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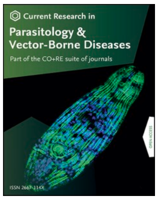

Bats from an area of the Colombian Caribbean reveal the circulation of *Alphacoronavirus*

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ABSTRACT

The evolutionary origin of coronaviruses is related to bats (order Chiroptera), and their association with pathologies in animals and humans is expected. Anthropic threats reduce bat diversity and expose humans to extraordinary transmission and spread of associated viruses, putting health and food security at risk owing to the multiple ecological roles that bats play. This study aimed to determine the presence of coronaviruses in bats in the Department of Córdoba, Colombia. Between 2022 and 2023, 11 municipalities were selected using non-probabilistic sampling methods. A total of 262 bats belonging to 16 species of five families were captured and identified. Serological tests were performed to detect SARS-CoV-2, and nested polymerase chain reaction (PCR) was performed to detect the coronavirus RdRp gene. RdRp-positive samples were sequenced using Sanger sequencing. Five specimens (2.7%) had antibodies against the coronavirus N protein, and the RdRp gene was detected in 55 specimens (21.0%), all belonging to the family Phyllostomidae. Phylogenetic analysis of the RdRp gene revealed that the newly generated sequences represented alphacoronaviruses. Bats tested in ecoregions with greater anthropogenic intervention were shown to be carriers of coronaviruses, unlike bats from conserved ecoregions. Coronavirus surveillance in bats has revealed previous infections through serology and circulating infections in natural populations of different ecoregions of the Department of Córdoba, where inter-species jumps could be generated by contact between bats and domestic/wild animals, or humans.

1. Introduction

Bats are a successful group of mammals and are probably the most diverse, with more than 1400 species of bats worldwide and 222 species recorded in Colombia, making it the country with the highest diversity in South America (Ramírez-Chaves et al., 2024). According to the One Health approach, bats are reservoirs of many zoonotic viruses that can jump species barriers and infect humans and other domestic or wild mammals, including lyssaviruses, henipaviruses, filoviruses, paramyxoviruses, and coronaviruses (Plowright et al., 2016).

Coronaviruses are enveloped viruses with single-stranded positive-sense RNA sequences of 26–32 kb. *Coronaviridae* is divided into four genera: *Alphacoronavirus* and *Betacoronavirus*, infecting mammals, and *Gammacoronavirus* and *Deltacoronavirus*, infecting mainly birds (Banerjee et al., 2019). Among alphacoronaviruses, the most notable are the porcine transmissible gastroenteritis virus (TGEV), feline infectious peritonitis virus (FIPV), porcine epidemic diarrhea virus (PEDV), and human coronaviruses (HCoV) 229E and NL63 (Colina et al., 2021). Betacoronaviruses cause emerging infectious diseases, such as severe acute respiratory syndrome (SARS) in 2003, Middle East respiratory syndrome in 2013, and COVID-19 in 2019 (Wong et al., 2019; Artika et al., 2020).

Coronavirus surveillance in bats has a great impact, not only because of the precedents of jumps between species but also because of the high mutation rates. Therefore, the World Health Organization and the World Organization for Animal Health called for the characterization of

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circulating coronaviruses with zoonotic potential to prevent epidemic events with high public health, social, and economic costs (Ruiz-Aravena et al., 2022; Horefti, 2023; WHO, 2024).

Research on the diversity of coronaviruses in Neotropical bats is scarce. Reports indicate that alphacoronaviruses are the most common worldwide and have been detected in 43 species of bats (Hernández-Aguilar et al., 2021). However, despite the richness of reported species, there are no reports of coronaviruses associated with bats in Colombia. In Córdoba, 61 species of the order Chiroptera are present in an ecosystem that is fragmented by disordered agricultural growth (Chacón et al., 2022). Ecosystem fragmentation increases the probability of interspecies jumps in the viruses associated with this group of flying mammals (Ruiz-Aravena et al., 2022).

The objective of this study was to evaluate the presence of coronaviruses in bats in the Department of Córdoba, Colombia.

2. Materials and methods

2.1. Study type, location and sample size

A prospective descriptive study was conducted between August 2022 and March 2023 using non-probabilistic convenience sampling in the Department of Córdoba, Caribbean area, north-west Colombia (9°25′–07°15′N and 75°26′–75°10′W). The area is classified as a tropical dry forest with an average annual temperature of 28 °C and an average annual rainfall of 1200 mm (Racero-Casarrubia et al., 2015). The 415 km-long Sinú River crosses the department and defines four major ecoregions, i.e. Upper, Middle and Lower Sinú, and Sabanas, bordered by the San Jorge River and the Caribbean coast. The sampling included 11 municipalities, covering all ecosystems of the department.

2.2. Bat capture and identification

Bats were captured using five mist nets (6 × 2 m) placed strategically in the forest, with surveillance every 15 min between 18:00 and 24:00 h for 540 h/net. Animals were handled according to biosecurity standards and taxonomically identified using taxonomic keys (Díaz et al., 2021). Biological data of interest were collected (sex, weight, age, reproductive status, and morphometric measurements). Blood samples and organs were collected in sterile cryovials and preserved in liquid nitrogen until they were transferred to the Instituto de Investigaciones Biológicas del Trópico of the Universidad de Córdoba, where they were stored at −80 °C until processing.

2.3. Seroprevalence of antibodies against coronaviruses in bats

The commercial ELISA kit ID Screen® SARS-CoV-2 Double Antigen Multi-species ELISA (Innovative Diagnostics, Grabels, France) was used to detect total antibodies directed against the nucleocapsid (N) of SARS-CoV-2. ODs were measured using a CLARIOstarTM reader (BMG Labtech, Ortenberg, Germany). OD values $\geq$ 0.350 were considered positive according to the manufacturer's instructions.

2.4. RNA extraction and molecular detection of coronaviruses

RNA was extracted from the intestines and lungs using a GeneJET RNA Purification Kit (Thermo Fisher Scientific, Waltham, MA, USA). RNA concentration was determined by spectrophotometry using a NanoDrop spectrophotometer (ND-2000/2000c; Thermo Fisher Scientific). cDNA was synthesized using Maxima H Minus cDNA Synthesis Master Mix (Thermo Fisher Scientific). The RdRp gene of the family Coronaviridae was detected using nested PCR, as described by Chu et al. (2011), which amplifies a 400-bp fragment. The primers for the first round were as follows: forward (5′-GGK TGG GAY TAY CCK AAR TG-3′); reverse: (5′-TGY TGT SWR CAR AAY TCR TG-3′). The primers used for the second round were as follows: forward (5′-GGT TGG GAC TAT CCT AAG TGT GA-3′); reverse (5′-CCA TCA TCA GAT AGA ATC ATC AT-3′). Amplicons were visualized by electrophoresis on a 1.5 % agarose gel.

2.5. Amplicon sequencing and phylogenetic analysis

Positive samples were processed using the Big Dye® reaction, with the primers of the second PCR round. Subsequently, automatic sequencing was performed using an ABI PRISM®-3500 (Applied Biosystems, Waltham, MA, USA). The generated sequencing files were analyzed using Geneious Prime® software (version 7.04, Biomatters, Boston, USA), and consensus sequences were compared using BLASTn. For the phylogenetic analysis, reference sequences for the four genera of the family *Coronaviridae* were retrieved from GenBank. Sequences were aligned using MAFFT® (Rozewicki et al., 2019), and a maximum likelihood tree was created using IQ-Tree2® (Minh et al., 2020) with 1000 bootstrap replicates. The resulting trees were visualized using FigTree software (http://tree.bio.ed.ac.uk/software/figtree/) and edited using ITol (https://itol.embl.de).

2.6. Statistical analysis

Comparative analyses of age and sex between coronavirus-positive and -negative bats were performed using the chi-square test. The normality of the data was analyzed for the two groups of bats grouped by size using the Shapiro-Wilk test. Young individuals were excluded from these analyses to avoid bias. Then, Student's t-test for independent samples was performed to compare the body condition (assessed based on the weight-to-forearm length ratio for each bat) between coronavirus-positive and -negative bats (grouping variable) (Jakob et al., 1996).

3. Results

A total of 262 bats belonging to 16 species of five families (Phyllostomidae, Noctilionidae, Emballonuridae, Molossidae, and Vespertilionidae) were captured. The family Phyllostomidae was the most prevalent, with 245 (93.5%) specimens, followed by the Noctilionidae, with 7 specimens. The species with the highest prevalence in all areas studied was the frugivore *Artibeus jamaicensis*, with 135 (51.5%) specimens, followed by 36 (13.74%) nectarivorous *Glossophaga soricina* and 28 (10.68%) omnivorous *Phyllostomus discolor.* The coronavirus-positive bat species found in each ecoregion are shown in Fig. 1.

3.1. Seroprevalence of total antibodies against coronaviruses

Antibodies against the SARS-CoV-2 N protein were detected in 5 of the 187 bats (2.7%). These were four *A. jamaicensis* from Cereté, Planeta Rica, and Moñitos, and one *Glossophaga soricina* from the municipality of Chimá. None of the specimens with positive serology presented molecular evidence of coronavirus infection.

3.2. Molecular detection of coronaviruses

A total of 21% (55/262) of bats were positive for the RdRp gene of coronaviruses. The gene was detected in the intestines of 36 bats and the lungs of 24 bats; in five positive specimens, the RdRp gene was detected in both the lungs and intestines. Coronaviruses was detected in bats in all municipalities except for Tierralta. The geographical distribution of bats carrying RdRp is illustrated in Fig. 1.

Eight of the 16 species studied presented evidence of RdRp belonging to the family *Coronaviridae*. All animals positive for coronavirus belonged to the family Phyllostomidae: *A. jamaicensis*, *A. lituratus*, *Carollia perspicillata*, *Desmodus rotundus*, *P. discolor*, *P. hastatus*, *Sturnira* sp. and *Uroderma bilobatum*. *Artibeus jamaicensis* was the most frequent host in the studied municipalities (Table 1).

There were no significant differences for the variables age (Chi-

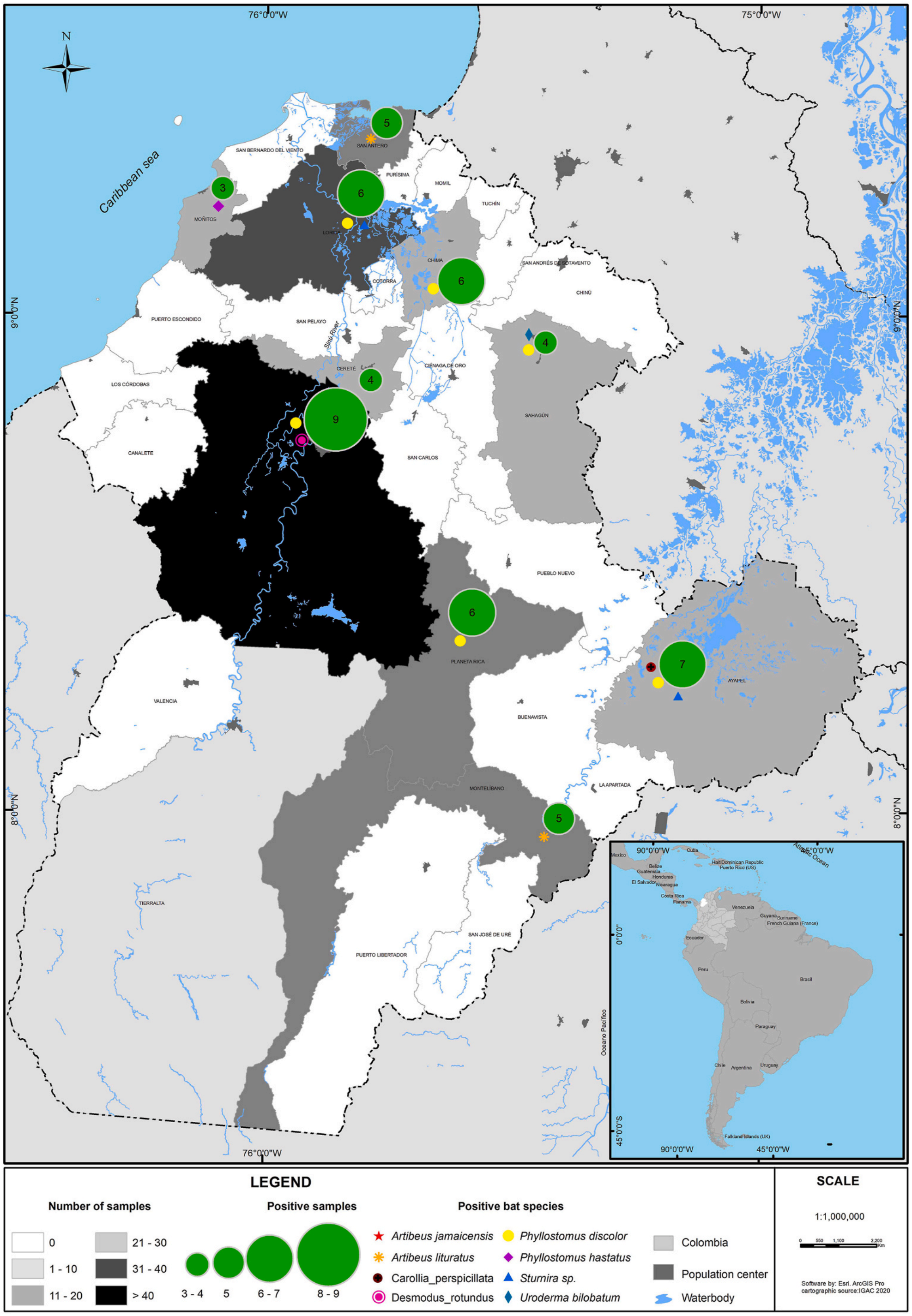

Fig. 1. Distribution of bats with the coronavirus RdRp gene detected in the Department of Córdoba, Colombia.

square test, $\chi^2 = 0.784$, $df = 1$, $P = 0.3761$) and sex (Chi-square test, $\chi^2 = 3.156$, $df = 1$, $P = 0.076$) with respect to the detection of coronavirus in the bat host. The body condition of adult bats positive for coronavirus was somewhat lower than that of bats negative for coronavirus. However, the Student's t-test used to compare the body condition of coronavirus-positive and -negative bats showed no significant differences in both large ($t = 1.0733$, $df = 156$, $P = 0.285$) and small ($t = 1.24$, $df = 80$, $P = 0.218$) bats.

3.3. Phylogenetic analysis

Of the 55 positive samples, 7 were sequenced based on their amplicon quality. Sequences of the RdRp gene, with an approximate length of 395 bp, were obtained and deposited in the GenBank database under the accession numbers OR250033-OR250038 and OR253787. Accession numbers correspond to *A. jamaicensis* ($n = 2$), *P. discolor* ($n = 3$), *P. hastatus* ($n = 1$), and *U. bilobatum* ($n = 1$).

A maximum likelihood phylogenetic tree was constructed using amino acid sequences corresponding to the RdRp gene of the novel coronavirus isolates and isolates of the *Coronaviridae* from bats, considered to be of importance in human and animal health, retrieved from GenBank. The analysis confirmed that the sequences generated in the present study belong to the genus *Alphacoronavirus* (Fig. 2). Five of the new RdRp sequences were grouped into the South American clade.

Table 1

Bat species in which natural coronavirus infection has been explored in the present study.

Bat species	Collection site	*n*/*N* (%)
Family Emballonuridae		
Saccopteryx leptura	Lo, Ce	0/2 (0)
Centronycteris centralis	Ms	0/1 (0)
Family Molossidae		
Molossus molossus	Ta, Lo	0/7 (0)
Family Vespertilionidae		
Myotis nigricans	Mo, Sh, Lo, Mtl	0/5 (0)
Family Noctilionidae		
Noctilio albiventris	Ch	0/1 (0)
Family Phyllostomidae		
Artibeus jamaicensis	Lo, Ce, Ms, Mo, Mtl, Sh, Sa, Ch, Ta, Pr, Ay	34/135 (25.1)
Artibeus lituratus	Mo, Mtl, Sa, Ms	2/8 (25.0)
Carollia perspicillata	Ay, Mo, Mtl, Ta, Sh	2/12 (16.6)
Centronycteris centralis	Ms	0/1 (0)
Dermanura phaeotis	Sh, Ms	0/2 (0)
Desmodus rotundus	Sa, Mo, Sh	1/4 (25.0)
Glossophaga soricina	Lo, Pr, Mo, Mtl, Sh, Ay, Ch	0/36 (0)
Phyllostomus discolor	Lo, Pr, Mo, Sa, Sh, Ay, Ch, Ta, Ce, Ms	12/28 (42.8)
Phyllostomus hastatus	Ms	1/1 (100)
Sturnira sp.	Ce, Mo, Lo, Ay	2/4 (50.0)
Uroderma bilobatum	Lo, Mtl, Sh, Mo, Ms	1/15 (6.6)
Total		55/262 (21.0)

Abbreviations: *n*, number of bats positive for coronavirus; *N*, number of bats examined. Collection sites: Lo, Lorica; Ce, Cereté; Ms, Moñitos; Mo, Montería; Mtl, Montelibano; Sh, Sahagún; Sa, San Antero; Ch, Chimá; Ta, Tierralat; Pr, Planeta Rica; Ay, Ayapel.

These sequences were related to those generated from bats in Argentina, Bolivia, Brazil, Costa Rica, Mexico, Panama, and Peru. In contrast, two sequences from *U. bilobatum* (238 Montería) and *A. jamaicensis* (208 Moñitos) were grouped in the clade of Old World alphacoronaviruses, which also contained sequences recorded from Argentine bats.

4. Discussion

To our knowledge, this is the first study on coronaviruses in bats in Colombia. Bats are non-human mammals with the highest number of genetic reports associated with coronaviruses worldwide. However, the diversity of registered hosts in South America is low, considering the number of bat species present on the continent (Ruiz-Aravena et al., 2022).

The coronavirus genes found in bats of the family Phyllostomidae in the present study coincide with reports of 88 species of this family that have been analyzed for coronaviruses in other countries, of which positive samples from 19 species (21%) have been reported (Ruiz-Aravena et al., 2022). Bats of the family Phyllostomidae occupy various trophic niches and adapt to anthropogenic disturbances (Galindo-Gónzalez, 2004). Similarly, previous studies have reported higher coronavirus detection rates in juvenile bats. However, in the present study, coronaviruses were detected in adult bats, indicating that these populations could play an essential role in maintaining virus circulation in the ecosystem for longer periods. On average, a bat's maximum recorded life expectancy is 3.5 times greater than that of a non-flying placental mammal of similar size. There are records of bats surviving for more than 30 years in the wild (Wilkinson and South, 2002).

Anthropic interventions in different regions of the Department of Córdoba have been described (MINCIT, 2024), with the Bajo Sinú region being notable because of its fishing activity and temporary crops. The Caribbean coast has a strong influence on the estuarine areas. San Jorge, Medio Sinú, and Sabanas are livestock and agricultural areas with high deforestation rates. Our study revealed that bat populations had the highest coronavirus prevalence in these ecosystems. On the contrary, no coronaviruses were detected in bats in the municipality of Tierralta, south of the Department of Córdoba, where native forests predominate. This finding positions bats as surveillance sentinels and reveals that ecological connections modulate the circulation of viruses and protect against an eventual inter-species jump, where bats not being stressed in conserved ecosystems such as Tierralta, could modulate the viral load and decrease pathogen excretion, as has been demonstrated for the Hendra virus (Eby et al., 2023).

Bats reported in this study used natural shelter sites such as caves, cracks, hollow logs, foliage, abandoned nests, and termite mounds. They can also use artificial shelters, such as sewers, houses, buildings, and bridges for resting, feeding, or breeding (Cortés-Delagado and Ferbans, 2014). Therefore, monitoring the circulation of coronaviruses in the ecosystem is essential, considering that shelters can be shared between different species, thereby facilitating virus spread (Gonzalez and Banerjee, 2022).

Artibeus jamaicensis is one of the largest bat species, which includes large fruits in its diet (Soriano and Ruiz, 2006; Calderón-Rangel et al., 2019; Calao-Ramos et al., 2021) and is distributed in all municipalities of the Department of Córdoba (Chacón et al., 2022). This species is the most common host of coronaviruses and can travel up to 10 km per night (Handley et al., 1991). It has been shown that viruses such as Marburg and Ebola can replicate in cell lines of this species when they reach flight-associated temperatures ranging between 37 °C and 41 °C (Miller et al., 2016).

The other species found with coronaviruses in the present study were *P. discolor* and *P. hastatus*, which are characterized by omnivorous diets and trophic plasticity with higher energy requirements (Chacón Pacheco et al., 2024). Both species are tolerant to environmental transformation and have been reported in fragmented environments (Galindo-Gónzalez, 2004; Aguilar-Garavito et al., 2014), expanding the possibilities of interaction with various ecosystem elements where they take refuge and search for food.

The presence of coronaviruses in *A. jamaicensis*, *A. lituratus*, *C. perspicillata*, *D. rotundus*, *P. discolor*, *P. hastatus*, *Sturnira* sp., and *U. bilobatum*, indicated that there was no association between coronaviruses and carrier bat species. Anthony et al. (2017) suggests that there is a significant correlation between the presence of coronaviruses and the taxonomic diversity of bats, highlighting their role as natural reservoirs in the evolution and dispersal of these viruses.

The search for antibodies demonstrating evidence of previous coronavirus infections revealed five seropositive bats, one *G. soricina* and four *A. jamaicensis*, the most abundant species. In another study, *A. jamaicensis* was used as an experimental animal model for MERS-CoV, and only one in ten bats produced neutralizing antibodies (Munster et al., 2016). The ability of coronaviruses to evade immune detection must have evolved in reservoir bats, benefiting the viruses without negatively affecting the bat populations (Matthews et al., 2014).

The presence of coronaviruses in different types of samples, such as in the intestines and lungs, shows cellular tropism towards these organs (Corman et al., 2015), which is associated with the fecal and oral elimination of aerosols from the respiratory tract. The fecal route is the most commonly reported route for these viruses (MacLachlan and Dubovi, 2017). Munster et al. (2016) reported that viral dissemination *via* the fecal route can occur for up to 12 days after infection. It is also possible to detect a high concentration of viral particles at the end of the digestive tract, allowing molecular techniques, such as PCR, to detect the virus in tissues. However, metagenomic sequencing is not helpful because it depends on the abundance of genetic material to obtain larger associated reads generated through overlapping DNA/RNA segments (Ko et al., 2022).

The partial RdRp sequences obtained by nested PCR showed differences, indicating that different alphacoronaviruses may be circulating in bat populations in the Department of Córdoba, given that even in the same sampling municipality and in different bat species, different

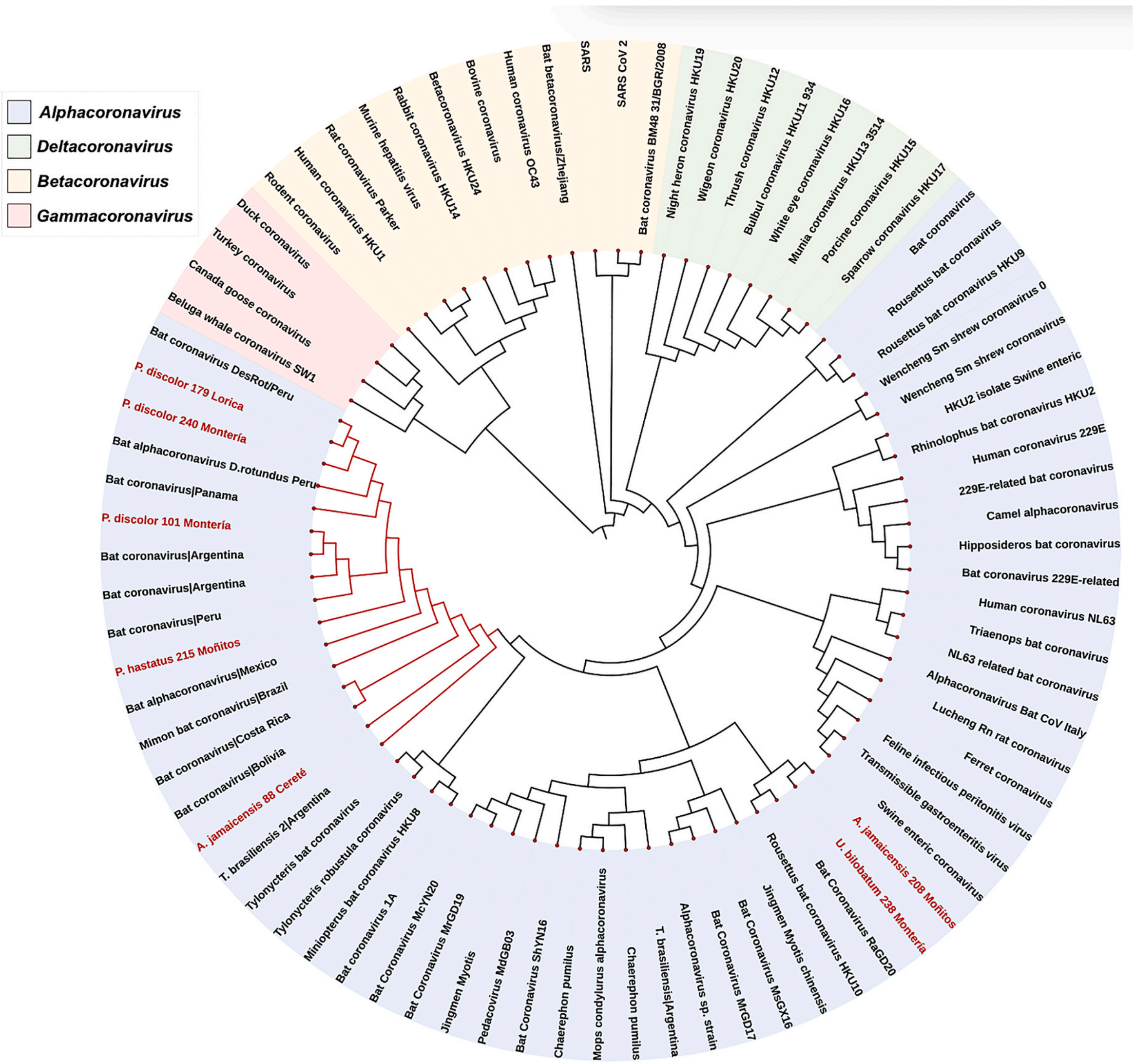

Fig. 2. Phylogenetic tree of the RdRp genomic region of coronaviruses from different genera and hosts. The alphacoronaviruses detected in this study and the branches of the American clade are indicated in red.

Alphacoronavirus sequences were recorded, as reported by Drexler et al. (2011). This suggests that coronavirus speciation may be more significant because of the presence of these viruses in hosts that have not been reported previously in nearby geographical locations. Additionally, high rates of genomic substitution and recombination allow coronaviruses to adapt rapidly to new hosts (Artika et al., 2020). Because the RdRp gene is a conserved region in the genome of coronaviruses and phylogeny shows structural and functional similarities across different strains, we are confident in their effectiveness in amplifying the RdRp gene region of coronaviruses (Góes et al., 2016; Lucero-Arteaga et al., 2023). Five coronavirus sequences were phylogenetically grouped in the genus *Alphacoronavirus* related to the South American clade (Bueno et al., 2022; Ruiz-Aravena et al., 2022).

Two of the RdRp sequences reported in this study were similar to those recorded for *Tadarida brasiliensis* (Molossidae) in Argentina (Cerri et al., 2023), located within the Old World *Alphacoronavirus* clade. This shows the circulation of *Alphacoronavirus* of different phylogenetic origins in South America and other host families such as Molossidae and Phyllostomidae (Anthony et al., 2017). This indicates that alphacoronaviruses in South American bats may have followed distinct evolutionary trajectories compared to those in other regions, influenced by geographical separation, niche specialization, and coevolution with specific hosts. These phylogenetic differences may provide insights into the virus evolutionary history, local adaptations, and factors influencing its ability to infect new species (Drexler et al., 2011; Hernández-Aguilar et al., 2021).

Our study has some limitations. First, serological surveillance revealed very few seropositive bats. Antibody responses in bats could be low due to various factors, such as weak infection or suppression of the innate immune response (Plowright et al., 2016). Therefore, the seroprevalence results should be interpreted with caution because the commercial kit detects coronavirus nucleocapsid proteins, which are relatively conserved; hence, significant antigenic cross-reactivity has been demonstrated in six human coronaviruses with N-protein residues (Oliveira et al., 2020; Dileepan et al., 2021; Lineburg et al., 2021). Another limitation of this study is the low sequencing output, which may be related to inadequate RNA concentration, resulting in weak signal strengths.

5. Conclusion

The search for coronaviruses in bat populations in the Department of Córdoba, Colombia, revealed the circulation of alphacoronaviruses in different ecoregions of the country. In these ecosystems, bats can interact with domestic animals and humans; therefore, the molecular characterization obtained is essential, as it is similar to the alphacoronaviruses circulating in South America.

CRediT authorship contribution statement

Caty Martínez: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **Daniel Echeverri:** Methodology, Investigation, Writing – review & editing. **Alfonso Calderón:** Conceptualization, Resources, Funding acquisition, Writing – review & editing. **Eliana Hurtado:** Methodology, Investigation, Validation, Writing – review & editing. **Bertha Gastelbondo:** Funding acquisition, Investigation, Writing – review & editing. **Yésica López:** Investigation, Methodology, Writing – review & editing. **Jairo Martínez:** Investigation, Conceptualization, Writing – review & editing. **Yeimy López:** Methodology, Conceptualization, Writing – review & editing. **Yesica Botero:** Investigation, Conceptualization, Writing – review & editing. **Camilo Guzmán:** Conceptualization, Investigation, Writing – review & editing. **Ketty Galeano:** Investigation, Methodology, Writing – review & editing. **Valeria Bertel:** Investigation, Methodology, Writing – review & editing. **Yonairo Herrera:** Investigation, Methodology, Writing – review & editing. **Germán Arrieta:** Resources, Methodology, Writing – review & editing. **Joao Pessoa Araujo:** Resources, Methodology, Writing – review & editing. **Salim Mattar:** Writing – review & editing, Supervision, Funding acquisition.

Ethical approval

The animals were captured under the permit for the capture and handling of fauna for non-commercial purposes, resolution 00914 of August 4, 2017, of the Autoridad Nacional de Licencias Ambientales (ANLA) and the authorization of the Ethics Committee of the Faculty of Veterinary Medicine and Zootechnics of the Universidad de Córdoba, Colombia (Act 003-06-12-2019). The pharmacological euthanasia was performed using an overdose of sodium pentobarbital (200 mg) at a dose of 0.05 mg/g body weight (Guzmán et al., 2019). The study received ethical approval from the Ethics Committee of the Faculty of Veterinary Medicine and Zootechnics of the Universidad de Córdoba, Colombia (Act 003–12.6.2019).

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this study.

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Data availability

All data generated or analyzed during this study are included in this published article. The newly generated sequences were submitted to the GenBank database under the accession numbers OR250033-OR250038 and OR253787.

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