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Novel Insights Into the Life History, Taxonomy, Host Use, and Biogeography of the Rare Ant Social Parasite *Acromyrmex argentinus* (Gallardo) comb. nov.

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ABSTRACT

Ant inquiline social parasites are brood parasites of free-living ant species that exploit the social colony services of their hosts for survival and reproduction. To trace the convergent evolutionary origins of inquiline social parasitism in ants, it is important to decipher the parasites' life histories. Here, we report novel observations on the rare inquiline social parasite *Pseudoatta argentina* Gallardo. In addition, we inferred a mitochondrial phylogeny for 15 leaf-cutting ant species. The phylogeny demonstrates that *P. argentina* is deeply nested inside the genus *Acromyrmex* rendering the genus *Acromyrmex* paraphyletic. On the basis of morphological and phylogenetic evidence, we synonymize the genus *Pseudoatta* under the name *Acromyrmex*. Our field study confirms that *Acromyrmex argentinus* (Gallardo) **comb. nov**. is an obligate, workerless inquiline social parasite of *Acromyrmex* leaf-cutting ants. We show that *A. argentinus* is likely monogynous, host-queen-intolerant, and reproduces semelparously. Winged males of *A. argentinus* are gynaecomorphic, that is, queen-like, and male and female offspring mate with their siblings. Mitochondrial DNA barcodes reveal that *A. argentinus* is highly inbred across its distribution, which was either caused by a genetic bottleneck during speciation or resulted from sib-mating. *Acromyrmex argentinus* is a generalist parasite exploiting at least four free-living *Acromyrmex* species including *A. ambiguus*, *A. crassispinus*, *A. heyeri*, and *A. lundii*. Furthermore, *A. argentinus* is distributed throughout northern-central Argentina, southern Brazil, and Uruguay, which constitutes the largest known geographic distribution range of any inquiline social parasite in the southern hemisphere. We suggest that repeated host shifts may have facilitated the geographic range expansion of the social parasite. Although widely distributed, *A. argentinus* is locally rare infecting ~1% of the colonies in a host population. In summary, our study suggests that the morphological, behavioral, and life history characters associated with the inquiline syndrome evolved convergently in a mosaic fashion across the fungus-growing ants.

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1 | Introduction

The complex societies of eusocial insects evolved repeatedly and convergently in bees, wasps, ants, and termites (Wheeler 1910; Wilson 1971, 1975; Michener 2000). In contrast to their solitary relatives, eusocial insects enjoy significant ecological and sociobiological benefits (Hamilton 1964; Davies et al. 2012). At the same time, group living and eusocial behavior provide opportunities for conflict and exploitation because in the eyes of parasites, pathogens, and predators, the densely packed societies of eusocial insects constitute a high concentration of valuable resources and nutrients (Hölldobler and Wilson 1990; Schmid-Hempel 1998; Hölldobler and Kwapich 2022).

Ant colonies are exploited by a phylogenetically diverse array of invertebrates, which are generally not closely related to the ants, and even by vertebrates. These ant guests or myrmecophiles scavenge for food scraps inside the colonies, parasitize individual ants, or prey on their brood (Hölldobler and Wilson 1990; Schmid-Hempel 1998; Parker 2016; Elizalde et al. 2018; Parker and Kronauer 2021; Hölldobler and Kwapich 2022). The consumer-resource interactions between ant colonies and their diverse symbionts span the spectrum of species interactions from mutualism over commensalism to parasitism, herbivory, and predation (Heil and McKey 2003; Rico-Gray and Oliveira 2008; Gray et al. 2018; Hölldobler and Kwapich 2022).

In addition to myrmecophiles, ant social parasites exploit the colonies of their ant hosts. Ant social parasites evolved a brood parasitic life history and obligately depend on the eusocial environment provided by their hosts for colony founding, survival, and reproduction (Hölldobler and Wilson 1990; Buschinger 2009; Rabeling 2021). The approximately 400 currently known ant social parasite species evolved at least 91 times across the ant tree of life (Gray and Rabeling 2023), and despite their high phylogenetic diversity, only three main life history syndromes evolved among ant social parasites: temporary, dulotic, and inquiline social parasitism (Seifert 2018; Borowiec et al. 2021; Stoldt and Foitzik 2021; Rabeling 2021). The inquiline social parasites are morphologically and behaviorally highly specialized, integrating seamlessly into the societies of hosts and exhibiting traits of the so-called "inquiline syndrome," which include morphological reductions and adaptations, such as reduced body size, smooth and shiny cuticle, reduced mouthparts, inside nest mating, and queen-like males (Kutter 1968; Wilson 1971, 1984; Cover and Rabeling 2024). Although inquiline ants evolved a high degree of behavioral specialization, they originated repeatedly and convergently in distantly related genera (Gray and Rabeling 2023). Despite their phylogenetic diversity, individual ant social parasite species are often rare and occur sporadically at low frequency in their host populations (Wilson 1963).

Globally, ant social parasites are distributed along an inverse latitudinal diversity gradient and are most diverse in the northern temperate regions (Gray and Rabeling 2023). However, in the Neotropical region, colonies of fungus-growing ants are exploited by a diverse group of inquiline social parasite species (Gallardo 1916; Schultz et al. 1998; De Souza et al. 2007; Rabeling and Bacci 2010; Rabeling et al. 2015, 2019). The fungus-growing ants consist of currently 247 extant described species, which evolved their obligate relationship with basidiomycete fungi some 66 million years ago (Mueller et al. 2005, 2017; Schultz et al. 2024). Among the fungus-growing ants, the leaf-cutting ants currently comprise a clade consisting of the three genera *Acromyrmex* Mayr, *Amoimyrmex* Cristiano et al., and *Atta* Fabricius (Branstetter et al. 2017; Cristiano et al. 2020; Barrera et al. 2022), which are unique because they use fresh leaves to grow their fungal cultivars (Wirth et al. 2013; Della Lucia 2011; Fernández et al. 2015).

The inquiline social parasite species of fungus-growing ants originated at least thrice convergently across the clade (Sumner et al. 2004; Schultz and Brady 2008; Rabeling, Schultz, et al. 2014; Rabeling et al. 2018; Schrader et al. 2021; Mera-Rodríguez et al. 2025), representing a series of natural experiments that are well-suited for studying the evolution of parasitic life history traits. *Mycocepurus castrator* Rabeling & Bacci is the sole social parasitic fungus-growing ant species outside the leaf-cutting ants, and *M. castrator* speciated directly from its host *Mycocepurus goeldii* (Forel) (Rabeling and Bacci 2010; Rabeling, Schultz, et al. 2014). The leaf-cutting ant genus *Acromyrmex* harbors a total of five inquiline social parasite species. Three of them, *Acromyrmex ameliae* De Souza et al., *Acromyrmex charruanus* Rabeling et al., and *Acromyrmex insinuator* Schultz et al., morphologically resemble their hosts, and both *A. ameliae* and *A. insinuator* still produce workers (Schultz et al. 1998; De Souza et al. 2007; Rabeling et al. 2015). In contrast, *Acromyrmex fowleri* Rabeling et al. and *Pseudoatta argentina* Gallardo are workerless and exhibit the marked behavioral and morphological modifications of the inquiline syndrome (Gallardo 1916, 1929; Bruch 1928; Delabie et al. 1993; Marsaro et al. 2017; Rabeling et al. 2019). Previous phylogenetic analyses inferred at least two independent evolutionary origins of inquilinism in the leaf-cutting ants, with *A. insinuator* being closely related to its host *A. octospinosus* (Reich), and both *A. charruanus* and *P. argentina* forming a clade that is closely related to two of their host species, *Acromyrmex heyeri* (Forel) and *Acromyrmex lundii* (Guérin-Méneville) (Sumner et al. 2004; Schultz and Brady 2008; Rabeling et al. 2018; Schrader et al. 2021; Mera-Rodríguez et al. 2025). Currently, the origins and evolution of *Acromyrmex* social parasites as well as behavioral and ecological traits associated with the transition from a cooperative to a social parasitic lifestyle are not well understood.

To reveal the ecological and sociobiological factors contributing to the independent evolutionary origins of social parasitism in ants, it is important to study the complex life histories of social parasites. In this study, we report novel observations on the rare inquiline social parasite *Pseudoatta argentina* from southern South America (Figures 1–5, Table 1). *Pseudoatta argentina* was described in 1916 and was the first inquiline social parasite species discovered in fungus-growing ants (Gallardo 1916), and the myrmecologists Angel Gallardo and Carlos Bruch made important natural history observations about the species' biology and

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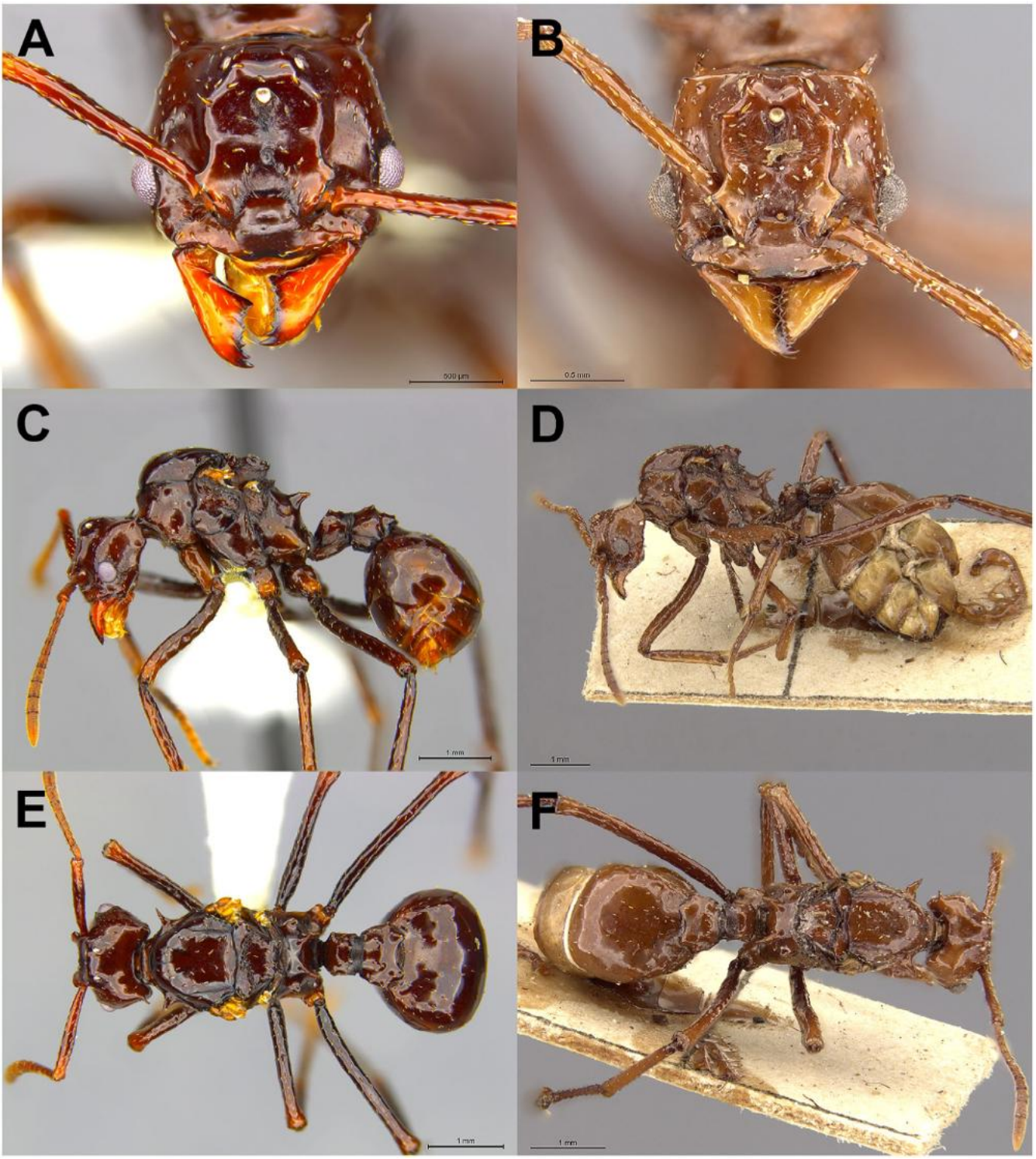


FIGURE 1 | Gynes of the inquiline social parasite *Acromyrmex argentinus* from Cerro Colorado in Uruguay (A, C, E) and the lectotype from Misiones in Argentina (B, D, F) in full-face (A, B), lateral (C, D), and dorsal (E, F) views. The scale bars represent 0.5 mm in figures (A, B), and 1 mm in figures (C–F).

life history (Gallardo 1916, 1929; Bruch 1928). After its discovery, *Pseudoatta argentina* remained uncollected and unstudied for almost a century. Between 2004 and 2017, we collected and observed *P. argentina* at multiple locations in Argentina, Brazil, and Uruguay. Our observations (i) answer unresolved questions about the parasite's life history and behavior, (ii) add new information about its host use, (iii) expand the known geographic distribution range, (iv) resolve the taxonomic classification, and (v) provide new ecological and sociobiological context for interpreting the evolution of social parasitism in leaf-cutting ants.

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2 | Materials and Methods

2.1 | Material Examined

Specimens from the following collections were examined and voucher specimens were deposited at these institutions.

CPDC	Laboratório de Mirmecologia at the Cocoa Research Center at CEPLAC, Itabuna, Bahia, Brazil
CRC	C. Rabeling Collection, University of Hohenheim, Stuttgart, Germany
DZUP	Coleção Entomológica Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brasil
IMLA	Instituto Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina
MACN	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina
MBC	Martin Bollazzi Collection, Universidad de la República, Montevideo, Uruguay
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MLP	Museo La Plata, Collection Entomología, La Plata, Argentina
NHMB	Naturhistorisches Museum Basel, Switzerland
MHNG	Muséum d'histoire naturelle de Genève, Switzerland

2.2 | Morphological Analysis

Specimens were examined using a Leica M205 C stereomicroscope. To generate composite images of the specimens we utilized a Leica DFC450 digital camera mounted on a Leica M205 C stereomicroscope. Composite images were assembled using the Leica Application Suite (Version 4.5) and the Helicon Focus (Version 6.2.2) software packages. Conventions for morphological terminology follow those utilized in recent taxonomic studies of socially parasitic fungus-growing ants (Rabeling et al. 2019).

2.3 | DNA Sequencing

To assess the genetic variability between *Pseudoatta argentina* populations, we sequenced the DNA barcoding region of the mitochondrial gene *cytochrome c oxidase subunit I* (COI) for recently collected individuals and compared the DNA sequence to that of a historical, museum-preserved specimen. Field-collected specimens were preserved in 100% ethanol. Before DNA extraction, individuals were removed from the ethanol, dried at room temperature, and then transferred to a 1.5 mL Eppendorf tube. We were granted permission to extract DNA from a single specimen of Carlos Bruch's *P. argentina* series, which he collected in La Plata, Argentina on April 27, 1924 (see Bruch 1928). The DNA extraction for this specimen was conducted in a separate laboratory, which had not been in contact with ant specimens or their DNA. For all specimens, DNA was extracted non-destructively using a Qiagen QIAamp DNA Micro Kit following the manufacturer's instructions for isolation of genomic DNA from tissues. DNA was re-suspended in 100 μL of ddH_2O. For recently collected specimens, the barcoding region of the mitochondrial gene COI was amplified using the primer pairs LCO1490 and HCO2198 (Folmer et al. 1994), resulting in a 658 bp fragment after trimming the primer sequences.

We did not succeed in amplifying the entire 658 bp COI barcoding fragment for Bruch's 1924 *P. argentina* sample (i.e., AC248), probably because the DNA was fragmented. Therefore, we designed eleven internal primers for the COI barcoding marker (Table 2), which yielded amplicons between 57 and 175 bp, depending on the primer pairings.

25 μL PCR reactions contained 1 μL of DNA extract, 12.5 μL Omega Taq polymerase Master Mix, 1 μL of forward and reverse primers at 10 μM concentration, and 9.5 μL of ddH_2O. COI fragments were amplified under the following conditions: initial denaturation at 94°C for 2 min; 34 cycles of denaturation at 94°C for 1 min, annealing at 45°C for 1 min, and extension at 70°C for 2 min; and a final extension at 70°C for 10 min. Four microliters of the PCR product were run on a 1.5% agarose gel and visualized with SYBR Safe DNA Gel Stain. The remaining 21 μL were purified utilizing the enzymatic ExoAp treatment (New England Biolabs: Ipswich, MA) and 1 μL of the purified PCR product was cycle-sequenced using the ABI BigDye Terminator Kit (version 3.1). Forward and reverse sequences were sequenced on an ABI 3730xl Genetic Analyzer.

2.4 | Phylogenetic Analysis

To test whether the recently collected *P. argentina* individuals from Brazil and Uruguay and the specimen collected by Bruch in La Plata in 1924 belong to the same clade and to unravel the phylogenetic relationships between *Pseudoatta* and free-living *Acromyrmex* species, we reconstructed a preliminary phylogeny based on the COI barcoding region including samples of *Pseudoatta argentina* as well as specimens from leaf-cutting ant species in the genera *Acromyrmex*, *Atta*, and *Amoimyrmex*.

Our DNA sequence alignment consisted of three samples of *Atta*, three samples of *Amoimyrmex*, 41 samples of *Acromyrmex*, and five samples of *P. argentina*. Hence, our phylogenetic inference included a total of 52 samples, of which 36 were newly sequenced for this study, and 16 were already available at NCBI Genbank (Tables S1 and S2). For the sequences already available at Genbank, ten were downloaded as COI sequences, two samples were extracted from off-target contigs of previously published Ultra Conserved Elements (UCE) data, and four were extracted using BLAST from published whole-genome assemblies. A detailed list of the samples sequenced in this study and additional samples used is provided in Tables S1 and S2.

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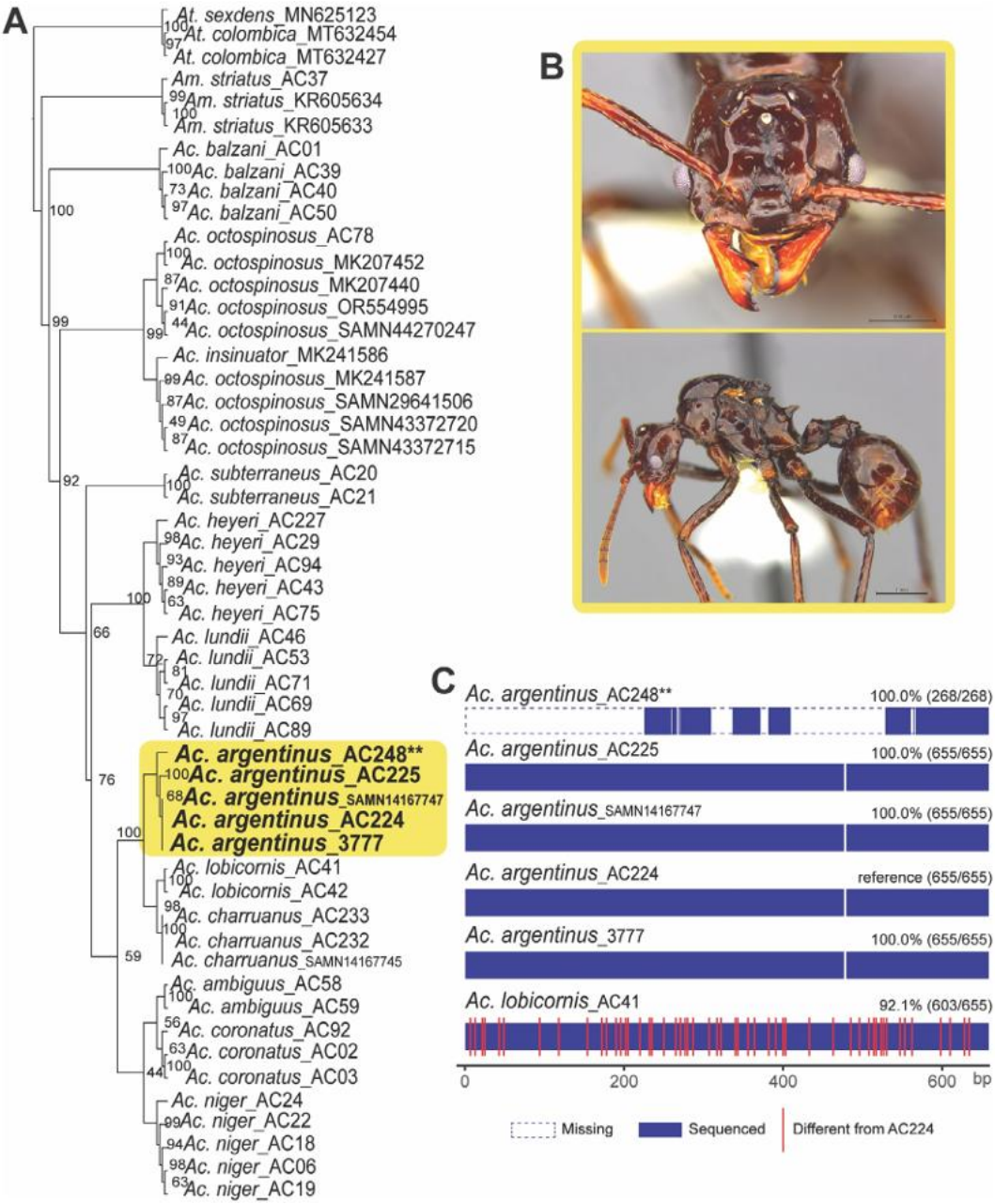


FIGURE 2 | Mitochondrial phylogeny of leaf-cutting ants and comparison of COI sequence similarity between *Acromyrmex argentinus* samples. (A) Maximum likelihood phylogeny inferred from COI barcoding sequences for 15 leaf-cutting ant species. Numbers at the nodes indicate ultrafast bootstrap support values (UFB). Samples of *A. argentinus* are highlighted in yellow. Tip labels correspond to species names and extraction/biosample/GenBank codes. "**" indicates sample AC248, one specimen from Bruch's historical nest series from which the two syntypes of "*P. argentina platensis*" were selected. Genera abbreviations: *At.* = *Atta*, *Am.* = *Amoimyrmex*, *Ac.* = *Acromyrmex*. (B) Gyne of *A. argentinus* collected in Cerro Colorado, Uruguay (col. code: CR130225-01) in frontal (top) and lateral (bottom) views. (C) Nucleotide-by-nucleotide comparison of the COI barcoding sequences for the five *A. argentinus* samples included in this study and the closely related species *A. lobicornis*. The *A. argentinus* sample AC224 from Cerro Colorado in Uruguay (CR130225-01) was utilized as the reference sequence.

We aligned all sequences for phylogenetic inference, excluding sample AC248 at first (see below), using MAFFT v7.525 (Katoh and Standley 2013). The initial alignment was trimmed to the COI barcode region by removing the primer sequences and three columns containing single-base insertions present in only one sequence, resulting in a final alignment of 658 positions. The alignment was checked for stop codons by translating the nucleotide sequence into amino acid triplets utilizing the invertebrate mitochondrial genetic code.

To build the consensus sequence for the Bruch 1924 sample AC248, we used eight sequenced fragments of 40 to 127 bp. We aligned the fragments using MAFFT employing the --addfragments, --adjustdirection, and --keeplength options

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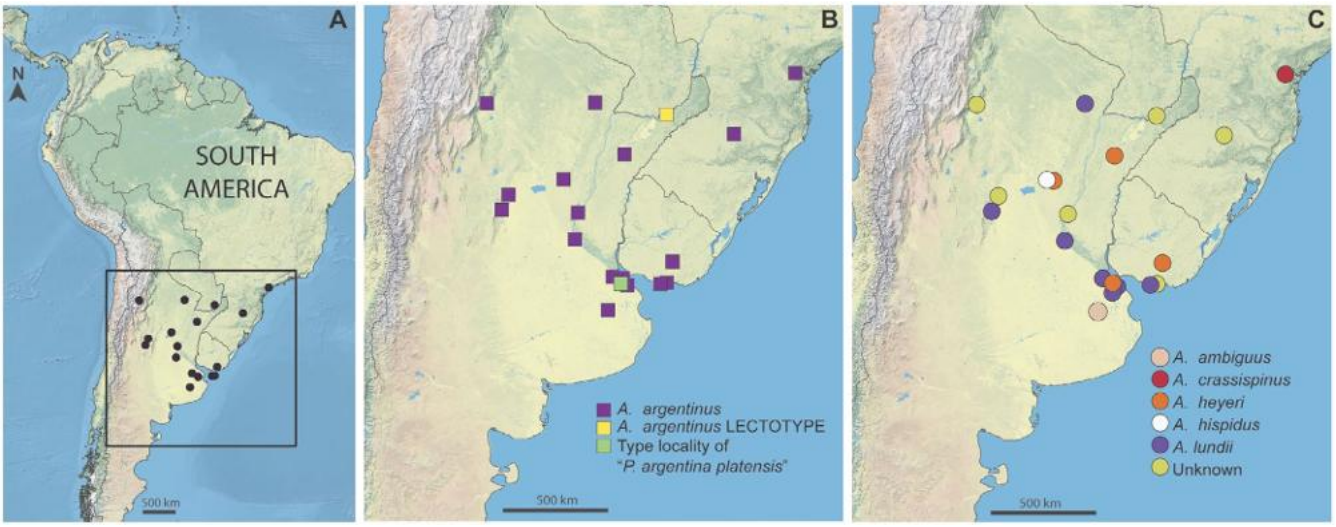


FIGURE 3 | Geographic distribution of the inquiline social parasite *Acromyrmex argentinus* (A, B) and its free-living *Acromyrmex* host species (A, C) in South America.



FIGURE 4 | Physogastric dealate queen of *Acromyrmex argentinus* that was collected in the nest of its host *A. crassispinus* in Curitiba, Brazil. Note the swollen metasoma. Due to the development of ovaries the white intersegmental membranes of the metasoma are exposed.



FIGURE 5 | Alate gyne and male of *Acromyrmex argentinus* copulating inside the *A. heyeri* host nest at Cerro Colorado, Uruguay.

(Katoh and Frith 2012). After examining the fragments, we built a consensus sequence for sample AC248. Positions where overlapping fragments agreed were called directly, conflicts were resolved by majority rule, positions where fragments disagreed without a majority were coded as ambiguous (N), and positions not covered by any amplicon data were coded as missing data. The resulting consensus sequence comprised 268 unambiguous bases, corresponding to 40.7% of the 658 bp COI barcode. Then, we added this consensus sequence to the final alignment for subsequent phylogenetic analysis. Finally, we performed our phylogenetic inference in IQ-TREE v3.1.4 (Wong et al. 2026). The best-fit model of sequence evolution was TIM2 + F + I + R3, which was selected using ModelFinder (Kalyaanamoorthy et al. 2017). Bootstrapping analyses used 1000 ultrafast bootstrap (UFB) replicates (Hoang et al. 2018) (Figure 2A).

To visualize the similarity of sample AC248 with recently collected *P. argentina* samples (Figure 2B), we compared each sequence position by position using sample AC224 from Uruguay as a reference. Only positions with unambiguous bases in both sequences were compared, and we calculated the percentage of similarity as the number of identical positions out of the total compared positions. We plotted the position comparison using ggplot2 (Wickham 2016) in R v4.6.0 (Figure 2C). Figures were edited in Adobe Illustrator.

3 | Results

3.1 | Phylogenetic Analysis

To infer the phylogenetic position of *Pseudoatta argentina* in the leaf-cutting ant tree of life, we estimated a mitochondrial phylogeny for 52 samples representing 15 species from the leaf-cutting ant genera *Acromyrmex*, *Amoimyrmex*, and *Atta*, as well as multiple samples of *Pseudoatta argentina* using COI barcoding sequences (Figure 2A). Our phylogenetic inference recovered the genus *Amoimyrmex* as the sister group to *Acromyrmex* and *Atta* as sister to both genera (Figure 2A, UFB = 100), which is consistent with previous studies (Branstetter et al. 2017; Cristiano

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TABLE 1 | Geographic distribution and host records of known *Acromyrmex argentinus* collections from South America.

Parasite	Host	Country	Province/state	Locality	Latitude	Longitude	Elevation asl. (m)	Collecting date	Collector	Specimen(s) examined	References
A. argentinus PARALECTOTYPE	*A. lundii*	Argentina	Buenos Aires	Bella Vista	−34.5621	−58.6909	25	February 1916	A. Gallardo's children	Yes	Gallardo (1916)
A. argentinus	*A. lundii*	Argentina	Buenos Aires	Bella Vista	−34.5621	−58.6909	25	5 January–4 February 1929	A. Gallardo and his children	No	Gallardo (1929)
A. argentinus PARALECTOTYPE	*Unknown*	Argentina	Buenos Aires	La Plata	−34.9091	−57.9354	24	March 1916	A. Zotta	No	Gallardo (1916)
A. argentinus	*A. lundii*	Argentina	Buenos Aires	La Plata	−34.9091	−57.9354	24	27 April–28 May 1924	C. Bruch	Yes	Bruch (1928)
A. argentinus	*A. heyeri*	Argentina	Buenos Aires	La Plata	−34.9091	−57.9354	24	28 December 2008	L. Elizalde	Yes	This study
A. argentinus platensis SYNTYPES	*A. lundii*	Argentina	Buenos Aires	La Plata	−34.9091	−57.9354	24	27 April 1924	C. Bruch	Yes	Santschi (1926)
A. argentinus	*A. ambiguus*	Argentina	Buenos Aires	Rosas, F.C. Sud, Las Flores	−35.9646	−58.9389	31	Probably 1930 (date not provided on label)	J. B. Daguerre	Yes	Bruch (1930)
A. argentinus	*A. lundii*	Argentina	Chaco	Parque Nacional Chaco	−26.8084	−59.6067	83	12 May 2004	L. Elizalde	Yes	This study
A. argentinus PARALECTOTYPE	*unknown*	Argentina	Córdoba	Alta Gracia	−31.6574	−64.4354	565	May 1913	A. Gallardo's children	No	Gallardo (1916)
A. argentinus	*A. lundii*	Argentina	Córdoba	Alta Gracia	−31.6574	−64.4354	565	February 1922	J. Hubrich	No	Bruch (1928)
A. argentinus	*unknown*	Argentina	Córdoba	Jesús María	−30.98	−64.09	534	6 January 1949	M. A. Terán coll. #7630	Yes	This study
A. argentinus	*A. heyeri*	Argentina	Corrientes	Mercedes	−29.18	−58.08	98	16 June 2006	L. Elizalde	Yes	This study

(Continues)

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TABLE 1 | (Continued)

Parasite	Host	Country	Province/state	Locality	Latitude	Longitude	Elevation asl. (m)	Collecting date	Collector	Specimen(s) examined	References
A. argentinus	*Unknown*	Argentina	Entre Rios	*Unknown*	−31.78[a]	−60.49[a]	59	*Unknown*	*Unknown*	No	F. Cuezzo pers. comm.
A. argentinus LECTOTYPE	[received with 2 *A. balzani* workers]	Argentina	Misiones	Posadas	−27.3643	−55.9014	114	February 1915	Dr. Marelli	Yes	Gallardo (1916); A. Roig Alsina pers. comm.
A. argentinus	*A. lundii*	Argentina	Santa Fe	Rosario	−32.9467	−60.6528	32	13 and 14 April 1924	J. Hubrich	Yes	Bruch (1928)
A. argentinus	*A. heyeri*	Argentina	Santa Fe	San Cristóbal	−30.31	−61.24	79	30 June, 1 and 8 November 2005; 6 February 2006	L. Elizalde	Yes	This study
A. argentinus	*A. hispidus*	Argentina	Santa Fe	San Cristóbal	−30.31	−61.24	79	14 January 2006	L. Elizalde	Yes	This study
A. argentinus	*Unknown*	Argentina	Tucumán	Unknown	−26.85[b]	−65.21[b]	443	*Unknown*	*Unknown*	No	Kusnezov (1953)
A. argentinus	*A. crassispinus*	Brazil	Paraná	Curitiba	−25.4489	−49.2330	920	30 September 2014	A. Casadei-Ferreira	Yes	This study
A. argentinus	*Unknown*	Brazil	Rio Grande do Sul	Passo Fundo	−28.2596	−52.4109	680	29 June 2015	A. L. Marsaro Jr.	No	Marsaro et al. (2017)
A. argentinus	*Unknown*	Uruguay	Canelones	El Pinar	−34.7970	−55.8912	15	28 March 2017	M. Bollazzi	Yes	This study
A. argentinus	*A. heyeri*	Uruguay	Florida	Cerro Colorado	−33.9042	−55.5942	224	22–27 February 2013	L. Tejera, M. Bollazzi, C. Rabeling	Yes	This study; see also Rabeling et al. (2015)
A. argentinus	*A. lundii*	Uruguay	Montevideo	Campus Univ. de la República, Facultad de Agronomía	−34.8381	−56.2205	40	22 February 2017	M. Bollazzi	Yes	This study

[a]In a personal communication, Dr. Fabiana Cuezzo alerted us to the presence of "*Pseudoatta argentina*" specimens from Entre Rios in the entomological collection of the Instituto Miguel Lillo at the Universidad Nacional de Tucumán. We did not have an opportunity to examine the specimens and provide the coordinates of the state capital, Paraná, as an approximation for the collection locality of *A. argentinus* in Entre Rios.
[b]In his checklist of ant species from Tucumán, Kusnezov (1953) included "*Pseudoatta argentina*", but unfortunately, he did not provide any details regarding the collection locality. For the purpose of this study, we provide the coordinates of the state capital, as an approximation for the collection locality of *A. argentinus* in Tucumán. The voucher specimen corresponding to this collection record could not be located.

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TABLE 2 | Internal primers used for PCR amplification and DNA sequencing of small, degraded fragments of the mitochondrial *cytochrome c oxidase subunit 1* (*COI*) gene from museum specimens.

Primer	Sequence (5′–3′)	Position	Source
LCO1490	GGTCAACAAATCATAAAGATATTGG	*D. yakuba* 1490-1515	Folmer et al. (1994)
LCO1532	TCAGGTATAGTAGGATCTGCCA	*D. yakuba*	This study
LCO1669	ACCATTCATAATTGGAGGATTCGGA	*D. yakuba*	This study
LCO1740	TCCCTTTAATACTAGGTTCCCCA	*D. yakuba*	This study
LCO1830	ACCGGTGCAGGATGAACTCT	*D. yakuba*	This study
LCO2023	TGATCCATCCTTATTACAGC	*D. yakuba*	This study
LCO2059	TCATTACCCGTTCTTGCTGGAG	*D. yakuba*	This study
LCO2128	GACCCATCTGGAGGTGGAGA	*D. yakuba*	This study
HCO1588	ACAAGAACCAAGTTCTAATCGGA	*D. yakuba*	This study
HCO1744	TCGAGGATATGCTATATCTGGGGA	*D. yakuba*	This study
HCO1835	TTCATCCTGCACCGGTTCCT	*D. yakuba*	This study
HCO1938	GCACCAAGAATGGATGATATACCTGC	*D. yakuba*	This study
HCO2198	TGATTTTTTGGTCACCCTGAAGTTTA	*D. yakuba* 2198-2223	Folmer et al. (1994)

Note: Position numbers correspond to *Drosophila yakuba* GenBank X03240 (COI). For all genes, the PCR product was amplified directly from the DNA extract.

et al. 2020; Barrera et al. 2022). *Pseudoatta argentina* was nested deep inside the *Acromyrmex* mitochondrial phylogeny rendering *Acromyrmex* paraphyletic (Figure 2A). The five samples of *P. argentina* formed a well-supported clade (Figure 2A, UFB = 100) that is sister to a clade comprising the free-living species *A. lobicornis* and the social parasite *A. charruanus* (Figure 2A, UFB = 100). The phylogenetic placement of *P. argentina* supports the hypothesis that *Pseudoatta* is not a distinct genus but instead shares a common ancestor with a subset of *Acromyrmex* species, and therefore, is a member of the genus *Acromyrmex* instead.

The COI sequences from different populations of *P. argentina* show a high degree of similarity (Figure 2C). In fact, all five COI barcoding sequences analyzed from different *P. argentina* individuals and/or populations were identical to each other (Figure 2C). Interestingly, the historical Bruch sample AC248 collected in 1924 is a specimen from Bruch's nest series from which Santschi (1926) selected two specimens to describe the subspecies *Pseudoatta argentina platensis*. For the sample AC248, we were able to sequence 268 base pairs of the 658 COI barcode (40.7%) using internal primers (Table 2) and the entire nucleotide sequence turned out to be identical to the COI barcodes from samples of *P. argentina* collected in Uruguay and Brazil (Figure 2C). The high degree of DNA sequence similarity and the lack of diagnostic morphological characters (see below) support the hypothesis that all sampled *P. argentina* individuals belong to a single species that exhibits a limited amount of genetic variability.

3.2 | Taxonomic Account

***Acromyrmex* Mayr 1865**

=*Pseudoatta* Gallardo 1916 **SYN. NOV.**

***Acromyrmex argentinus* (Gallardo 1916) COMB. NOV.**

= *Pseudoatta argentina* Gallardo, 1916: 320–323, figs. 1, 2 (g,m). Lectotype gyne designated secondarily by Santschi 1926: 7. Lectotype gyne, Posadas, Misiones, Argentina (leg. Marelli; February 1915) (MACN) [examined]. Two paralectotype gynes: Bella Vista, Buenos Aires, Argentina (leg. A. Gallardo's children, February 1916) (MHNG) [examined]; La Plata, Buenos Aires, Argentina (leg. A. Zotta, March 1916) (repository unknown) [not examined]. One paralectotype male: Alta Gracia, Córdoba, Argentina (leg. A. Gallardo's children, May 1913) (repository unknown) [not examined].

= *Pseudoatta argentina* v. *platensis* Santschi, 1926: 7. Syntype series consisting of a single gyne and a single male, La Plata, Buenos Aires, Argentina (leg. C. Bruch, 27 April 1924) (NHMB) [gyne examined] **SYN. NOV.**

3.3 | Comments on Taxonomic Changes

Gallardo (1916) described *Pseudoatta argentina* based on three gynes and a single male that were collected in Argentina in the provinces of Misiones, Buenos Aires, and Córdoba (Figures 1 and 3, Table 1). Gallardo did not designate a holotype for *P. argentina* but instead labeled all four specimens as "Cotypus," of which we examined two: one gyne from Posadas, Misiones and one gyne from Bella Vista, Buenos Aires. Santschi (1926, 7) referred to the *P. argentina* gyne from Misiones (Figure 1B,D,F) as "type," because Gallardo described this specimen in detail and depicted it in his figure no. 1 (see Gallardo 1916, 321–323, fig. 1 on p. 321). We consider Santschi's reference to the Misiones specimen as the lectotype designation according to the recommendations of the IUCN, article 74. The two gynes from Bella Vista and La Plata, as well

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as the single male specimen from Alta Gracia, we consider to be paralectotypes.

Because *P. argentina* is a morphologically highly derived inquiline social parasite, Gallardo proposed the monotypic satellite genus *Pseudoatta*, which was a common taxonomic practice at the time (see other monotypic social parasite genera for example, "*Bruchomyrma*" (jun. syn. of *Pheidole*) *acutidens* (Santschi) or "*Labauchena*" (jun. syn. of *Solenopsis*) *daguerrei* (Santschi); Santschi 1922, 1930; see also Casadei-Ferreira et al. 2016). However, entomologists also recognized that socially parasitic species and their hosts were often close relatives (Emery 1909; Wheeler 1919). Modern integrative taxonomic studies reconcile evolutionary history with taxonomic classification and evaluate whether parasites are part of their host clades (Rabeling, Schultz, et al. 2014; Ward et al. 2015; Prebus et al. 2023; Mera-Rodríguez et al. 2023, 2025). In the case of *P. argentina*, our COI phylogeny recovered *P. argentina* as deeply nested inside the *Acromyrmex* phylogeny and sister to a clade comprising *A. charruanus* and *A. lobicornis* (Figure 2A). Although COI represents a single maternally inherited mitochondrial marker, this result is congruent with previous studies which also showed (a) that *P. argentina* is closely related to the social parasite species *A. charruanus* and (b) that both parasite species are phylogenetically nested deeply inside the genus *Acromyrmex* (Figure 2A; see also Rabeling et al. 2018; Schrader et al. 2021). Therefore, we interpret the morphological modifications of *P. argentina* as typical reductions and potential adaptations to the inquiline syndrome instead of being diagnostic traits of a distinct genus. Consequently, we consider the genus *Pseudoatta* Gallardo a junior synonym of *Acromyrmex* Mayr and refer to this inquiline species as *Acromyrmex argentinus* (Gallardo) **comb. nov**. In the original species description, Gallardo (1916, 321–323) used the species epithet "*argentina*" as an adjective, which he derived from the toponym "Argentina" in the sense of "argentine." Accordingly, the species epithet must agree in gender with the generic name, which is masculine in the case of *Acromyrmex*. For the adjectival ending to agree with the masculine gender of *Acromyrmex*, we changed the species name to *Acromyrmex argentinus* (Gallardo).

Prior to this study, Brown (1973) proposed a generic and subgeneric classification for ants, where he already asked whether *Pseudoatta* should be a junior synonym of *Acromyrmex*. In their landmark monograph "The Ants," Hölldobler and Wilson (1990, 442 and 607) shared Brown's opinion. However, the taxonomic classification of *A. argentinus* was never addressed in detail, which was in part due to the lack of freshly collected material.

In addition, Santschi (1926) described the subspecies *Pseudoatta argentina* v. *platensis* based on a single gyne and a single male, which were collected by Carlos Bruch in the nest of *Acromyrmex lundii* on April 27th, 1924. Santschi's decision to erect this new taxon was based on the longer occipital and pronotal spines of the gyne, as well as the higher and shorter petiole of the male. To test whether this subspecies is either synonymous with *A. argentinus* or constitutes a distinct species, we compared the gyne of Santschi's type series to the lectotype of *A. argentinus* and to specimens that were collected across the species distribution range, including a large series of more than 600 specimens collected by Carlos Bruch in La Plata (Bruch 1928), from which the types of *P. a. platensis* originated (Table 1). The morphological variation Santschi described falls well within the variation present in *A. argentinus* populations. In addition, the 268 bp fragment of the mitochondrial barcoding gene COI, which we sequenced for one of Bruch's 1924 specimens and which was part of the same nest series as the two syntype individuals of *P. argentina platensis*, was identical to the COI fragment obtained from the recently collected *A. argentinus* specimens collected in Brazil and Uruguay (Figure 2C). In combination, both the morphological and the molecular genetic evidence are consistent with the hypothesis that *A. argentinus* is a single, monophyletic species with minimal genetic divergence between populations. We therefore synonymize *P. argentina* v. *platensis* Santschi, 1926 **syn. nov**. under *A. argentinus* (Gallardo).

A single specimen in the Santschi collection (deposited at NHMB) was identified as *Pseudoatta argentina v. attenuata*. The specimen carries a Santschi identification label from 1925. This specimen was collected by Jose Hubrich in Rosario, Province of Santa Fe, Argentina on either the 13th or 14th of April 1924. To our knowledge, this taxon was never described in the literature. Additional *A. argentinus* specimens from Rosario, which were also collected by Hubrich (deposited at MACN), were examined, and morphological characters that are unique to specimens from this population could not be identified. Therefore, this specimen does not warrant taxonomic description. Since the name "*attenuata*" was not used in the literature and only seems to exist on the specimen label, it has no status in zoological nomenclature.

3.4 | Natural History Observations

3.4.1 | Uruguay

On February 22, 2013, we first found few (3–4) winged gynes and males of *A. argentinus* on the mound of an *A. heyeri* nest at "Plantación Cruz Roja," which is an *Eucalyptus* tree plantation located 6 km southwest of Cerro Colorado in the Department of Florida in Uruguay (GPS coordinates: S33.9042°, W055.5942°, ±600 m; elevation 224 m above sea level) (Figures 1, 3, and 5, Table 1). We observed the winged gynes and males on top of a mound of a decaying *A. heyeri* nest. The *A. heyeri* nest was located in the shade next to the trunk of a ~5-year-old *Eucalyptus* tree. It was relatively small, falling within the lower 25% size group of *A. heyeri* nests in the same population, and it was not covered by a prominent thatch mound. For comparison, the size of a mature *A. heyeri* nest in south-central Uruguay can easily extend to a diameter of ~1 m at the base and be covered by a thatch mound of ~1 m height (Roces and Bollazzi 2026). After finding the first *A. argentinus* alates on the nest mound, we opened the nest and removed five 50 mL cups of fungus garden and ants. Between February 25 and 27, 2013, we returned to the same nest and collected two additional 400 mL containers of fungus garden and ants. All samples were brought to the laboratory and kept alive for behavioral observations. After careful examination, we censused the *A. argentinus* individuals and found 4 dealate gynes, 724 alate gynes, 80 alate males, 100 gyne pupae,

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and 6 male pupae, as well as 47 larvae of unknown sex in a total of 1050 mL of fungus garden. In sum, the colony contained 961 *A. argentinus* individuals. The female to male sex ratio of the offspring in this colony was almost 10:1 [numerical sex ratio = number of female sexuals ÷ total number of sexuals = 824 (724 alate gynes + 100 gyne pupae) ÷ 910 (sum of female and male sexuals) = 0.91], and therefore highly female-biased. Since none of the four dealate gynes was physogastric, we cannot tell whether any or all of these individuals were the reproductively active queen(s) of this colony or whether they were merely unmated offspring gynes that had lost their wings.

The host colony showed significant signs of decay. For example, we did not find a reproductively active queen of *A. heyeri* in the nest. In addition, the colony consisted mostly of minor and fewer small medium-size host workers. Large-size host workers that are found in healthy, mature *A. heyeri* colonies were absent. Three weeks after our first observation, the host colony was dead. Therefore, we believe that the host queen was absent from the colony and had either died of natural causes or was killed by the parasite queen(s). *Acromyrmex heyeri* was previously unknown to be a host of *A. argentinus* and this observation constitutes a new host record.

During two periods of fieldwork (austral fall: 22–27 February 2013; austral spring: 1–5 November 2013), we further studied the *A. heyeri* host population to better understand host ecology, potentially detect additional social parasites, and collect samples of host and parasite species. We opened a total of 200 *A. heyeri* nests, 100 nests per season (note: some of the same nests were probably opened twice, during spring and fall surveys), as well as nests of related species, such as *A. crassispinus* (Forel), *A. lobicornis* (Emery), and *A. lundii* (Guérin-Méneville). We found a total of three *A. heyeri* nests that were occupied by two social parasite species: one host colony was exploited by *A. argentinus* (reported here) and two colonies were usurped by *A. charruanus* (see Rabeling et al. 2015). Since social parasites are more likely to be detected prior to their mating flights during the austral fall, it is possible that we missed additional parasites during our spring survey. Therefore, we estimate that approximately 3% of the *A. heyeri* colonies in this Uruguayan population were infiltrated by at least two social parasite species with 1 of 100 host nests by *A. argentinus* (1%) and 2 of 100 host nests by *A. charruanus* (2%). The host nest density at "Plantación Cruz Roja" was estimated at approximately 3–4 nests per hectare and literally hundreds of *A. heyeri* nests could be observed in the neighboring tree plantation and Pampa habitat. The high number and density of potential host nests provide excellent conditions for social parasites seeking new host colonies.

3.4.2 | Brazil

In Brazil, we observed a single dealate queen of *A. argentinus* in a colony of *A. crassispinus* at the Centro Politécnico campus of the Universidade Federal do Paraná in Curitiba, Paraná, on September 30, 2014 (GPS coordinates: S25.4489°, W049.2330°, elevation 920 m above sea level) (Figures 3 and 4, Table 1). The single *A. argentinus* queen was highly physogastric (Figure 4), which means she had an expanded metasoma due to the development of her ovaries, indicating that she was the reproductively active queen of this colony. Additional individuals of the social parasite were not observed.

Prior to this study, *A. crassispinus* was never observed as a host of *A. argentinus*. Therefore, this observation also constitutes a new host record. The host colony did not contain a reproductively active *A. crassispinus* queen, which is consistent with our observation from Uruguay, indicating that *A. argentinus* parasitizes queen-less host colonies or actively kills the host queen. However, the *A. crassispinus* colony did contain host alates, indicating that these alates were produced prior to the death of the host queen. Four additional nests of *A. crassispinus* were excavated at the same locality, but additional parasites could not be detected. Similar to the other hosts, *A. heyeri* and *A. lundii*, *A. crassispinus* is a commonly found species in the pampas and open grassland areas of southern Brazil, Paraguay, Uruguay, and northern Argentina (Gonçalves 1961; Sánchez-Restrepo et al. 2019). Its nest mounds consist of dry leaves, branches, and soil, under which the single fungus chamber is located (Nickele et al. 2009; Roces and Bollazzi 2026).

3.4.3 | Argentina

In Argentina, we sporadically observed winged gynes and males of *A. argentinus* emerging from *A. heyeri* and *A. lundii* host nests and collected isolated individuals of *A. argentinus* at multiple localities, including the provinces Buenos Aires, Chaco, Corrientes, and Santa Fe. These observations were made between May 2004 and December 2008 (Figure 3, Table 1). *Acromyrmex heyeri* and *A. lundii* were repeatedly identified as hosts, and once a worker of *Acromyrmex hispidus* Santschi was observed to carry a dealate gyne of *A. argentinus*. Whether *A. hispidus* is a true and novel host for *A. argentinus* needs to be evaluated.

4 | Discussion

4.1 | Inquiline Syndrome

Acromyrmex argentinus is a morphologically and behaviorally highly specialized, workerless inquiline social parasite that exploits at least four, potentially five free-living *Acromyrmex* leaf-cutting ant species in southern South America (Figures 1 and 3–5, Table 1). Both females and males of *A. argentinus* show marked modifications characteristic of the inquiline syndrome (Wilson 1984; Rabeling et al. 2019; Cover and Rabeling 2024). In comparison to its host species, *A. argentinus* is smaller in body size, has elongated scapes, lost the worker caste, has reduced pilosity and sculpturing on the body surface and therefore appears smooth and shiny, has a reduced number of maxillary palps (reduction from 4 to 3), and a reduced number of antennal segments in males (reduction from 13 to 11). Furthermore, *A. argentinus* seems to be monogynous, host-queen-intolerant, mates with siblings inside and on the host nest (Figure 5), and males are highly modified and are similar to females (i.e., gynaecomorphism). Overall, *A. argentinus* shows an extremely high degree of morphological and behavioral modifications associated with its social parasitic life history.

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Currently, six inquiline social parasite species are known in the fungus-growing ants, and no two species are identical in the combination of inquiline syndrome traits (Rabeling and Bacci 2010; Rabeling et al. 2015, 2019). Superficially, the degree of modifications observed in *A. argentinus* resembles that of *M. castrator* and *A. fowleri*. All three species are reduced in size, lost the worker caste, and are smooth and shiny. However, only *A. argentinus* is host-queen-intolerant, whereas the other two species coexist with the resident queen inside the host colony. Also, unlike the males of *A. argentinus* and *M. castrator*, the males of *A. fowleri* are not gynaecomorphic and are more similar to males of free-living, non-parasitic *Acromyrmex*.

Our mitochondrial phylogeny inferred *A. argentinus* as sister to a clade consisting of the free-living species *A. lobicornis* and *A. charruanus*, an inquiline parasite of *A. heyeri*, which is consistent with previous phylogenetic analyses (Rabeling et al. 2018; Schrader et al. 2021). *Acromyrmex charruanus* differs significantly from *A. argentinus* in morphology and life history in that *A. charruanus* resembles its host, does not possess some of the morphological modifications associated with the inquiline syndrome (i.e., reduced mouthparts, reduced antennae, gynaecomorphism), is host-queen-tolerant, and performs nuptial flights (Rabeling et al. 2015). The close relatedness of these two parasites with different life histories, morphologies, and behaviors suggests that the characteristics associated with the inquiline parasite syndrome evolved convergently in a mosaic fashion across leaf-cutting ants and small differences in the parasites' life histories may have led to individual deviations from the ancestral inquiline syndrome "Bauplan".

4.2 | Host Use

Information about the host biology is essential for understanding the behavioral and ecological interactions between hosts and social parasites, as well as for interpreting their evolutionary origins and coevolutionary dynamics. When *A. argentinus* was discovered, the parasite was reported to exploit *A. lundii* in Argentina (Gallardo 1916, 1929; Bruch 1928). In a footnote of a paper about a *Solenopsis* social parasite, Bruch (1930) observed *A. argentinus* alates on the nest of *A. ambiguus* (Emery). In addition, we observed *A. crassispinus* and *A. heyeri*, and potentially *A. hispidus*, as novel host species in Argentina, Brazil, and Uruguay (Figure 3, Table 1). Furthermore, Gallardo (1916) received two workers of *Acromyrmex balzani* (Emery) in the same vial with specimens of *A. argentinus*, which prompted some myrmecologists to suggest that *A. balzani* could be a host of *A. argentinus*. However, Gallardo (1916) did not report any biological observation that *A. argentinus* lived in or emerged from an *A. balzani* nest. Interestingly, phylogenetic analyses revealed the four hosts of *A. argentinus* as close relatives that are part of the same clade, whereas *A. balzani* is a distant relative of the confirmed host species with a distinctly different sociobiology (Figure 2A; see also Schultz and Brady 2008; Elizalde et al. 2019; Mera-Rodríguez et al. 2025). Considering the lack of conclusive evidence and the markedly different ecology and sociobiology of *A. balzani* from the confirmed *Acromyrmex* host species, we currently do not consider *A. balzani* a host of *A. argentinus*. Hence, a total of four *Acromyrmex* species are confirmed host species of *A. argentinus*, and the host association with *A. hispidus* needs confirmation.

With four hosts, *A. argentinus* is the only known generalist inquiline parasite in South America to date. All other inquiline social parasites of fungus-growing ants are known to exploit a single host species (Rabeling and Bacci 2010). The Panamanian inquiline *A. insinuator* was previously thought to exploit two host species (Schultz et al. 1998; Sumner et al. 2004), but one of the host species, *A. echinatior* (Forel), was recently synonymized under *A. octospinosus* (Reich) (Mera-Rodríguez et al. 2025). Hence, the widely distributed *A. octospinosus* is the single known host species of *A. insinuator*.

In eusocial insects, the social structure of the host colony is thought to be tightly linked to the evolutionary origins of social parasitism. One of the prevailing hypotheses is that polygyny, the coexistence of multiple reproductively active queens in a single colony, provides the opportunity for social parasitism because the presence of multiple queens allows for reproductive cheating and/or polygynous colonies are more prone to accepting additional, potentially unrelated egg-laying queens (Bourke and Franks 1991; Dahan and Rabeling 2022). A recent sociogenetic study of leaf-cutting ants in South America showed that at least three of the four confirmed hosts of *A. argentinus* are facultatively polygynous including *A. ambiguus*, *A. crassispinus*, and *A. heyeri* (Dahan et al. 2022). For these three species, 11%–25% of the sampled colonies were polygynous, with 2–3 reproductively active queens per colony, and each queen mated with 4–6 males (Dahan et al. 2022). Interestingly, the high queen numbers and mating frequencies significantly reduced the average relatedness (r) in the host colonies to 0.36–0.46, which is well below the maximum relatedness, that is, $r = 0.75$, in colonies of monogynous, singly-mated haplodiploid eusocial organisms (Hamilton 1964; Dahan et al. 2022). These deviations from an ancestral monogamous life history seem to provide the sociobiological breeding ground for reproductive cheating and social parasitism in leaf-cutting ants. The only host species that was inferred to be strictly monogynous is *A. lundii*, and the social structure of the potential host *A. hispidus* remains unstudied (Dahan et al. 2022). According to the sociobiological results, one would expect that *A. argentinus* evolved either from or in tight association with one of the facultatively polygynous species and that the use of *A. lundii* likely constitutes a secondary host shift.

Interestingly, the mitochondrial phylogeny inferred *A. argentinus* as sister to a clade consisting of *A. lobicornis* and *A. charruanus* (Figure 2A). Although, Dahan et al. (2022) characterized *A. lobicornis* as a facultative polygynous species with 22% of the sampled colonies ($n = 18$) being polygynous, polygynous colonies containing 2–4 reproductively active queens per colony, each queen mating with 1–4 males, and average relatedness (r) being reduced to 0.46 (±0.04), *A. lobicornis* was never observed to be the host of *A. argentinus*. This suggests that *A. argentinus* is either not the closest relative of one of its hosts, or alternatively, *A. lobicornis* was simply not yet discovered to be a host of *A. argentinus*. A forthcoming phylogenetic study using nuclear

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markers will examine the puzzling host–parasite relationships between *A. argentinus* and its hosts in more detail (Rabeling et al., unpubl. data).

4.3 | Host-Queen-Intolerance and Reproductive Strategy

The behavioral interactions between host and social parasite queens are decisive for characterizing the parasites' life histories. Most inquiline social parasites are host-queen-tolerant (Buschinger 2009; Rabeling 2021). They coexist with the host queen for extended periods of time and enjoy the crucial advantage of being supplied with workers that provide social colony services, such as foraging, nest construction, and brood care. The stable host environment allows for continuous reproduction of the social parasite and therefore, host-queen-tolerant inquilines can be considered K-strategists (MacArthur and Wilson 1967; Pianka 1970).

In contrast, host-queen-intolerance is a highly specialized life history strategy in inquilines because in the absence of the host queen, new host workers are not being produced (Cover and Rabeling 2024). Therefore, the inquiline's lifespan is expected to be short and the parasite needs to rapidly produce a large quantity of offspring. Thus, host-queen-intolerant inquilines can be considered r-strategists.

Host-queen-intolerance consists of two distinct behavioral strategies (Cover and Rabeling 2024). First, an aggressive behavior, where some inquiline species attack and eliminate the host queen(s) actively, which has been observed in *Leptothorax goesswaldi* Kutter, *Leptothorax wilsoni* Heinze, *Monomorium santschii* (Forel), and *Pseudomyrmex leptosus* Ward (Forel 1905; Kutter 1967; Klein 1987; Buschinger and Klump 1988; Heinze 1989), as well as in some inquilines that likely evolved from a dulotic ancestor, such as species in the *Temnothorax corsicus* and *T. muellerianus* species groups (Buschinger 1989; Prebus 2017). Second, an opportunistic behavior exists, where other so-called host-queen-intolerant inquilines do not aggressively replace the host queen but instead parasitize old or queenless host colonies, such as the microgyne of *Myrmica rubra* (Linnaeus), *Formica talbotae* Wilson, *Pheidole acutidens*, possibly *Tapinoma inflatiscapus* Cover & Rabeling, and *Tetramorium atratulum* (Schenk) (Kutter 1968; Talbot 1976; Schär and Nash 2014; Casadei-Ferreira et al. 2016; Cover and Rabeling 2024).

Acromyrmex argentinus shows the typical adaptations of a r-selected, host-queen-intolerant social parasite. When reproductively active, the queen of *A. argentinus* becomes physogastric, which is visible by the expanded metasoma and exposed intersegmental membranes (Figures 1C vs. 1D and 4). In the physogastric state, the queen's ovaries develop rapidly and expand to produce large numbers of eggs in a short time. After the parasite brood develops, the available fungus garden resources are exhausted, and both the parasite queen and the remaining host colony die after a single bout of semelparous parasite reproduction (Bruch 1928; Gallardo 1929; this study).

In ants, physogastric queens are common in army ants with a migratory lifecycle (Gotwald 1995; Kronauer 2020), and are expected to be common among inquiline social parasites. However, physogastry was only documented in some species so far, including, for example, the host-queen-tolerant *Tetramorium inquilinum* Ward et al., as well as the host-queen-intolerant *T. atratulum* (Kutter 1950, 1968) and *Pheidole acutidens* (Santschi) (Casadei-Ferreira et al. 2016). *Acromyrmex argentinus*, *P. acutidens*, and *T. atratulum* are host-queen-intolerant and physogastric, which allows for the rapid production of sexual offspring before the collapse of the queenless host colony; whereas *T. inquilinum* is host-queen-tolerant, and physogastry might enable successful reproduction during the short summer season in alpine habitats of Central Europe (Kutter 1968).

Interestingly, the *A. argentinus* sexual offspring emerging from the *A. heyeri* host nest in Uruguay showed a highly skewed sex ratio towards females. The colony contained 910 winged *A. argentinus* individuals (including pupae), of which 824 were female and 86 were male (numerical sex ratio: 0.91). Both Bruch (1928) and Gallardo (1929) reported the observations that Hubrich made in 1924 on the mating flight of the same *A. argentinus* colony from La Plata, Argentina. Hubrich observed ~600 alates in a mating flight with roughly one third being males (numerical sex ratio: ~0.67). These observations of a highly female-biased sex ratio are consistent with Hamilton's local mate competition (LMC) theory (Hamilton 1967), which predicts that natural selection favors female-biased sex ratios when the offspring of a single mother mate with their siblings before the females disperse because the increased number of mates for males is expected to reduce competition among brothers. Empirical support for Hamilton's LMC theory was provided by numerous studies of parasitic wasps (Shuker et al. 2005; Abe et al. 2014), and ant social parasites apparently respond to the same selective pressures (Heinze et al. 2007; this study). Hamilton's LMC theory also postulates that males mate repeatedly with their siblings, which is unusual for eusocial insects, because the male aedeagus carries hooks that lock into the female genitalia during copulation, and males usually die after copulation (Baer 2010). Interestingly, these aedeagal hooks are reduced in the inquiline *M. castrator* and males were observed to mate repeatedly in laboratory colonies (Rabeling and Bacci 2010). Similarly, males of the inquiline *T. atratulum* were also reported to mate thrice under laboratory conditions (Heinze et al. 2007). Hence, some inquiline social parasites show multiple hallmarks of LMC including (i) reproduction by a single queen, (ii) intranidal mating of offspring with siblings, (iii) female-biased sex ratios, and (iv) multiple copulations by individual males. Future comparative studies need to (a) examine the degree to which different social parasite species evolved characteristics expected under LMC and (b) test whether ant social parasites evolved optimal sex ratios for females.

As expected under LMC, *A. argentinus* is adelphogamous with alate males and females mating inside or on the host nest (Figure 5; see also Bruch 1928; Gallardo 1929). Adelphogamy is a common mating strategy in inquiline social parasites and was also observed in other inquilines, such as *M. castrator* (Rabeling and Bacci 2010), *T. atratulum* (Heinze et al. 2007), and some *Temnothorax* species in the *T. corsicus* species group (Buschinger 1989). Sib-mating is expected to cause inbreeding, and to test whether the social parasite *A. argentinus* is inbred, we previously developed highly variable short tandem repeat

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markers for one of the host species, *A. lundii*, that also cross-amplify in *A. argentinus* (Rabeling, Bollazzi, et al. 2014; Dahan et al. 2022). For the parasite population in Cerro Colorado, Uruguay and the single individual from Curitiba, Brazil, which are separated by approximately 1140 km and parasitize two different host species, all individuals were homozygous across the 22 loci studied (Dahan et al. 2022). The complete absence of genetic variation in the COI barcoding sequences (Figure 2C) and across microsatellite loci supports the hypothesis that *A. argentinus* is highly inbred. However, it is currently not understood whether genetic homogeneity was caused by an extreme bottleneck at the origin of the parasitic lineage or whether the absence of genetic variation is a consequence of sib mating.

4.4 | Biogeography

Globally, the species richness of ant social parasites peaks in the northern hemisphere outside of the equatorial tropics and the species are distributed along an inverse latitudinal diversity gradient (Gray and Rabeling 2023). Since its discovery in 1916, *A. argentinus* was known from the provinces of Buenos Aires, Córdoba, Misiones, Santa Fe, and Tucumán (Gallardo 1916, 1929; Bruch 1928; Kusnezov 1953). Our study adds distribution records from 17 localities across northern Argentina, southern Brazil and Uruguay, which considerably expands the distribution range of *A. argentinus* (Figure 3, Table 1). The current geographic range covers approximately 1.050.000 km^2, which is roughly equivalent to the size of Bolivia. Accordingly, *A. argentinus* is probably the inquiline species with the most extensive biogeographic range in South America. In Brazil, the discovery of *A. fowleri* in Mato Grosso do Sul also extended the distribution of that inquiline social parasite significantly, which was previously only known from the type locality in Bahia (Santos-Neto et al. 2026). To our knowledge, only very few inquiline parasite species are distributed over a similarly large area, including *T. atratulum*, which is known to occur throughout Europe, extending east to Türkiye and which was recently introduced to North America, where it now almost reaches the west coast (Dash and Sanchez 2009; Seifert 2018). Frequent host shifts of *A. argentinus* could have allowed the parasite to expand to geographic areas that the original host species did not occupy. It would be interesting to further explore the hypothesis that frequent host shifts are associated with biogeographic range expansions in ant social parasites.

On the population level, highly specialized inquiline social parasites are usually rare and locally distributed (Wilson 1963; Kutter 1968; Cover and Rabeling 2024). Despite its extensive distribution range, *A. argentinus* was only sporadically encountered over the past 100 years and occurred locally at low frequencies. Therefore, we consider this species widely distributed but locally rare.

5 | Conclusions and Outlook

Novel observations on the rarely collected inquiline social parasite *A. argentinus* reveal new information about its behavior, life history, host use, geographic distribution, and taxonomic classification. Furthermore, the results provide additional context for interpreting the evolution of social parasitism in the leaf-cutting ants.

Our results demonstrate and confirm that *A. argentinus* is a workerless, likely monogynous, host-queen-intolerant inquiline social parasite. *Acromyrmex argentinus* seems to be a r-selected parasite that is well adapted to semelparous reproduction in queenless host colonies, as evident from the physogastric metasoma and the abridged life cycle. The winged parasite offspring mate with siblings on and inside the host nest, and population genetic analyses showed that *A. argentinus* is highly inbred. The sex ratio of the parasite offspring is highly skewed towards females, which is consistent with Hamilton's local mate competition theory.

In addition, our study reveals previously undocumented host associations of *A. argentinus* showing that *A. argentinus* usurps the social colony structure of at least four free-living *Acromyrmex* leaf-cutting ant species including *A. ambiguus*, *A. crassispinus*, *A. heyeri*, and *A. lundii*. The host association with *A. hispidus* needs to be confirmed. So far, *A. argentinus* seems to be the only known generalist social parasite in South America that is capable of exploiting multiple host species.

Furthermore, *A. argentinus* is much more widely distributed in the South American subtropics than previously documented. Its biogeographic range includes southern Brazil, northern-central Argentina, and Uruguay. We suggest that frequent host shifts may have facilitated the parasite's significant geographic range expansion.

Although covering a broad distribution range, we consider *A. argentinus* locally rare. The studied Uruguayan *A. heyeri* host population was populous and had high nest densities, but only 1% of the nests were detected to be parasitized by *A. argentinus*. The low infection rate supports the notion that host-queen-intolerant parasites depend on dense host populations where colony turnover provides sufficient queenless colonies to support a population of a host-queen-intolerant social parasite.

The new collections of *A. argentinus* also provided fresh material to re-examine its morphology and taxonomic classification. Our morphological analyses show that *A. argentinus* exhibits a number of morphological reductions that are typical for the inquiline syndrome. Our mitochondrial phylogeny inferred *A. argentinus* as deeply nested inside the genus *Acromyrmex*, which is congruent with previous studies. Therefore, we synonymize the genus name *Pseudoatta* under *Acromyrmex* and Santschi's subspecies *Pseudoatta argentina platensis* under the species name *Acromyrmex argentinus*. These taxonomic changes reconcile taxonomic classification with evolutionary history and provide direct biological information about the parasite's ancestry and host use.

Lastly, our study provides new information for interpreting the evolution of social parasitism in leaf-cutting ants. *Acromyrmex argentinus* and *A. charruanus* were inferred as members of the same clade, and other studies inferred sympatric speciation patterns for *M. castrator* and *A. insinuator*, suggesting that the highly derived morphological and behavioral characteristics of

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the inquiline syndrome evolved at least thrice independently across the fungus-growing ants.

Considering that not two of the six social parasitic fungus-growing ant species are identical in their combination of morphological and behavioral traits, we suggest that the derived characters of the inquiline syndrome evolved in a mosaic fashion. The traits of the inquiline syndrome seem to evolve rapidly and convergently in response to the selective pressures that socially parasitic lineages experience when interacting with their host species.

Future studies need to confirm that *A. argentinus* is a monogynous, host-queen intolerant inquiline social parasite. While we assume that *A. argentinus* is an "opportunistic" host-queen-intolerant inquiline that specializes on usurping old, queenless host colonies, behavioral interactions between inquiline and host queens were never observed. Carefully planned behavioral experiments would provide novel insights into how *A. argentinus* queens invade new hosts and allow us to distinguish whether *A. argentinus* is an aggressive or opportunistic host-queen-intolerant inquiline. Field studies should also pay attention to the host use of *A. argentinus* because, due to the facultative polygynous colony organization of *A. lobicornis* and the close relatedness between *A. argentinus* and *A. lobicornis*, *A. lobicornis* could potentially be a suitable host for *A. argentinus* that, so far, may have escaped detection. In addition, a comprehensive phylogenetic study needs to test conflicting hypotheses about the origins and evolution of social parasitism in *Acromyrmex* leaf-cutting ants as well as examine the role of host-shifting in social parasite evolution.

Author Contributions

Christian Rabeling: conceptualization (lead), data curation (lead), formal analysis (lead), funding acquisition (lead), investigation (lead), methodology (equal), project administration (lead), resources (lead), software (equal), supervision (lead), validation (lead), visualization (equal), writing – original draft (lead), writing – review and editing (lead). **Alexandre Casadei-Ferreira:** data curation (equal), investigation (equal), validation (equal), writing – review and editing (equal). **Rodrigo M. Feitosa:** data curation (equal), investigation (equal), supervision (equal), validation (equal), writing – review and editing (equal). **Luciana Elizalde:** data curation (equal), investigation (equal), validation (equal), writing – review and editing (equal). **Daniela Mera-Rodríguez:** data curation (equal), formal analysis (equal), investigation (equal), software (equal), visualization (equal), writing – review and editing (equal). **Leticia Tejera:** investigation (equal), validation (equal), writing – review and editing (equal). **Martín Bollazzi:** conceptualization (equal), investigation (equal), methodology (equal), resources (equal), validation (equal), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Voucher specimens are deposited in natural history collections listed in the methods. Newly generated DNA sequence data are deposited in NCBI GenBank (submission SUB16548042). Accession numbers and links to the previously published sequence data are provided in Tables S1 and S2. All other data are contained within this manuscript. Additional specimen information is available upon request from C. Rabeling.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** ece374686-sup-0001-TableS1.xlsx. **Table S2:** ece374686-sup-0002-TableS2.xlsx.

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