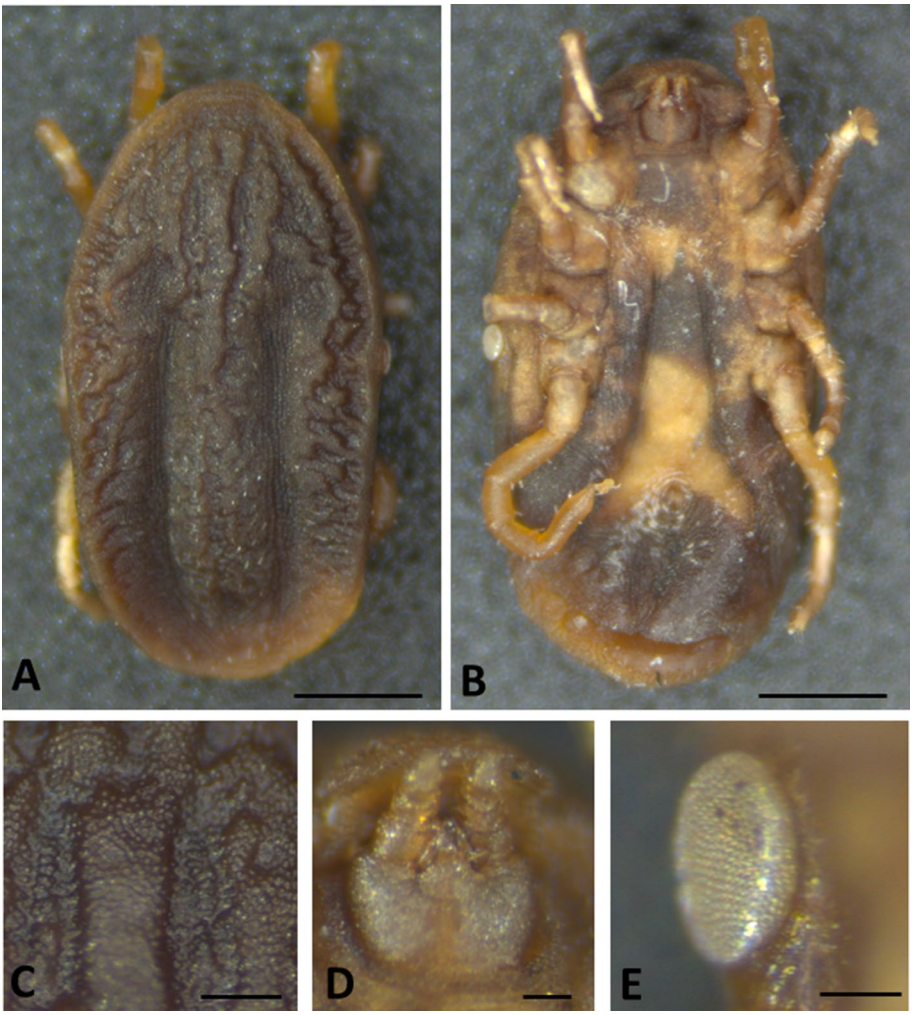

Fig. 4 *Ornithodoros marinkellei* nymph. **a** Dorsal view, bar: 0.5 mm. **b** Ventral view, bar: 0.5 mm. **c** Detail of the dorsal mammillae at the anterior half of the idiosoma, bar: 0.1 mm. **d** Gnatosoma, bar: 0.05 mm. **e** Spiracular plate, bar: 0.05 mm

Ventral

Entire idiosoma micromammillated, without elevations in integument. Distinct median and transverse postanal grooves; coxal folds extending from coxa I to posterior-lateral end, where they diverge; transverse preanal groove straight. Anus broadly circular (length 0.098, width 0.068). Anterior end of idiosoma with flap-like projected extension of dorsal idiosoma protecting gnathosoma anteriorly; capitulum in well-developed camerostome; cheeks indistinct.

Capitulum

Short, not visible dorsally, length 0.245, width 2221; basis capituli rectangular with rounded angles. Hypostome almost indistinct (vestigial), reduced to a triangular pit (length 0.036) devoid of denticles, not reaching beyond the level of palpal article 2. Palpi length 0.120, rounded laterally. Length of palpal article 1: 0.039, article 2: 0.027; article 3: 0.020; article 4: 0.034.

Legs

With micromamillated surface, especially on anterior segments; sparsely setose. All coxae contiguous, decreasing in size from I to IV, without spurs. Coxa I 0.307 long, 0.246 broad; coxa II 0.297 long, 0.245 broad; coxa III 0.225 long, 0.218 broad; coxa IV 0.224 long, 0.216 broad. Tarsi with claws and pulvilli, lacking dorsal humps. Tarsus I 0.397 long, 0.081 broad; tarsus IV 0.335 long, 0.087 broad.

Description based on 1 nymph collected on the wall of a cave in the Rincón García, Villanueva Municipality, Chinandega Department, Nicaragua, 31 May 2012 (CNC-3703).

Discussion

In this study, adults of *O. marinkellei* were collected from hot caves inhabited by *Pteronotus* bats in Colombia and Nicaragua, similarly to the caves where this tick species was previously collected in Brazil (Labruna et al. 2011; Henrique-Simões et al. 2012). Hot caves are characterized by temperatures between 28 and 40 °C, and RH > 90%, conditions generated by the large populations of bats (e.g. *Pteronotus* spp.) that colonize internal chambers of the caves (de la Cruz 1992). It seems that the presence of *O. marinkellei* is strictly associated to hot caves, where the tick will find suitable hosts such as *Pteronotus* bats. This assumption is corroborated by the fact that all host records of *O. marinkellei* larvae have been on *Pteronotus* bats (Kohls et al. 1969; Jones et al. 1972; Labruna et al. 2011; Luz et al. 2016). Such hot caves are also the preferable habitat for ticks of the genus *Antricola* (de la Cruz 1992). In fact, large numbers of *Antricola* were found sympatrically with *O. marinkellei* in the Brazilian hot cave reported by Labruna et al. (2011), and also in the caves of Colombia and Nicaragua sampled in the present study (data not shown).

Labruna et al. (2011) claimed that the larval stage of *O. marinkellei* from Brazil was generally larger than the type specimens from Colombia reported by Kohls et al. (1969). Herein, we collected new larval specimens from the type locality in Colombia, and from a new locality in Nicaragua. Our PCA analysis of larval morphometric variables corroborates the results of Labruna et al. (2011), showing that the larval specimens from Brazil are larger than those from Colombia and Nicaragua; larvae from the two later countries had similar morphometric values (Fig. 2). These results were corroborated by the morphometric analysis of adult ticks, which also showed that ticks from Colombia and Nicaragua had similar metrics, and at the same size, smaller than the morphometric values of the Brazilian adult specimens (Table 1). In order to expand this investigation, we performed a phylogenetic analysis of these ticks, which corroborated the morphometric results; i.e., ticks from Colombia and Nicaragua were more genetically related than any of them with ticks from Brazil (Fig. 3). Besides the difference in size, no other morphological difference was

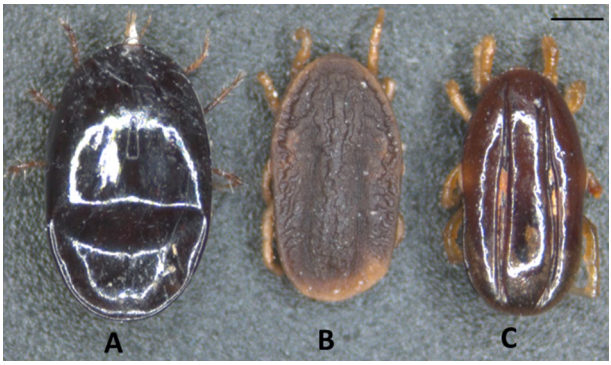

Fig. 5 Dorsal view of *Ornithodoros marinkellei* engorged larva (**a**), nymph (**b**), and an adult male (**c**) from Nicaragua. Bar: 0.5 mm

found between *O. marinkellei* ticks from Brazil and from Colombia/Nicaragua. In addition, the overall 16S rRNA genetic divergence of *O. marinkellei* ticks between Brazil and Colombia/Nicaragua (5%) is only slightly higher than the 3.5% differences reported for two geographically related populations of *Ornithodoros rietcorreai* Labruna et al. ticks that were reproductively compatible (Labruna et al. 2016). The above arguments led us to adopt a conservative assumption at this moment, in which the ticks identified as *O. marinkellei* from Colombia, Nicaragua, and Brazil represent the same taxon, and that the genetic and morphological differences between them are likely to have a geographical bias. Indeed, additional data from additional geographically distinct populations of *O. marinkellei* are required to confirm this assumption.

Labruna et al. (2011) reported an adult of *O. marinkellei* attached superficially to a human skin. Herein, we confirmed that *O. marinkellei* adults can effectively feed on humans, as demonstrated by 4 ticks that became engorged after feeding for 10-20 min on a human. While these observations highlight the vector potential of *O. marinkellei* to tick-borne zoonotic pathogens, this condition is likely to be limited to those persons entering hot caves, the typical habitat of *O. marinkellei.* At the same time, our morphological analysis of the *O. marinkellei* nymph showed a vestigial hypostome, probably incompatible with blood feeding, similarly to the hypostome morphology of the non-feeding adult stage of the argasid tick *Otobius megnini* (Dugès) (Lindquist et al. 2016). The fact that the size of a full engorged larvae, a nymph, and an adult of *O. marinkellei* are generally very similar (Fig. 5), coupled with the above statements, support the hypothesis that *O. marinkellei* has a single nymphal stage that does not feed or engorge on a host. Interestingly, a single, non-feeding nymphal stage was recently demonstrated for the life cycle of another neotropical argasid species, *Ornithodoros peropteryx* Kohls, Clifford and Jones (Venzal et al. 2013).

The present study extends the distribution of *O. marinkellei* to Nicaragua. In addition, the CNC tick collection contains an unpublished lot of an *O. marinkellei* larva that was collected on *Pteronotus parnelli* Gray from Kaw Mountain, French Guiana, at 3 June 2013 (CNC-3705). Therefore, the current distribution of *O. marinkellei* includes Nicaragua, Panama, Colombia, Venezuela, Guyana, French Guiana, and northern Brazil. These areas are within the geographical distribution of *Pteronotus* bats (Emmons and Feer 1997), which so far is the only bat genus that has been recorded as hosts of *O. marinkellei*. Although hot caves inhabited by *Pteronotus* bats have a wide range of temperature (28–40 °C) (de la Cruz 1992; Nava et al. 2010), the cave chambers where *O. marinkellei* adult ticks have been collected are at the upper limit of this temperature range, namely > 35 °C (Labruna et al. 2011, present study). This abiotic condition could be a limiting factor for the occurrence of this tick species.

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