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RESEARCH ARTICLE

Acromyrmex fowleri: a new inquiline social parasite species of leaf-cutting ants from South America, with a discussion of social parasite biogeography in the Neotropical region

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Abstract

Ant inquiline social parasites obligately depend on their hosts for survival and reproduction. Because of their shift from a eusocial to a socially parasitic life history, inquiline social parasites are interesting study systems for exploring the dynamics between conflict and cooperation in eusocial insect colonies. In addition, inquiline social parasites are of interest to evolutionary biology, because some species evolved directly from their hosts via sympatric speciation. With five described species, inquiline social parasites are relatively diverse in the fungus-growing ants. So far, four species have been reported from the leaf-cutting ant genus *Acromyrmex* and its closely affiliated social parasite genus *Pseudoatta*. In contrast, only a single parasite species was described from the lower attine genus *Mycocepurus*. Here, we describe a new species of inquiline social parasite, *Acromyrmex fowleri* sp. nov., which was discovered 27 years ago in the tropical region of Brazil (State of Bahia), living inside the colonies of its host *Acromyrmex rugosus*. We also report observations on the behavioral ecology and natural history of *A. fowleri* and its host. Our study suggests that *A. fowleri* is an obligate, queen-tolerant, workerless inquiline social parasite of *A. rugosus* and that *A. fowleri* represents some but not all morphological and life history characters of the inquiline syndrome, supporting the hypothesis that the complex traits of the inquiline syndrome evolve in a mosaic fashion. Considering that *A. fowleri* is a new social parasite species from tropical Brazil, we discuss the paradoxical biogeographic distribution of ant social parasites, which we refer to as the "Kutter–Wilson Paradox", and conclude that the Kutter–Wilson Paradox is a genuine biogeographical pattern, instead of being a mere sampling artifact.

Keywords Attini · Biogeography · Formicidae · Fungus-growing ants · Inquilinism · Kutter–Wilson Paradox · Latitudinal diversity gradient · Myrmecosymbiosis · Social parasitism

Introduction

The fungus-growing ants (Myrmicinae, Attini, Attina) (sensu Ward et al. 2015) are a monophyletic clade in the ant subfamily Myrmicinae that live in an obligate mutualistic relationship with a basidiomycete fungus and associated microorganisms (Craven et al. 1970; Hölldobler and Wilson 1990, 2011; Currie et al. 1999; Mueller et al. 2005; Schultz et al. 2005; Little and Currie 2007). The fungus-growing behavior of the ants evolved 50–60 million years ago (Schultz and Brady 2008, Nygaard et al. 2016) and currently approximately 260 extant species of fungus-growing ants are recognized across nineteen genera (Sosa-Calvo et al. 2018; Solomon et al. 2019). The fungus-growing ants are exclusive to the New World, ranging from the 41st parallel north (Long Island, New York, USA) to the 44th parallel

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south (Patagonia, Argentina) (Fowler 1983; Farji Brener and Ruggiero 1994; Rabeling et al. 2007; Delabie et al. 2011).

The leaf-cutting ants are the ecologically dominant, polyphagous herbivores of the Neotropical region (Fowler et al. 1989; Wirth et al. 2003), and due to their impact on their environment, they have attracted the attention of biologists and agronomists for centuries (Cherrett 1986; Fowler et al. 1986; Lofgren and Vander Meer 1986; Hölldobler and Wilson 1990, 2011; Mueller and Rabeling 2008; Della Lucia 2011). During the nineteenth century, naturalists discovered that the leaf-cutting ants utilize harvested leaf fragments to cultivate a fungus garden in their subterranean nest chambers for food (Belt 1874; Müller 1874). In fact, leaf-cutting ants, their symbiotic fungi, and associated microbes have been sharing a co-evolutionary history for approximately 15 million years (Nygaard et al. 2016; Mueller et al. 2017, Li et al. 2018), and as a result, both partners evolved specific morphological and behavioral adaptations that are exclusive to this mutualism (Mueller 2002; De Fine Licht et al. 2014). The leaf-cutting ants are currently comprised of the two genera *Acromyrmex* and *Atta*, containing 34 and 17 species, respectively (Borgmeier 1959; Fowler 1985, 1988; Fernández et al. 2015; Rabeling et al. 2015).

The colonies of the leaf-cutting ants are extremely populous, and in the eyes of parasites and predators, leaf-cutting ant nests constitute large accumulations of resources and nutrients (Autuori 1942; Moser 1963; Jonkman 1980; Schmid-Hempel 1998; Moreira et al. 2004; Powell and Clark 2004; Forti et al. 2011). Not surprisingly, the colonies of leaf-cutting ants host a high diversity of parasites and commensals (Mehdiabadi and Schultz 2010). In addition, colonies of *Acromyrmex* leaf-cutting ants are hosts to ant social parasites, i.e., ant species that depends on the care of another ant species for survival and reproduction (Buschinger 1986, 2009). So far, four obligate inquiline social parasites were described: *Pseudoatta argentina* Gallardo (1916), *Acromyrmex insinuator* Schultz et al. (1998), *Acromyrmex ameliae* De Souza et al. (2007), and *Acromyrmex charruanus* Rabeling et al. (2015). The high diversity of social parasites is noteworthy because *Acromyrmex* leaf-cutting ants represent only 13% (34 of 260) of the total species diversity in the fungus-growing ants. In contrast, among all other fungus-growing ant species, only a single inquiline social parasite is known from the genus *Mycocepurus* (Rabeling and Bacci 2010). In addition to inquiline social parasites, *Gnamptogenys hartmanni* and eight *Megalomyrmex* species are trophic and social parasites of non-leaf-cutting fungus-growing ants (Wheeler 1925; Brandão 1990, 2003; Adams et al. 2000; Dijkstra and Boomsma 2003; Longino 2010; Boudinot et al. 2013).

Here, we describe *Acromyrmex fowleri* sp. nov., a new inquiline social parasite species of leaf-cutting ants from the State of Bahia in Brazil that was discovered by one of us (JHC Delabie) 27 years ago. We report first observations on the behavioral ecology and natural history of *A. fowleri* and discuss our findings in the context of social parasite biology, evolution, and biogeography.

Materials and methods

Material examined

The specimens examined have been deposited in the institutions listed below:

CPDC	Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, Itabuna, Bahia, Brazil
DZUP	Coleção Entomológica "Padre Jesus Santiago Moure", Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil
IMLA	Instituto Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina
MCZC	Museum of Comparative Zoology Collection, Harvard University, Cambridge, MA, USA
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil
SIBR	Social Insect Biodiversity Repository, School of Life Sciences, Arizona State University, Tempe, AZ, USA
USNM	United States National Museum of Natural History, Washington, DC, USA

Morphological analysis

Specimens were examined and measured using a Leica M125 C stereomicroscope fitted with an ocular micrometer. Measurements were recorded to the nearest 0.01 mm at the maximum magnification allowed for each measurement without exceeding the bounds of the micrometer. Composite images were generated using a Leica DFC450 digital camera mounted to a Leica M205 C stereomicroscope and assembled using Leica Application Suite (version 4.5) and Helicon Focus (version 6.6.1) software packages. Scanning Electron Micrographs were taken at the Muséum National d'Histoire Naturelle (MNHN) in Paris, France, using the JEOL JSM-840 scanning electron microscope of the MNHN's Common Service of Electronic Microscopy facility. Morphological terminology, measurements and indices used for taxonomic description follow recent taxonomic studies of fungus-growing ants (Rabeling et al. 2015; Sosa-Calvo et al. 2018). Measurements are given in millimeters and abbreviations for measurements and indices are as follows:

Cephalic index (CI) HW/HL × 100.

Eye length (EL) Maximum diameter of the eye from the dorsal to the ventral margin, measured in full-face view.
Eye width (EW) Maximum diameter of the eye between both lateral margins, measured in lateral view.
Frontal lobe distance (FLD) Maximum horizontal distance between the outer borders of the frontal lobes, measured in full-face view.
Gaster length (GL) Maximum length of the gaster, measured from the meeting of the fourth abdominal tergum and sternum at their anterior ends to the posteriormost point of the last segment, measured in lateral view.
Head length (HL) Maximum vertical distance of the head in full-face view, excluding mandibles, measured in a straight line from the midpoint of the anterior clypeal margin to the midpoint of the posterior margin of the head. In species where the posterior margin of the head or the clypeal margin (or both) is concave, the measurement is taken from the midpoint of a transverse line spanning the anteriormost or posteriormost projecting points, respectively.
Head width (HW) Maximum horizontal width of the cephalic capsule, excluding the eyes, measured in full-face view.
Interocular distance (IOD) Maximum horizontal width of the head, including the eyes, measured in full-face view.
Mandible length (ML) Maximum mandible length, measured in a straight line from the mandibular insertion into the head capsule to the distal end of the apical tooth, measured in full-face view.
Mandibular index (MI) ML/HL × 100.
Metafemur length (FL) Maximum length of metafemur, measured in dorsal view.
Petiolar width (PW) Maximum width of petiole, measured in dorsal view.
Petiole length (PL) Maximum length of the petiole, measured in lateral view from the posteriormost margin of the metapleural lobe to the posteriormost margin of the petiole.
Postpetiolar width (PPW) Maximum width of postpetiole, measured in dorsal view.
Postpetiole length (PPL) Maximum length of the postpetiole, measured in lateral view along the margin where postpetiolar tergite and sternite meet.
Pronotal width (PrW) Maximum width of the pronotum, measured in dorsal view.
Scape index (SI) SL/HW × 100.
Scape length (SL) Maximum length of the antennal scape, excluding the condylar bulb.
Total length (TL) Sum of ML, HL, WL, PL, PPL, and GL.
Weber length (WL) Diagonal length of the mesosoma from the point at which the pronotum meets the cervical shield to the posterior base of the metapleuron, measured in lateral view.

Results and discussion

Here, we describe a new inquiline social parasite species, *Acromyrmex fowleri* sp. nov., which was discovered 27 years ago near Ilhéus in the state of Bahia in Brazil (see Taxonomic Account below). The combined morphological, behavioral, life history, and natural history data suggest that *Acromyrmex fowleri* is a queen-tolerant, obligate, workerless inquiline social parasite of the leaf-cutting ant *Acromyrmex rugosus*. The observed combination of morphological, behavioral, and life history characteristics is indicative of the inquiline syndrome, a combination of traits shared by the approximately 100 inquiline social parasite species that evolved across the ant tree of life from predominantly independent evolutionary origins.

The inquiline syndrome of *Acromyrmex fowleri*

Mixed colonies

In 1992, Jacques H. C. Delabie discovered winged queens and males of *Acromyrmex fowleri* inside the nests of *A. rugosus*. These mixed colonies consisted of *A. fowleri* alates as well as a single dealate queen, many workers, as well as winged queens and males of *A. rugosus*. Observing a mixed colony in eusocial insects is immediately indicative of a socially parasitic interaction between different species (Wasmann 1891, Wheeler 1910, Hölldobler and Wilson 1990). In contrast, the interactions of different species sharing a compound nests, defined as ant species sharing a nest space but keeping their brood separately, can be predatory, parasitic, commensalistic, or mutualistic (Menzel and Blüthgen 2010; Gray et al. 2018).

Polygyny and host queen tolerance

To examine the mixed colonies of *A. fowleri* and *A. rugosus* in detail, multiple nests were excavated revealing several dealate *A. fowleri* queens inside a single *A. rugosus* host colony, suggesting that *A. fowleri* is polygynous (Delabie et al. 2002). *Acromyrmex fowleri* was also observed to live alongside the *A. rugosus* queen in parasitized colonies (Delabie et al. 2002), suggesting that *A. fowleri* is a queen-tolerant inquiline social parasite. The observations that alates of *A. rugosus* were present in parasitized colonies (Delabie et al. 1993) further corroborates the interpretation that *A. fowleri* is host queen-tolerant and also indicates that the *A. rugosus* queen was reproductively active in the presence of *A. fowleri* and that the social parasite did not suppress the host queen's production of sexual offspring. Host queen tolerance is observed in all other inquiline parasites of fungus-growing ants (Schultz et al. 1998; De Souza et al. 2007; Rabeling and Bacci 2010; Rabeling et al. 2015), except for *P. argentina,* which either kills the host queen(s) or preferentially parasitizes queenless host colonies (Bruch 1928; Gallardo 1929; Rabeling and Bollazzi, unpubl. data).

Absence of the worker caste

During the excavations of mixed colonies, workers of *A. fowleri* were never encountered, suggesting that *A. fowleri* lost the worker caste and is a workerless inquiline social parasite (Delabie et al. 1993). In general, inquiline social parasites preferentially produce sexual offspring and most inquiline species lost the sterile worker caste. Among the inquilines of fungus-growing ants, *P. argentina*, *M. castrator*, and *A. charruanus* also lost their worker caste (Gallardo 1916; Rabeling and Bacci 2010; Rabeling et al. 2015), whereas *A. ameliae* and *A. insinuator* still maintain a reduced number of workers in their colonies (Schultz et al. 1998; Bekkevold and Boomsma 2000; De Souza et al. 2007; Soares et al. 2011).

Morphological traits of the inquiline syndrome

Acromyrmex fowleri exhibits some but not all of the morphological traits characteristic of the inquiline syndrome (sensu Kutter 1968; Wilson 1971; Hölldobler and Wilson 1990). Most notably, *A. fowleri* is significantly smaller than its host *A. rugosus* and the integumental sculpturing is completely reduced; therefore, individuals appear smooth and shiny (Figs. 1 and 2). Superficially, *A. fowleri* resembles the socially parasitic fungus-growing ant species *P. argentina* and *M. castrator*. However, *A. fowleri* lacks some of the highly derived morphological characteristics of the inquiline syndrome present in *P. argentina* and *M. castrator*. For example, *A. fowleri* retains four maxillary and two labial palp segments (Fig. 3c, d), representing the plesiotypic condition in fungus-growing ants, whereas the maxillary palps of *P. argentina* and *M. castrator* are reduced to three segments (Gallardo 1916; Rabeling and Bacci 2010). In addition, the males of *A. fowleri* retain the plesiotypic condition of 13 antennal segments (Fig. 3a), whereas males of *P. argentina* and *M. castrator* reduced the number of antennal segments to 11. Interestingly, the aedeagus of *A. rugosus* bears a very large dorsal lobe that is absent from *A. fowleri* (Fig. 4). Lastly, *A. fowleri* is only known from the coast of Ilhéus in the State of Bahia in the Brazilian Northeast. *Mycocepurus castrator* occurs significantly further south in Rio Claro, State of São Paulo, Brazil, and *P. argentina* is distributed throughout southern Brazil (States of Paraná and Rio Grande do Sul), Uruguay, and northern Argentina (Rabeling et al. unpublished data).

The comparative morphological analysis reveals that *A. fowleri* is in fact remarkably similar to its host species, *A. rugosus* (Figs. 1 and 2). Notwithstanding, the gyne of *A. fowleri* can easily be distinguished from *A. rugosus* by the smaller size, the smooth and shiny integument, and the presence of appressed and transversally flattened setae (Figs. 1 and 3b). The male of *A. fowleri* resembles the male of *A. rugosus* closely, and interestingly, the male of *A. fowleri* is not gynaecomorphic (Fig. 2). In contrast, the males of many highly modified inquiline social parasites resemble the queen caste or become pupoid (Wilson 1971). The males of *P. argentina* and *M. castrator* are gynaecomorphic and closely resemble the queen, whereas the males of all other attine inquilines can be clearly recognized as *Acromyrmex* males (Rabeling and Bacci 2010).

In conclusion, the character analysis of the inquiline syndrome in fungus-growing ants reveals that *Acromyrmex* social parasites are an example of parallel evolution, and the different social parasite species evolved the traits of the inquiline syndrome in a mosaic fashion, where not all parasites are specialized to the same degree. The evolutionary pattern of phenotypic and life history evolution in *Acromyrmex* social parasites exhibits striking parallels to the mosaic evolution of inquiline social parasites in the ant genus *Pheidole* (Wilson 1984).

Biology of *A. fowleri* and its host *A. rugosus*

Parasitism rate and colony census

Delabie et al. (1993) noted that the nest density was unusually high among parasitized *A. rugosus* populations, with nest entrances being approximately 10 meters apart from each other (Delabie et al. 1993). To test the frequency of parasitized host colonies, Delabie and colleagues excavated a total of 65 nests and in five of them (7.7%) alate queens and males were detected (Delabie et al. 1993, 2002). For two parasitized colonies, a full colony census of parasite alates was taken, revealing 30 females and eight males in the first, as well as 38 females and ten males in the second host colony (Delabie et al. 1993). The numerical male–female sex ratio was biased towards females for both colonies (1:3.75 and 1:3.8).

Interestingly, *A. fowl*eri seemed to have been a common species in the Ilhéus region at the time when behavioral observations were first conducted (1992–1996), and the nest densities of its host *A. rugosus* were locally very high with an estimated number of about 20 nests per hectare (Delabie, pers. observation). High host nest density is one of the ecological conditions predicted to favor the evolution of a social parasitism (Wilson 1971; Buschinger 1990). During the past 15 years, however, it seems that *A. rugosus* has become uncommon along the coast near

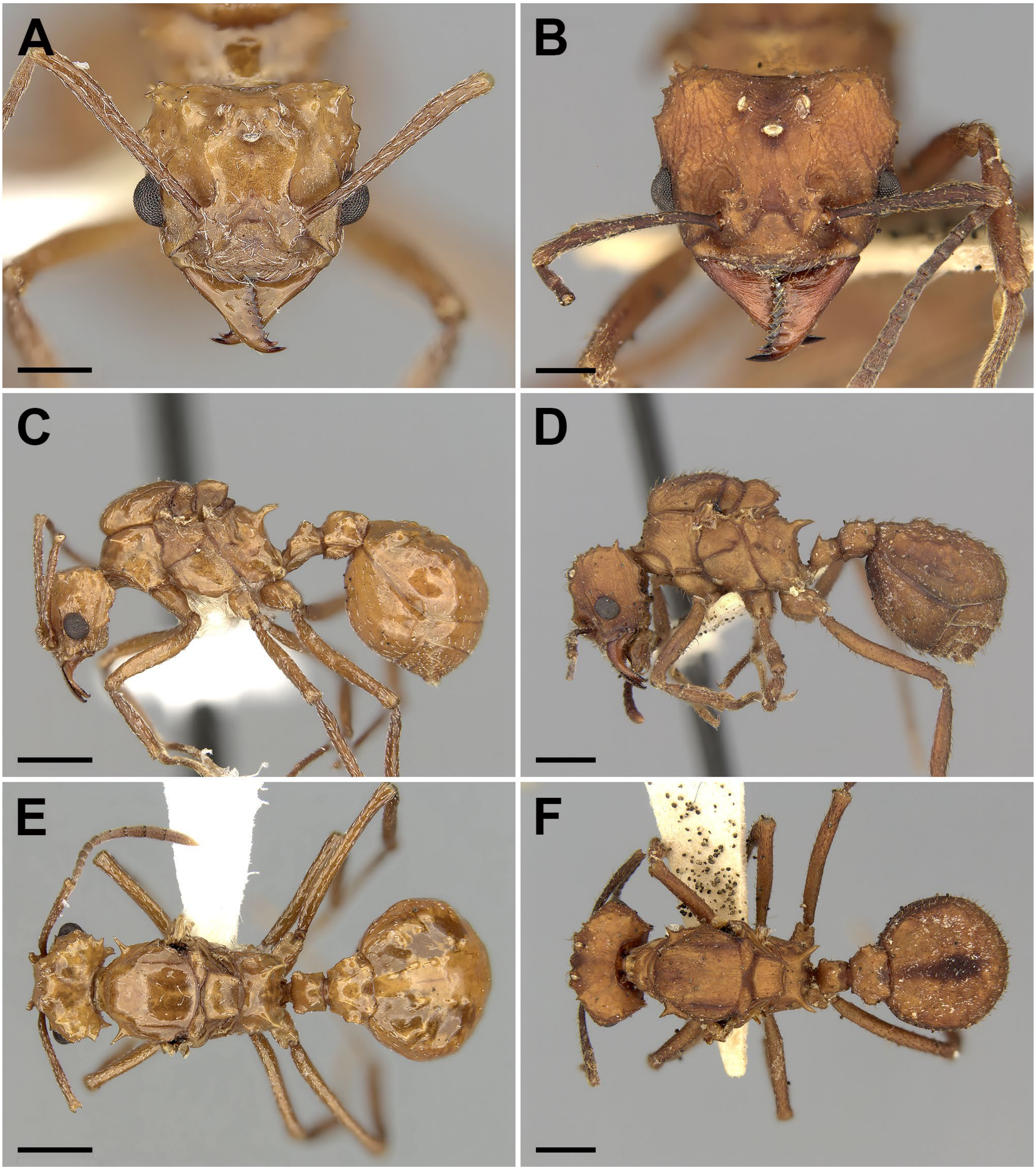

Fig. 1 Gynes of the social parasite *Acromyrmex fowleri* (**a**, **c**, **e**) and its host *Acromyrmex rugosus* (**b**, **d**, **f**) in full-face (**a**, **b**), lateral (**c**, **d**), and dorsal (**e**, **f**) views. The scale bars represent 0.5 mm in **a** and **b**, and 1 mm in **c**–**f**

Ilhéus, and *A. fowleri* could not be encountered anymore. The last systematic attempt to find *A. fowleri* was made in 2004, when one of us (I. C. do Nascimento) collected alates from mating flights for the entire year from January to December along a 6-km beach transect, including one of the sites where *A. fowleri* was commonly encountered between 1993 and 1996. Only five *A. fowleri* alates were found during the year-long survey, while alates of the

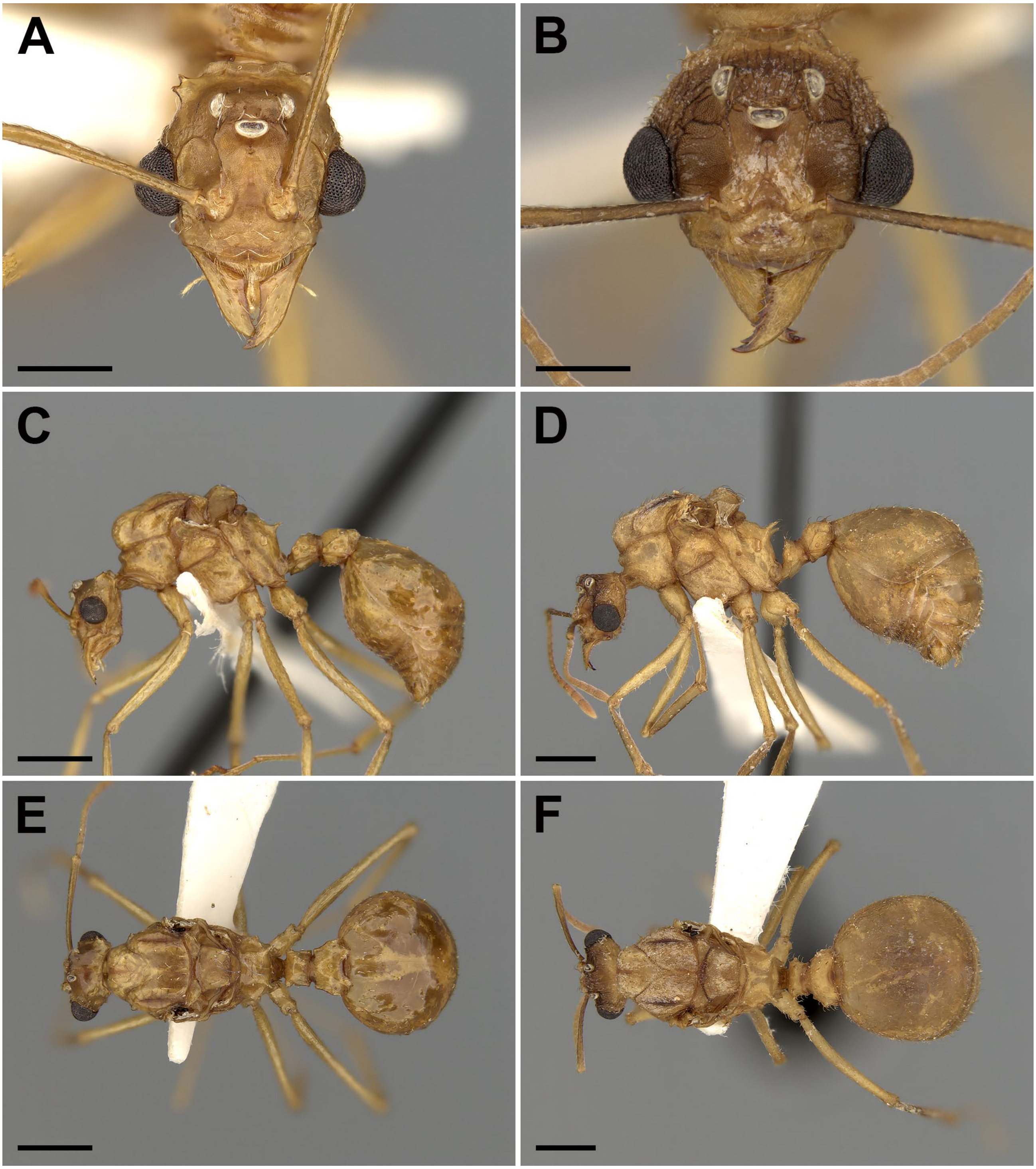

Fig. 2 Males of the social parasite *Acromyrmex fowleri* (**a**, **c**, **e**) and its host *Acromyrmex rugosus* (**b**, **d**, **f**) in full-face (**a**, **b**), lateral (**c**, **d**), and dorsal (**e**, **f**) views. The scale bars represent 0.5 mm in **a** and **b**, and 1 mm in **c**–**f**

host were most regularly reported (I. C. do Nascimento et al. pers. observations). It is unknown whether the high parasite density caused the decline of the host species in this habitat, or whether the population density of *A. rugosus* declined for other reasons and is now too small to support a viable social parasite population. Irrespective of the causes of the population decline, it is possible that *A. fowleri* is locally extinct.

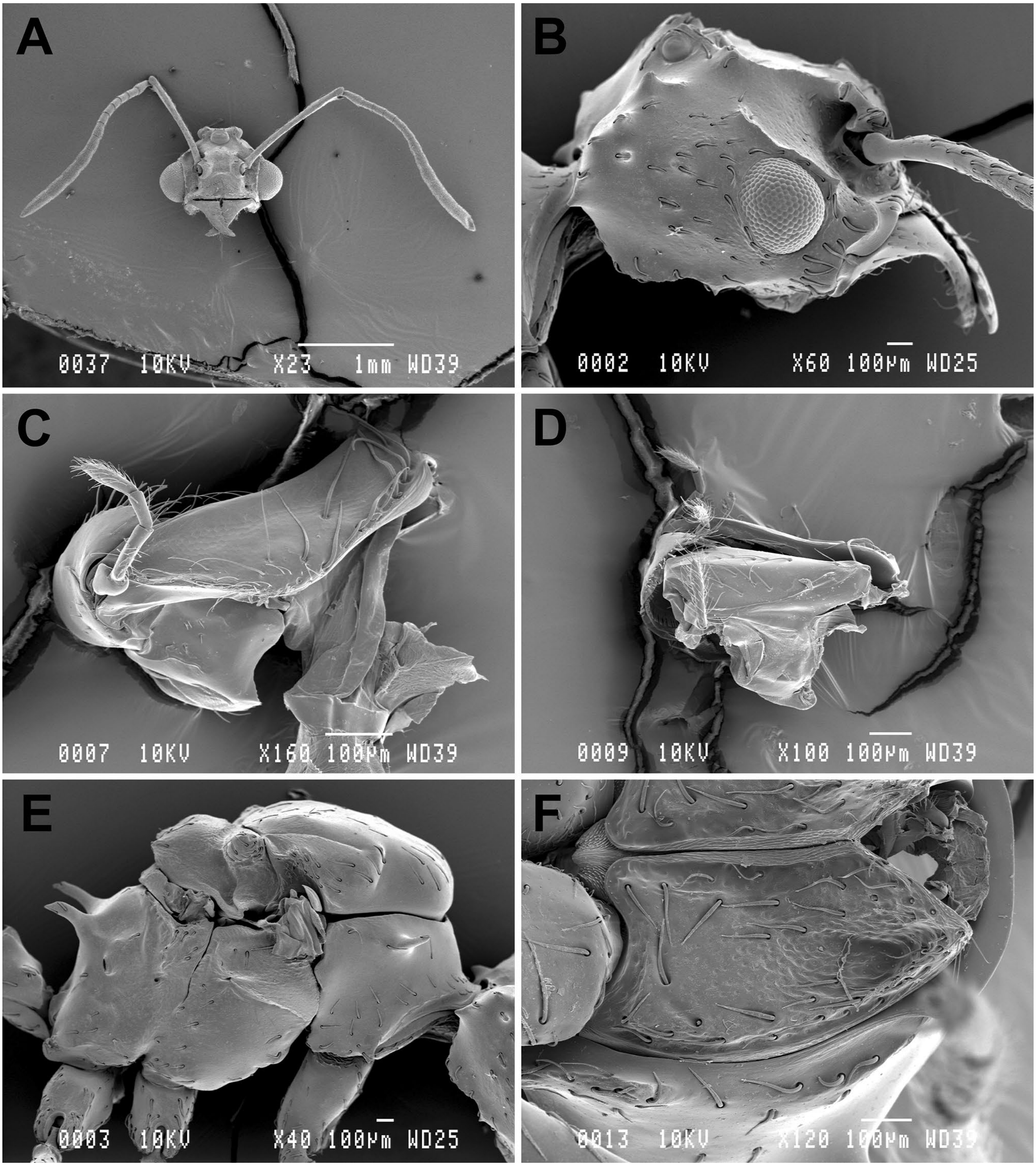

Fig. 3 Scanning electron micrographs of an *Acromyrmex fowleri* male (**a**) and female (**b**–**f**) depicting **a** the male head in frontal view, **b** the female head in lateral view, **c** the female maxilla showing the maxillary palp, **d** the female labium showing the labial palp, **e** the female mesosoma, and **f** the left female propleuron. The scale bars represent 1 mm in **a** and 100 μm in **b**–**f**

Mating flights

Large numbers of alate *A. fowleri* queens and males were found during the morning hours (6–7 h) along the drift line on the beach at the Atlantic Ocean, indicating that *A. fowleri* performs pre-dawn mating flights. The existence of mating flights further suggests that *A. fowleri* alates mate outside the host nest. Among the social parasites of fungus-growing

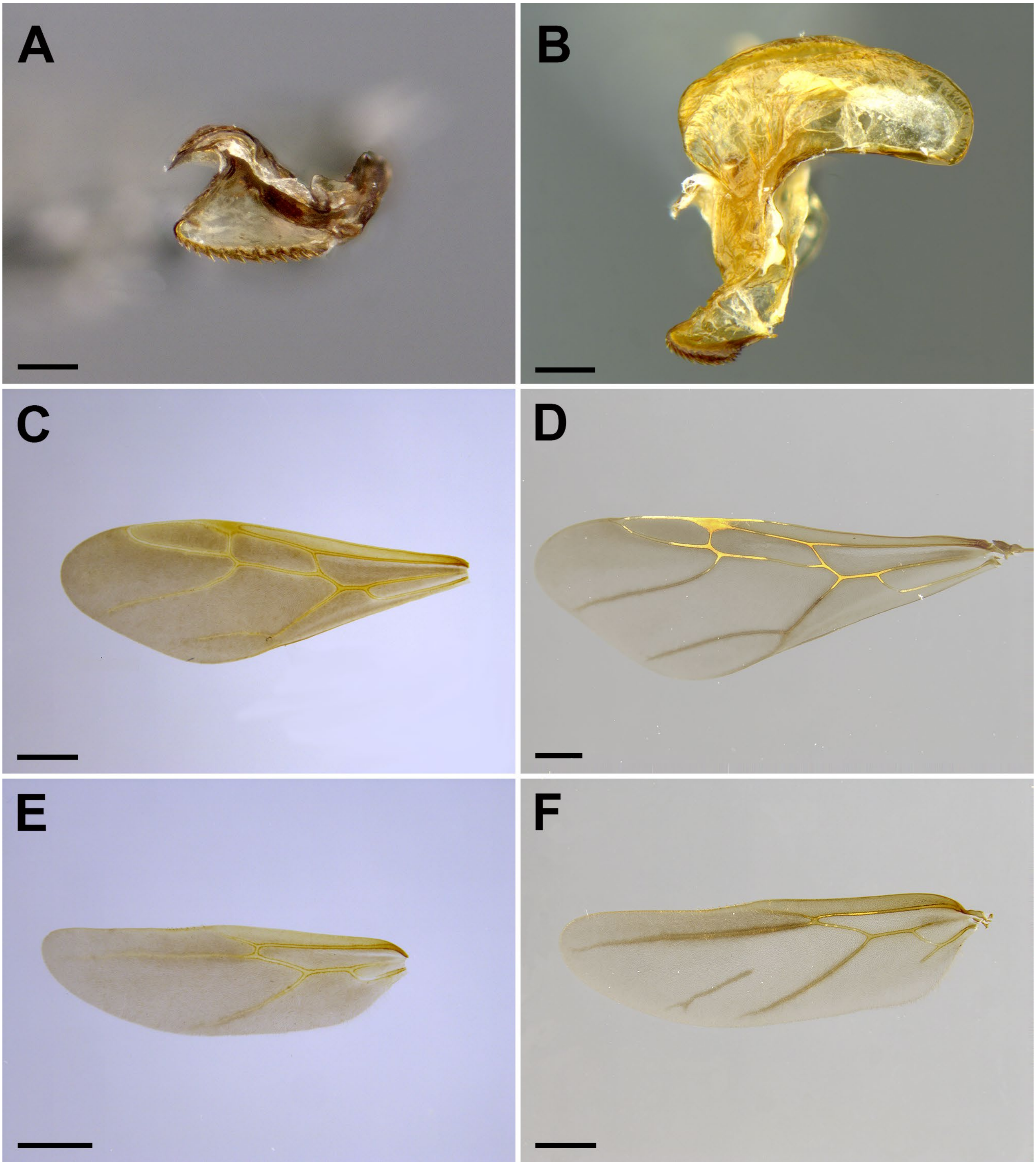

Fig. 4 Comparative anatomy of male genitalia (**a**, **b**), female forewings (**c**, **d**), and female hindwings (**e**, **f**) of *Acromyrmex fowleri* (**a**, **c**, **e**) and *Acromyrmex rugosus* (**b**, **d**, **f**). The scale bars represent 0.1 mm in **a**, 0.2 mm in **b**, and 1 mm in **c**–**f**

ants, the morphologically less specialized inquilines, such as *A. insinuator*, *A. ameliae*, and *A. charruanus*, are known to conduct mating flights (Schultz et al. 1998; Soares et al. 2010; De Souza et al. 2011; Rabeling et al. 2015), whereas the highly specialized inquiline parasites, such as *P. argentina* and *M. castrator*, are adelphogamous and mate inside the host colony, presumably with their siblings (Bruch 1928; Gallardo 1929; Rabeling and Bacci 2010).

Mating flights of *A. fowleri* were observed year-round at a low rate; however, from October to March/April the

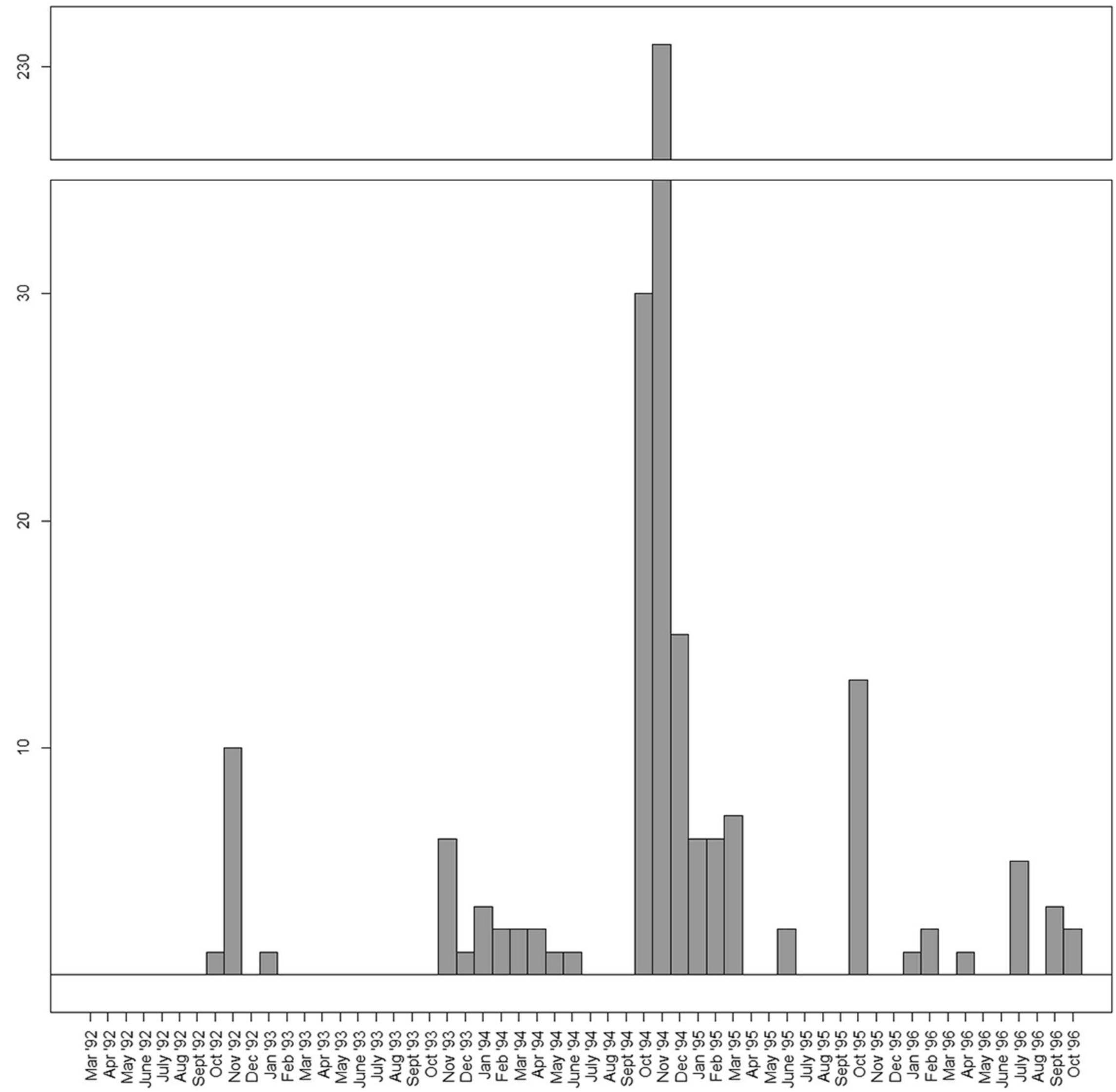

Fig. 5 Mating flight activity of *Acromyrmex fowleri* alates recorded between 1994 and 1996. The number of alate *A. fowleri* individuals is depicted on the *y*-axis and the time period of our collections is depicted on the *x*-axis

number of dispersing alates increased significantly (Fig. 5) (Delabie et al. 2002). The majority of all alates (70%; 247 of 354 individuals) was collected during the month of November in 1994. Approximately, 13% (45 of 354 individuals) of all alates were collected outside of the peak dispersal months, suggesting that low-frequency dispersal occurs throughout the year. The mating flights of parasite and host were not fully synchronized, but the time periods of their mating flights overlapped broadly, with *A. rugosus* dispersing from December to March (Delabie et al. 2002). The mating flights of *A. fowleri* and *A. rugosus,* therefore, coincide with the warmer and rainier austral summer, which is a frequently observed pattern for fungus-growing ants (Mehdiabadi and Schultz 2010).

Most of the parasite behavior following the mating flight is unknown, but Fowler (Fowler, pers. observation; cited in Schultz et al. 1998) observed that newly mated *A. fowleri* queens were detected by host workers and repulsed from the nest when they tried to enter mature colonies of *A. rugosus*, suggesting that *A. rugosus* is capable of detecting and evicting invading social parasites. It is currently unknown whether *A. fowleri* reproduces semelparously or iteroparously. Delabie's observations that the fungus garden of parasitized *A. rugosus* colonies looked healthy and showed no evidence of colony decline provide circumstantial evidence for semelparous reproduction of the parasite, similar to *M. castrator* (Rabeling and Bacci 2010). In contrast, *A. insinuator* and *A. charruanus* reproduce iteroparously and the host colonies do not seem to be able to recover from the mass production of parasite alates and collapse after the parasites' nuptial flights (Bekkevold and Boomsma 2000; Rabeling et al. 2015).

Host ecology

So far, *Acromyrmex fowleri* has only been found in nests of *Acromyrmex rugosus*. *Acromyrmex rugosus* is a geographically widespread leaf-cutting ant species in South America and can be found between the 2nd and 31st parallel south (Gonçalves 1961; Fowler 1985; Delabie et al. 2011). *Acromyrmex rugosus* inhabits a wide variety of ecologically distinct habitats, such as cerrado, campo, caatinga, restinga, and Amazon rainforest. In Bahia, *A. rugosus* is frequently found associated with human settlements, but this leaf-cutter ant species was recorded to have a low impact on agriculture. Nests of *A. rugosus* can be large, and single nests were found to contain a maximum number of 26 chambers (Forti et al. 2006, 2011; Verza et al. 2007). *Acromyrmex rugosus* is one of the few leaf-cutting ant species that deposits exhausted fungal substrate and other waste in underground chambers (Verza et al. 2007). In comparison to the enormous colonies of some leaf-cutting ant species, the colonies of *A. rugosus* are of moderate size with an average number of 519 workers per colony (Soares et al. 2006). Colonies of *A. rugosus* were reported to usually be monogynous (Soares et al. 2006; Verza et al. 2007, 2017).

The parasitized *A. rugosus* population around Ilhéus was characterized by high nest densities, and 7.7% (5 out of 65) colonies were parasitized by *A. fowleri* (Delabie et al. 1993). *Acromyrmex balzani* and *A. subterraneus* are restinga-inhabiting leaf-cutting ants that nest in sympatry with *A. rugosus* around Ilhéus, but *A. fowleri* was only found in association with *A. rugosus*.

Social parasite evolution

Since the turn of twentieth century, entomologists have recognized that social parasites are close relatives of their hosts (Wasmann 1891, 1915; Emery 1909; Wheeler 1910, 1919), and Le Masne (1956) coined the term "Emery's rule" for this general pattern. In the aftermath of the modern synthesis of evolutionary biology, these earlier studies were interpreted in a phylogenetic and speciation context, which led to the then controversial hypothesis that parasites could have evolved directly from their hosts via sympatric speciation. Phylogenetic tests of Emery's rule demonstrated that some inquiline social parasite species originated directly from their hosts via sympatric speciation (Savolainen and Vepsäläinen 2003; Jansen et al. 2010; Rabeling et al. 2014; Leppänen et al. 2015), whereas slave-making and temporary social parasites were more likely to speciate in allopatry and began parasitizing their hosts subsequently (Hasegawa et al. 2002; Kronauer et al. 2003; Janda et al. 2004; Beibl et al. 2005, 2007; Maruyama et al. 2008; Heinze et al. 2015; Prebus 2017). A mitochondrial phylogeny of a subset of *Acromyrmex* species inferred *A. fowleri* as a distant relative to *A. rugosus* suggesting that *A. fowleri* evolved via allopatric speciation (Sumner et al. 2004). In contrast to this earlier study, our ongoing studies that utilize a complete taxon sampling of all *Acromyrmex* species and are based on multiple nuclear as well as genomic markers infer *A. fowleri* as a close relative of its host *A. rugosus*, suggesting that *A. fowleri* originated via the *intra*specific, sympatric route of social parasite evolution (Rabeling et al. unpublished manuscript). Our molecular phylogenetic analyses are also consistent with the morphological analysis, demonstrating that *A. fowleri* and *A. rugosus* share many key morphological characters (Figs. 1 and 2). The evolution of social parasitism in *Acromyrmex* leaf-cutting ants will be discussed in detail in a forthcoming publication (Rabeling et al. unpublished manuscript).

Social parasite diversity in tropical regions: the "Kutter–Wilson Paradox"

During the past centuries, myrmecologists unearthed a remarkable diversity of social parasite species (Wheeler 1910; Hölldobler and Wilson 1990; Buschinger 2009). Currently, more than 300 species of ant social parasites are known and the majority of these species occur in the temperate regions of the northern hemisphere (Kutter 1968; Hölldobler and Wilson 1990; Buschinger 2009; Gray and Rabeling, unpublished data). The higher parasite diversity towards high latitudes contradicts the general biogeographic distribution of free-living ant species, which are distributed along a latitudinal diversity gradient with an increase in biodiversity towards the equator (Economo et al. 2018). Kutter (1968) emphasized the paradoxical biogeographic distribution of ant social parasites and estimated that 30% of the Swiss ant diversity were social parasites, whereas the global social parasite diversity amounted to a mere 2% of the world's ant species. In Kutter's opinion, the disproportionally low number of social parasite species in the tropics reflected a sampling bias, testifying to the incomplete knowledge about tropical ant biology and natural history (Kutter 1968). Wilson (1971, 1984; see also Hölldobler and Wilson 1990) confirmed Kutter's biogeographic observations but suggested that the disproportionally high number of social parasites in temperate climates was linked to ecological and physiological factors that favored the evolution of social parasitism instead of being a mere sampling artifact. Furthermore, Kutter, Wilson, and other authors emphasized that only temporary and inquiline social parasites are known from the tropical regions, whereas slave-making social parasites seem to be restricted to the temperate regions (Wheeler 1919, 1925; Kutter 1968; Wilson 1971; Hölldobler and Wilson 1990, Buschinger 2009).

Since Kutter and Wilson described the paradoxical biogeographic distribution of ant social parasites, which we refer to as the "Kutter–Wilson Paradox", the pattern did not change significantly. Dulotic social parasites remain unknown from the Earth's tropical regions, and current estimates reveal that approximately 2.2% of the global ant species are social parasites. The proportion of social parasites remains higher among the Nearctic (12%) and Palearctic (6%) ant faunas. In contrast, only 1.1% of the Neotropical and 0.6% of the Afrotropical and Malagasy ant species are socially parasitic. Despite the fact that the number of known Neotropical social parasite species doubled to currently 45 described species during the past 50 years (Longino 2003, 2006, 2007; Feitosa et al. 2008; Guerrero et al. 2010; Rabeling and Bacci 2010; Rabeling et al. 2015; Prebus and Lubertazzi 2016), the number of free-living ant species also increased significantly (Kempf 1972, Brandão 1991, Fernández and Sendoya 2004). Consequently, the proportion of social parasite to free-living species in the Neotropical region did not change significantly since Kutter's (1968) census.

The underlying causes responsible for this biogeographic pattern are not well understood, and every new social parasite species from the world's tropical regions contributes additional information to this biogeographic puzzle. Wilson (1971) and Hölldobler and Wilson (1990) suggested that a combination of ecological, life history, and climatic factors, such as cool climate, polygyny and potentially polydomy of the host species, as well as high putative host population densities, may facilitate the evolutionary transition from eusociality to social parasitism in temperate regions. In a review of the evolution and distribution of social parasites in the aculeate Hymenoptera, Wcislo (1981) emphasized that developmental synchrony between host and parasite is particularly important for the evolution of brood parasitic behavior, and that populations in temperate regions are more tightly synchronized than in tropical regions.

Our observations of *A. fowleri* and its host *A. rugosus* are in part consistent with the ecological, life history, and climatic conditions under which social parasitism is expected to evolve. Importantly, the nest densities of *A. rugosus* were locally very high when parasitized colonies were observed (Delabie et al. 2002), allowing the parasite ample access to new host colonies. This observation is important because in general, tropical ant faunas are characterized by high species diversity and low abundance (i.e., nest densities) of individual species; whereas, temperate faunas are less diverse but individual species occur at higher densities. Therefore, species that occur at high densities in tropical regions, could potentially provide fertile breeding grounds for social parasite evolution.

The time periods when *A. fowleri* and *A. rugosus* conduct their nuptial flights broadly overlap, which could contribute to the synchronization of host and parasite development. In contrast to the predicted colony organization, the colonies of the host *A. rugosus* seem to be predominantly monogynous in the population where the social parasite *A. fowleri* was encountered, which is inconsistent with the expectation that hosts of inquiline social parasites have polygynous and/or polydomous colonies. Additional studies need to verify whether *A. rugosus* is monogynous across its geographic distribution, or whether host colonies in parasitized populations could have shifted from facultative polygyny to monogyny, potentially as a response to being parasitized, as was hypothesized for *Mycocepurus goeldii*, the host of *M. castrator* (Rabeling and Bacci 2010).

To conclude the biogeographic observations, the comparison of historic and current biogeographic patterns, as well as our increased knowledge about the biology and taxonomy of tropical social parasite species and their hosts, indicates that the "Kutter–Wilson Paradox" is a genuine biogeographical phenomenon instead of being a mere sampling artifact. Empirical observations suggest that a combination of ecological and life history traits, including high host population density, synchrony of colony development, and colony organization, needs to be present simultaneously in a population for social parasitism to evolve in tropical habitats.

Taxonomic account

Species description

Acromyrmex fowleri Rabeling, Messer, Lacau and Delabie, NEW SPECIES

Zoobank record: http://zoobank.org/D96C94C2-AF2D-4543-965E−49AB99DFE652.

Holotype, alate gyne BRAZIL, Bahia, Ilhéus, Praia do Norte, 18 km N Ilhéus; S14.6197°, W039.0607°; elevation above sea level: 0 m; collection date: 27 November 1994, 07.00 h; col. Jacques Delabie; individual was collected from the drift line of the Atlantic Ocean on the beach. Presumably alates of *A. fowleri* participated in a predawn nuptial flight and drowned in the sea. The holotype is deposited at the Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, Itabuna, Bahia, Brazil (CPCD) and carries the unique specimen identifier No. ASUSIBR00000001.

Description, holotype gyne Measurements: TL 7.90, WL 2.47, HL 1.30, HW 1.45, IOD 1.59, ML 0.97, FLD 0.75, SL 1.59, EL 0.37, EW 0.33, PrW 1.38, FL 1.73, PL 0.52, PW 0.57, PPL 0.50, PPW 0.92, GL 2.15, CI 110, MI 73, SI

109. A small species of *Acromyrmex* fungus-growing ants (WL 2.47, TL 7.90) that is immediately recognizable as a social parasite due to its smaller body size and shiny integument. Mandibles (MI 73) and appendages (FL 1.73, SI 109) long relative to head and body size, respectively. Integument smooth and shiny, in part translucent, characteristic of the inquiline syndrome. Body surface, antennal scapes, and legs (except for tarsi) sparsely covered with pale, transversally flattened, appressed setae; only tarsi covered with semi-erect setae. *Color* uniformly light orange brown; anepisternum, scutellum, and masticatory margin of mandibles slightly darker, reddish-brown. *Head* head shape subquadrate, slightly wider than long (CI 110); lateral margins parallel to each other; posterior margin with median concavity; posterior and lateral margins with numerous distinct tubercles. Mandibles long and slender in full-face view; external margins sinuate; masticatory margins with 12 teeth; apical and preapical teeth distinctly larger, followed by five small teeth that are interspersed by smaller denticles; mandible surface smooth and shiny, not striate. Palp formula 4:2, representing the plesiomorphic condition of fungus-growing ants. Posterior margin of clypeus trapezoidal, broadly inserted between frontal lobes; anterior margin of clypeus shiny and median portion concave. Unpaired median clypeal seta short (0.09 mm), semi-erect, transversally flattened, only barely projecting over the anterior clypeal margin. Frontal lobes broadly rounded, fully covering condylar bulbs in full-face view; lateral margin of frontal lobe serrated with two distinct tooth-like projections. Frontal carinae extending towards the level of the ocelli, not forming a fully shaped antennal scrobe. Preocular carina forming a straight line in lateral view and traversing the area of the antennal scrobe by one-third of the scrobe's width behind the level of the eye. Eyes large (EL 0.37, EW 0.33) and strongly convex. The three ocelli are small and embedded in the integument. Antennae with 11 segments. Antennal scapes long (SL 1.59, SI 109) with abundant, appressed setae, surpassing the posterior margin of the head by more than one-third of its length. *Mesosoma* Mesosoma slender with caste-specific modifications related to wing bearing. Dorsolateral pronotal spine long, slender, and sharply pointed in dorsal view. Ventrolateral pronotal spine reduced, triangular, with blunt, rounded tip. Dorsum of mesosoma smooth and shiny. Posterior margin of scutellum concave, but not distinctly bidentate. Bulla and meatus of metapleural gland not notably modified from the condition in the host species. Propodeal spines straight, slender, sharply pointed, projecting away from the propodeum at a 90° angle in lateral view. *Metasoma* Anterior peduncle of petiole short, about one-fourth the length of the petiolar node. Dorsum of petiolar node with a pair of irregularly shaped ridges. Postpetiole wider (PPW 0.92) than long (PPL 0.50) in dorsal view, posterior margin slightly concave. Gaster large (GL 2.15). First gastric tergite notably smooth with few broadly rounded, reduced tubercles; on median portion of anterior half tubercles form a pair of shallow, longitudinal ridges. Except for the smaller size, fore- and hindwings resemble the wings of the host species, *A. rugosus*.

Measurements, paratype gynes (*n* = 25): TL 7.33–8.13, WL 2.34–2.69, HL 1.25–1.31, HW 1.38–1.47, IOD 1.53–1.61, ML 0.89–0.98, FLD 0.73–0.78, SL 1.51–1.71, EL 0.36–0.39, EW 0.33–0.37, PrW 1.23–1.44, FL 1.65–1.76, PL 0.48–0.58, PW 0.56–0.63, PPL 0.43–0.55, PPW 0.91–1.02, GL 1.90–2.22, CI 106–114, MI 69–76, SI 107–120.

Paratypes 279 alate gynes and 84 males, ASUSIBR00000002-00000364, from three collection sites along a 40 km stretch of "restinga" habitat (i.e., tropical and subtropical coastal forest habitats that form on sandy, acidic, nutrient-poor soils) along the coastline with the city of Ilhéus at its center.

First collection site: BRAZIL, Bahia, Ilhéus, Praia do Sul, STAC camping, 13 km south of Ilhéus; near the entrance of a subterranean nest of *Acromyrmex rugosus* dug in the sand about 100 m from the beach, S14.91210°, W039.02095°; elevation above sea level: 5 m; collection date: 29 October 1992; col. Jacques H. C. Delabie (1 alate gyne, ASUSIBR00000002); same as above, but 05 November 1992 (7 alate gynes and 6 males, ASUSIBR00000003-15); same as above, but 15 January 1993; col. Harold G. Fowler (1 alate gyne ASUSIBR00000016).

Second collection site: BRAZIL, Bahia, Ilhéus, Praia do Norte, Barramares village, 18 km north of Ilhéus, from the drift line of the Atlantic Ocean on the beach; S14.6197°, W039.0607°; elevation above sea level: 0 m; collection date: 01 November 1993; col Jacques H. C. Delabie (1 male, ASUSIBR00000017); same as above, but 06 November 1993 (2 males, ASUSIBR00000018-19); same as above, but 14 November 1993 (3 males, ASUSIBR00000020-22); same as above, but 13 December 1993 (1 male, ASUSIBR00000023); same as above, but 08 January 1994, 18:00 h (1 male, ASUSIBR00000024); same as above, but 14 January 1994 (2 alate gynes ASUSIBR00000025-26); same as above, but 06 February 1994, 08:00 h (1 alate gyne and 1 male, ASUSIBR00000027-28); same as above, but 06 March 1994, 07:00 h (1 alate gyne, ASUSIBR00000029); same as above, but 20 March 1994, 07:00 h (1 alate gyne, ASUSIBR00000030); same as above, but 01 April 1994, 07:00 h (1 alate gyne, ASUSIBR00000031); same as above, but 02 April 1994, 07:00 h (1 male, ASUSIBR00000032); same as above, but 21 May 1994, 08:00 h (1 male, ASUSIBR00000033); same as above, but 12 June 1994, 08:00 h; col. Ivan C. do Nascimento (1 alate gyne, ASUSIBR00000034); same as above, but 12 October 1994; col. Clayton R. R. Delabie (2 alate gynes and 2 males, ASUSIBR00000035-38); same as above, but 16 October 1994, 07:00 h; col. Clayton R. R. Delabie (1 alate gyne and 4 males, ASUSIBR00000039-43); same as above, but 29 October 1994, 07:00 h; col. Jacques H. C. Delabie and Clayton R. R. Delabie (17 alate gynes and 4 males, ASUSIBR00000044-64); same as above, but 13 November 1994, 07:00-08:00 h; col. Clayton R. R. Delabie (84 alate gynes and 9 males, ASUSIBR00000066-158); same as above, but 20 November 1994, 07:00 h; col. Clayton R. R. Delabie (1 alate gyne and 1 male, ASUSIBR00000159-160); same as above, but 24 November 1994 (1 alate gyne, ASUSIBR00000161); same as above, but 27 November 1994, 07:00 h (112 alate gynes and 26 males, ASUSIBR00000162-298); same as above, but 04 December 1994, 07:00 h (4 alate gynes and 1 male, ASUSIBR00000299-303); same as above, but 18 December 1994, 06:00 h; col. Clayton R. R. Delabie (2 alate gynes and 3 males, ASUSIBR00000304-308); same as above, but 27 December 1994, 07:00 h; col. Ivan C. do Nascimento (2 alate gynes and 2 males, ASUSIBR00000309-312); same as above, but 31 December 1994, 06:00 h; col. Clayton R. R. Delabie (1 alate gyne, ASUSIBR00000313); same as above, but 01 January 1995, 06:00 h; col. Clayton R. R. Delabie (3 alate gynes, ASUSIBR00000314-316); same as above, but 15 January 1995, 06:00 h (1 alate gyne, ASUSIBR00000317); same as above, but 19 January 1995, 07:00 h; col. Ivan C. do Nascimento (1 male, ASUSIBR00000318); same as above, but 27 January 1995 (1 male, ASUSIBR00000319); same as above, but 12 February 1995, 07:00 h (2 alate gynes, ASUSIBR00000320-321); same as above, but 26 February 1995, 06:00 h (1 alate gyne, ASUSIBR00000322); same as above, but 28 February 1995, 06:00 h (2 alate gynes and 1 male, ASUSIBR00000323-235); same as above, but 01 March 1995, 06:00 h (1 alate gyne and 1 male, ASUSIBR00000326-327); same as above, but 03 March 1995, 06:00 h (1 alate gyne and 2 males, ASUSIBR00000328-330); same as above, but 11 March 1995, 07:00 h (1 alate gyne, ASUSIBR00000331); same as above, but 17 March 1995, 07:00 h (1 alate gyne, ASUSIBR00000332); same as above, but 01 June 1995, 06:00 h (1 alate gyne and 1 male, ASUSIBR00000333-334); same as above, but 29 October 1995, 09:00 h (8 alate gynes and 8 males, ASUSIBR00000335-350); same as above, but 01 January 1996, 07:00 h (1 alate gyne, ASUSIBR00000351); same as above, but 10 February 1996, 07:00 h; col. Clayton R. R. Delabie (1 alate gyne, ASUSIBR00000352); same as above, but 20 February 1996, 08:00 h (1 alate gyne, ASUSIBR00000353); same as above, but 06 April 1996, 07:00 h (1 male, ASUSIBR00000354); same as above, but 14 July 1996 (5 alate gynes, ASUSIBR00000355-359); same as above, but 22 September 1996 (3 alate gynes, ASUSIBR00000360-362); same as above, but 26 October 1996 (2 alate gynes, ASUSIBR00000363-364).

Third collection site: BRAZIL, Bahia, Ilhéus, Praia do Malhado, from the drift line of the Atlantic Ocean on the beach; S14.781°, W039.045°; elevation above sea level: 0 m; collection date: 02 November 1994; col. Ivan C. do Nascimento (1 alate gyne, ASUSIBR00000065).

Description, paratype males Measurements ($n=25$): TL 6.89–7.32, WL 2.25–2.47, HL 0.96–1.02, HW 1.00–1.07, IOD 1.25–1.33, ML 0.64–0.70, FLD 0.49–0.51, SL 1.31–1.45, EL 0.37–0.41, EW 0.38–0.43, PrW 1.23–1.44, FL 1.67–1.76, PL 0.37–0.44, PW 0.50–0.61, PPL 0.37–0.44, PPW 0.79–0.92, GL 2.15–2.47, CI 99–108, MI 64–71, SI 128-140. A small male (WL 2.25–2.47, TL 6.89–7.32), distinctly smaller than the male of the host species, *A. rugosus*. Integument smooth and shiny, thin, partly translucent. Body surface covered with few appressed, transversally flattened setae. *Color* uniformly pale yellow- to reddish-brown. *Head* Approximately as wide as long (CI 99–108); behind the level of the eyes, sides rounded and tapering towards the posterior margin of head; head size small relative to mesosoma. Mandibles long, slender, with distinct apical and preapical teeth, followed by seven to eight smaller, irregularly spaced teeth of irregular size; mandible surface smooth, shiny. Palp formula 4:2. Clypeus shape as in gyne; unpaired clypeal seta projecting over the anterior clypeal margin by two-thirds its length. Frontal lobes narrow, leaving the anterior half of the condylar bulbs exposed in full-face view. Preocular carina distinct, traversing the area of the antennal scrobe almost completely, nearly touching frontal carina. Eyes very large (EL 0.37–0.41, EW 0.38–0.43), strongly convex. Ocelli large, raised above the surface of the head; unpaired median ocellus approximately one and a half times wider than paired lateral ocelli. Antennae with 13 segments. Antennal scape long (SL 1.31–1.45) with appressed setae, surpassing the posterior margin of the head by half its length. *Mesosoma* Mesosoma with sex-specific modifications related to wing bearing. Anteriodorsal portion of pronotum inflated. Dorsolateral pronotal spine short, broadly triangular, and blunt in dorsal view. Ventrolateral pronotal spine absent. Dorsum of mesosoma smooth. Scutellum shape as in gyne; sculpture granulate with fine rugae. Bulla and meatus of metapleural gland small, orifice of metapleural gland tiny and round, pointing posteriorly, not notably modified from the condition in *A. rugosus*. Propodeal spines short, narrowly triangular, sharply pointed. *Metasoma* Petiole and postpetiole as in gyne. Gaster less bulbous than in host. First gastric tergite smooth, shiny, laterally with few reduced, rounded tubercles; sparsely covered with few appressed setae. Fore- and hindwings resemble the wings of its host, except for smaller size and a missing detached vein at the posterior end of the hindwing. *Genitalia* In toto, excluding the basal ring, parameres longer (1.04 mm) than wide (0.83 mm);

Table 1 Morphological and life history traits characteristic of the inquiline syndrome in fungus-growing ants

	A. insinuator	*A. ameliae*	*A. charruanus*	*A. fowleri*	*P. argentina*	*M. castrator*
Elongated antennal scapes relative to the host species	×	×	×	×	×	×
Multiple egg laying parasite queens coexist in host colony (polygyny)	×	×	?	×	–	×
Coexisting with host queen (host queen tolerance)	×	×	×	×	–	×
Reduced body size	×	×	×	×	×	×
Loss of worker caste	–	–	×	×	×	×
Shiny integument	–	–	–	×	×	×
Reduced pilosity	–	–	–	×	×	×
Number of antennal segments reduced in the male	–	–	–	–	×	×
Number of maxillary pals reduced	–	–	–	–	×	×
Gynaecomorphism	–	–	–	–	×	×
Adelphogamy	–	–	–	–	×	×

apical lobe of paramere evenly rounded with less than 10 long, erect setae. In lateral view, aedeagus small (0.26 mm), ventral border of penis valve bearing 12 recurved teeth of uniform length; the anterior two and posteriormost of which are small and weakly sclerotized, whereas teeth 3-11 are distinctly larger and heavily sclerotized, as notable by the darker brown coloration.

Differential diagnosis The comparative morphological analysis reveals that *A. fowleri* is remarkably similar to its host species, *A. rugosus* (Figs. 1 and 2). Notwithstanding, the gyne of *A. fowleri* can easily be distinguished from *A. rugosus* by the smaller size, the smooth and shiny integument, and the presence of appressed and transversally flattened setae (Figs. 1 and 3b). Relative to its smaller body size, *A. fowleri* is also characterized by longer appendages, and antennal scapes, as well as by a broader postpetiole (Fig. 1, Table 1). In the field, *A. fowleri* can be distinguished from its host by the significantly smaller size, the shiny appearance, the distinctly orange–brown coloration, the slowness of its movements, and the occurrence of alate females and males in some host nests throughout the year, whereas alates of *A. rugosus* typically occur during the rainier and warmer summer months (December–March) in coastal Bahia.

The male of *A. fowleri* resembles the male of *A. rugosus* and is not gynaecomorphic (Fig. 2). Large males of *A. fowleri* reach the same size as small and medium size of *A. rugosus* males, but never reach the body size of large *A. rugosus* males. Despite slightly overlapping size ranges, the males of *A. folweri* can be distinguished from the *A. rugosus* males by their shiny integument, the slenderer and less bulbous gaster, the relatively longer antennal scapes, the absence of the inferior pronotal spine, the more pronounced tubercles on the first gastral tergite, and the presence of few, dorsoventrally flattened, appressed setae (Fig. 2, Table 1). The parasites' genitalia are smaller than the hosts' genitalia (paramere length: *A. fowleri* = 1.04 mm, *A. rugosus* = 1.66 mm), the length of the ventral aedeagal lobe is smaller in *A. rugosus* (*A. fowleri* = 0.26 mm, *A. rugosus* = 0.21–0.22 mm; Fig. 4). It is important to note that the aedeagus of *A. rugosus* bears a very large dorsal lobe that is absent from *A. fowleri* (Fig. 4). The ventral border of the aedeagus bears 12 teeth in *A. fowleri* and 12–14 teeth in *A. rugosus* (Fig. 4).

Worker caste The worker caste is unknown and potentially nonexistent.

Etymology This inquiline social parasite is named in honor of our colleague, the late Harold Gordon Fowler, in recognition of his numerous important contributions to leaf-cutting ant biology, taxonomy, biogeography, and pest management in Brazil and Paraguay.

Previous studies referring to A. fowleri *Acromyrmex fowleri* was discovered 27 years ago and aspects of its biology were discussed in previous publications, where *A. fowleri* was referred to as either "*Pseudoatta* new species", "*Pseudoatta* from Bahia", "*Pseudoatta* from Brazil", or "*Acromyrmex* new species" (Delabie et al. 1993, Delabie et al. 2002; Schultz et al. 1998; Sumner et al. 2004; Schultz and Brady 2008; Rabeling and Bacci 2010; Soares et al. 2011; Rabeling et al. 2015). In this paper, we summarized the published and unpublished observations on the biology of *A. fowleri*. Key aspects of *A. fowleri*'s biology and life history remain unknown and will require detailed field studies as well as conclusive behavioral experiments.

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