
**PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
(BIOLOGIA CELULAR E MOLECULAR)**

**FILOGENIA E BIOGEOGRAFIA DO GÊNERO *ATTA* FABRICIUS, 1804 (FORMICIDAE:
ATTINI) A PARTIR DE ELEMENTOS ULTRA-CONSERVADOS (UCes): EVIDÊNCIAS
DE RECENTE E RÁPIDA ESPECIAÇÃO.**

CORINA ANAHÍ BARRERA

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ciência Biológicas (Área: Biologia Celular e Molecular).

**Rio Claro - SP
Março - 2021**

CORINA ANAHÍ BARRERA

**FILOGENIA E BIOGEOGRAFIA DO GÊNERO *ATTA* FABRICIUS, 1804
(FORMICIDAE: ATTINI) A PARTIR DE ELEMENTOS ULTRA-CONSERVADOS
(UCEs): EVIDÊNCIAS DE RECENTE E RÁPIDA ESPECIAÇÃO.**

Tese apresentada ao Instituto de
Biociências do Câmpus de Rio
Claro, Universidade Estadual
Paulista Júlio de Mesquita Filho,
como parte dos requisitos para
obtenção do título de Doutor em
Ciências Biológicas (Área: Biologia
Celular e Molecular).

Orientador: Maurício Bacci Jr.
Coorientador: Christian Rabeling

**Rio Claro - SP
2021**

B272f

Barrera, Corina Anahí

Filogenia e biogeografia do gênero *Atta* Fabricius, 1804 (Formicidae: Attini) a partir de Elementos Ultra-conservados (UCEs): evidências de recente e rápida especiação. / Corina Anahí Barrera. -- Rio Claro, 2021

114 f. : il., tabs., fotos, mapas

Tese (doutorado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro

Orientador: Maurício Bacci

Coorientador: Christian Rabeling

1. Formiga-cortadeira. 2. Genética animal. 3. Evolução. 4. Análise cladística. 5. Biogeografia. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Biblioteca do Instituto de Biociências, Rio Claro. Dados fornecidos pelo autor(a).

Essa ficha não pode ser modificada.

UNIVERSIDADE ESTADUAL PAULISTA
Câmpus de Rio Claro

CERTIFICADO DE APROVAÇÃO

TÍTULO DA TESE:

FILOGENIA E FILOGEOGRAFIA DO GÊNERO ATTA
FABRICIUS, 1804 (FORMICIDAE: ATTINI) A PARTIR
DE ELEMENTOS ULTRA-CONSERVADOS (UCes):
EVIDÊNCIAS DE RECENTE E RÁPIDA ESPECIAÇÃO

AUTORA: CORINA ANAHÍ BARRERA

ORIENTADOR: MAURICIO BACCI JUNIOR

COORIENTADOR: CHRISTIAN RABELING

Aprovada como parte das exigências para obtenção do Título de Doutora em CIÊNCIAS
BIOLÓGICAS (BIOLOGIA CELULAR E MOLECULAR), pela Comissão Examinadora:

Prof. Dr. MAURÍCIO BACCI JÚNIOR
(Participação Virtual) /
Departamento de Biologia Geral e Aplicada / IB Rio
Claro

Profa. Dra. GABRIELA PROCÓPIO CAMACHO
(Participação Virtual)
Department of Entomology / California Academy of
Sciences

Prof. Dr. HERALDO LUIS DE VASCONCELOS
(Participação Virtual)
Instituto de Biologia / Universidade Federal de
Uberlândia

Prof. Dr. FERNANDO FERNANDEZ
(Participação Virtual)
Instituto de Ciências Naturais / Universidade Nacional
de Colombia

Prof. Dr. ANDRÉS FERNANDO SÁNCHEZ RESTREPO (Participação Virtual)
(FuEDEI) / Fundación para el Estudio de Especies Invasivas

Rio Claro, 25 de março de 2021.

Título alterado para: "FILOGENIA E BIOGEOGRAFIA DO GÊNERO ATTA FABRICIUS, 1804 (FORMICIDAE: ATTINI) A PARTIR
DE ELEMENTOS ULTRA-CONSERVADOS (UCes): EVIDÊNCIAS DE RECENTE E RÁPIDA ESPECIAÇÃO"

*Dedico este trabalho aos meus pais, Sílvia e Héctor, aos pais
dos meus pais e a todos aqueles que por amor, permitiram
que chegasse até mim o presente mais valioso, a minha vida.*

Sem vocês nada houvesse sido possível.

AGRADECIMENTOS

Eu quero agradecer em primeiro lugar a toda minha família, principalmente, os meus pais, meu irmão Marcos, Carlina, meus sobrinhos, Aimé e Caetano, minha avó Erlina e ao Rodriguito, pelo amor e apoio incondicional de sempre e particularmente durante o doutorado, por senti-los perto mesmo longe fisicamente, por sempre confiar em mim e na força da nossa família, por me receber de volta da melhor forma todas as vezes. Amo muito vocês!

À Universidade Estadual Paulista (UNESP), campus Rio Claro e à Coordenação de Pós-Graduação do Instituto de Biociências pela oportunidade de realização do curso e por abrir as portas da instituição para o desenvolvimento deste trabalho.

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001.

A meus professores, orientadores e colaboradores nesse importante trabalho da minha carreira. Me sinto muito grata e privilegiada pela oportunidade de trabalhar na mesma equipe. Ao Prof. Dr. Maurício Bacci Jr. pela oportunidade, confiança, orientação, ensinamentos e apoio durante todo o período. Ao Dr. Christian Rabeling, pela oportunidade de formar parte da sua equipe de pesquisa nos EUA e me receber no seu laboratório, por todo apoio acadêmico e financeiro que fizeram possível grande parte desse estudo. Ao meu colega e amigo Dr. Jeffrey Sosa-Calvo, por ter sido o primeiro em me incentivar a encarar esta importante pesquisa, pelo treinamento no laboratório, todos os ensinamentos, acompanhamento, conselhos e todo auxílio brindado nas análises de dados. Ao Dr. Ted Schultz, por ter sido o primeiro a dizer sim no momento de decidir tomar a frente do projeto, pelo apoio acadêmico e orientações.

Aos meus colegas e amigos do Laboratório de Evolução Molecular (LEM), Milene, Renata, Miagui e Dayane. Obrigada pelo apoio acadêmico, mas especialmente o apoio emocional. Os cafezinhos compartilhados e os bons almoços. À Milene em particular, pelos ensinamentos, pelo carinho e toda a ajuda brindada, no laboratório, durante minha estadia nos EUA e sempre que eu precisei de você, muchas gracias!

Ao departamento de Biologia, ao professor e coordenador do programa de Pós-Graduação em Biologia Celular e Molecular, o Prof. Diogo Cabral de Mello e aos funcionários e professores especialmente do Centro de Estudos de Insetos Sociais (CEIS), Necis, Bibi, Mari L., professores Odair Correa Bueno, André Rodrigues e Osmar Malaspina, pelo apoio brindado sempre que solicitado.

Aos membros da banca examinadora do exame de qualificação e defesa da Tese: Scott Solomon, Heraldo Vasconcelos, Gabriela Procópio Camacho, Fernando Fernandez e Andrés F. Sánchez-Restrepo, pelas avaliações, sugestões, comentários e considerações construtivas que contribuíram muito no polimento e melhora do produto final desse trabalho.

Aos meus colegas de programa e grandes amigos: Rafael, Allison, Amanda O., Caio, Luís A., Manu R., Laka, Lore, Tati, Adna, Quimi, Maria e muitos outros pelas experiências compartilhadas, a amizade forjada, toda ajuda e apoio.

A todos os professores e profissionais, membros dessa grande família de mirmecólogos, pela inspiração durante toda minha carreira, ensinamentos, apoio e incentivo, pela contribuição moral, acadêmica e técnica e me receber tão bem cada vez que visitei seus

laboratórios; Doutoradas e Doutores: Inara Leal, Fabiana Cuezze, Luciana Elizalde, Mariana Nickele, Rodrigo Feitosa, Jacques Delabie, John Lattke, Jarbas M. Queiroz, Fernando Fernandez, Antônio Mayhé-Nunes, Bert Hölldobler, Jack Longino, Phil Ward, Fabricio Baccaro, Heraldo Vasconcelos, Marcio Oliveira, Martín Bollazzi, Andrés F. Sánchez-Restrepo.

A meus colegas biólogos, mirmecólogos e todos os amigos queridos de diferentes partes do Brasil e outros países, pelo apoio, inspiração, pela ajuda nos trabalhos de campo, amostras coletadas, os congressos vividos, por toda a amizade e momentos tão felizes compartilhados, de longe ou juntos: Thalles, Janete, Emília, Pedro. S., Pedro E., Manu, Mayara, Deh, Rodrigo, Iris, Karla, Juci R., Bella, Rodolfo, Eder, Matheus, Mari P., William, Raquel C., Marina O., Nadia, Z., Clarissa K., Bia Caitano, Rafaela, Rick, Júlio, Tiago F., Thiago S., Livia P., Itanna O., Gabi C., Clarisa D, Mônica U., Kelli R., Sabrina S., Jamid, Gibran.

A meus colegas e amigos que fiz durante o tempo que passei nos EUA: Emília, Flora, Dani, Juliana, Eva, Matt, Kyle, Steven, Laura, Rick, Christina, Romain. Em especial ao Kevin (e a Gargoyle), meu amigo e 'hermano de la vida', pela parceria, acolhimento, todo o suporte e apoio durante meu tempo nos EUA, por me receber com tanto carinho na sua casa e me fazer sentir como se fosse também a minha.

Eu quero agradecer de forma muito especial a todos meus amigos e família que fiz em Rio Claro: Mari, Fran, Helô, Mão, Lucas, Yuri, Fer, Viscondi, Roger, Ju, Mah, Clara, Lara, Kawe, Dani F., Edu, Daniel, Thiago, Pedro, Rafa e Murilo, obrigada por TUDO! Sem vocês não teria sido tão especial e importante. Obrigada por todo o apoio e amor que vocês e suas famílias me brindaram, por me ajudar a crescer, evoluir, me tornar uma pessoa e profissional melhor, por todos os momentos e experiências compartilhadas, por reforçar cada dia quão especial o Brasil é e será sempre para mim.

Um agradecimento muito especial, a minha amiga Mariana Ferraz, pela maravilhosa amizade que construímos em tão pouco tempo, por toda a entrega e apoio incondicional nesse último período tão intenso, desafiador e importante que foi o final do doutorado.

Aos meus amigos da Argentina, a TODOS e cada um deles que são muitos: Becha, Sandra, Marce, Sole, Dani, Nadia, Gise, Lau, e com um agradecimento especial a minha amiga da vida Lu, por estar sempre, não importa o tempo, não importa o espaço, você está e isso basta para mim. Muchas gracias mi gran AMIGA!

Aos meus terapeutas e mestres espirituais: Igor, Amélia, Ceci, Elisa, Jade, Larissa e Géssica, por todo apoio e acompanhamento nesse longo processo que é o autoconhecimento. Graças a vocês foi mais fácil e amoroso.

Ao meu amor.

A mim mesma, por cada pequena vitória alcançada, por resistir e persistir, por nunca desistir.

A todos e cada um dos que de alguma maneira formaram parte desta etapa tão importante.

Muito obrigada!

*“Felicidade é quando o que você
pensa, o que você diz e o que você
faz estão em harmonia”*

Mahatma Gandhi

PREFÁCIO

Nesta Tese de Doutorado, apresenta-se uma introdução geral e um capítulo, seguidos das conclusões do trabalho. A introdução geral contém uma revisão bibliográfica sobre a família Formicidae, as formigas Attini, as formigas cortadeiras, particularmente do gênero *Atta*, e questões científicas relacionadas aos objetivos do presente estudo. O Capítulo 1 trata-se do manuscrito científico obtido como produto desta pesquisa e composto pelos principais resultados da Tese. Este é intitulado “*Phylogenomic reconstruction reveals new insights into the evolution and biogeography of Atta leaf-cutting ants (Hymenoptera: Formicidae)*” e foi submetido para a sua publicação na revista *Systematic Entomology*. Ao final, se descrevem as considerações finais com as principais contribuições e conclusões alcançadas.

RESUMO

As formigas (Hymenoptera: Formicidae) constituem um grupo monofilético e são considerados os insetos eussociais mais bem-sucedidos da Terra. O ancestral comum das formigas existentes teve origem há 103–128 milhões de anos atrás (Ma). No final do Cretáceo, junto com expansão das angiospermas, através de múltiplos eventos de especiação, as formigas converteram-se em um grupo extremamente abundante e diverso nos ecossistemas terrestres. Um grupo muito característico de formigas são as cultivadoras de fungos, comumente chamadas de attíneas, capazes de praticar a agricultura de fungos e manter uma associação simbiótica com seus cultivares. Existem cinco sistemas simbióticos de associação entre formigas attíneas e seus cultivares de fungos e o mais especializado deles é representado pelas formigas *Attina* superiores, incluindo as formigas cortadeiras (gêneros *Atta* Fabricius, *Acromyrmex* Mayr e *Amoimyrmex* Cristiano, Cardoso & Sandoval). As formigas cortadeiras são chamadas assim pelo particular hábito que elas têm de cortar os fragmentos de material vegetal que utilizam como substrato para o cultivo do fungo simbiote. As formigas cortadeiras tiveram sua origem há aproximadamente 17–19 Ma, são endêmicas das Américas e consideradas os herbívoros dominantes da Região Neotropical. Estas formigas também apresentam uma grande importância ecológica e econômica, principalmente as do gênero *Atta*, conhecidas no Brasil como saúvas. As saúvas desempenham papéis fundamentais como engenheiros de ecossistemas, por meio da remoção de grandes quantidades de biomassa vegetal, participação em complexas interações biológicas, construção de enormes ninhos e até como pragas agrícolas. Formigas do gênero *Atta* têm uma distribuição muito ampla, que abrange a maior parte do Continente Americano e são reconhecidas atualmente por 15 espécies. Apesar de ser um gênero muito bem estudado, aspectos na sua evolução, biogeografia e taxonomia ainda permanecem sem resolução. O avanço nos estudos moleculares e a aplicação de técnicas de Sequenciamento de Nova Geração permitem o progresso no conhecimento das relações filogenéticas e evolução nos diversos grupos de formigas. O uso de Elementos Ultra-conservados (UCEs) como marcadores genéticos é um dos recursos mais explorados na ciência moderna e tem permitido a obtenção de relevantes evidências sobre as relações filogenéticas dentro de Formicidae e particularmente no grupo das formigas attíneas. Na presente Tese de Doutorado, os UCEs são utilizados para aprofundar os conhecimentos acerca da sistemática, biogeografia e história evolutiva das formigas do gênero *Atta*.

Palavras-Chaves: Formicidae. Formigas cortadeiras. Gênero *Atta*. Sequenciamento de Nova Geração.

ABSTRACT

Ants (Hymenoptera: Formicidae) are a monophyletic group and considered the most successful eusocial insects on Earth. The ancestor of extant ants originated 103–128 million years ago (Ma). During the late Cretaceous, along with the expansion of angiosperms, through multiple speciation events, the ants became an extremely abundant and diverse group in terrestrial ecosystems. A very characteristic group of ants is the fungus-growing ants, also known as ‘attine’ ants, which are capable of practicing fungal agriculture and maintaining a symbiotic association with their fungal cultivars. There are five ant agricultural systems practiced by attine ants and the most specialized of them belongs to the higher-attine, including the leaf-cutting ants (genera *Atta* Fabricius, *Acromyrmex* Mayr, and *Amoimyrmex* Cristiano, Cardoso & Sandoval). Leaf-cutting ants are so called because of the particular habit of cutting the fragments of plants that they use as a substrate for farming the symbiotic fungus. Leaf-cutting ants arose approximately 17–19 Ma, they are endemic to the Americas and considered the dominant herbivores of the Neotropical Region. These ants also have a great ecological and economic importance, especially in the genus *Atta*, known in Brazil as *saúvas*. *Saúvas* play a key role as ecosystem engineers, harvesting large amounts of vegetal biomass, due to their complex biological interactions, building gigantic nests and even as agricultural pests. Ants of the genus *Atta* have wide distribution in the American continent and are currently recognized in 15 extant species. Despite being a well-studied genus, aspects in its evolution, biogeography and taxonomy still remain uncertain. The advancement in molecular studies and the application of Next Generation Sequencing techniques allow progress in the knowledge of phylogenetic relationships and evolution in different groups of ants. The use of ultraconserved elements (UCEs) as genetic markers is one of the most explored resources of modern science and a tool that allows obtaining relevant evidence on phylogenetic relationships within Formicidae and particularly in attine ants group. In the present PhD study, we used UCE data to get a deeper understanding on systematics, biogeography and evolutionary history of ants in the genus *Atta*.

Keywords: Formicidae. Leaf-cutting ants. Genus *Atta*. Next Generation Sequencing.

SUMÁRIO

1.	INTRODUÇÃO GERAL	13
1.1	Família Formicidae	13
1.2	Tribo Attini	15
1.3	Attina: Formigas cultivadoras de fungos	15
1.4	Formigas cortadeiras.....	18
1.5	O gênero <i>Atta</i>.....	20
1.6	A filogenômica como ferramenta para estudos em sistemática e evolução de formigas	25
1.7	Objetivo Geral	26
	COLABORAÇÃO EXTERNA	27
	REFERÊNCIAS	28
2.	CAPÍTULO 1	39
	RESUMO	40
	ABSTRACT	41
2.1	Introduction	42
2.2	Materials and Methods	46
2.2.1	Taxon sampling.....	46
2.2.2	UCE data collection	48
2.2.2.1	Taxon selection and specimen conditioning.....	48
2.2.2.2	DNA extraction and library preparation.....	49
2.2.2.3	Sample pooling and target enrichment of libraries.....	50
2.2.2.4	Processing of UCE sequence data	51
2.2.2.5	UCE phylogenomic analysis	52
2.2.3	Divergence time inference.....	53
2.2.4	Biogeographical analysis.....	54
2.3	Results.....	55
2.3.1	UCE sequencing.....	55
2.3.2	Phylogenetic reconstruction and divergence dating.....	55
2.3.3	Historical biogeography	58
2.4.	Discussion	60
2.4.1	Reconstruction of <i>Atta</i> phylogeny and divergence dating.....	60
2.4.2	Phylogenetic relationships within the genus <i>Atta</i>	62
2.4.3	Historical biogeography and evolution.....	66

	ACKNOWLEDGMENTS.....	70
	REFERENCES	71
	FIGURES	85
	SUPPLEMENTARY TABLES	96
3.	CONSIDERAÇÕES FINAIS.....	112

Introdução Geral

1. INTRODUÇÃO GERAL

1.1 Família Formicidae

As formigas pertencem a uma única família da ordem Hymenoptera, a família Formicidae, e são considerados o grupo de insetos eussociais mais bem-sucedido da Terra (BRADY *et al.*, 2006; HÖLLDOBLER; WILSON, 1990; WILSON, 1990). Sua condição eussocial é caracterizada pela divisão de trabalho com produção de castas estéreis (operárias) e reprodutivas, criação e cuidado cooperativo da prole, assim como também a sobreposição de gerações (HÖLLDOBLER; WILSON, 1990; WILSON, 1971; WILSON; HÖLLDOBLER, 2005a). Estudos de história evolutiva demonstraram que as formigas constituem um grupo natural, monofilético, ou seja, descendente de um único ancestral comum. Esta hipótese é apoiada por evidências filogenéticas (BOROWIEC *et al.*, 2019; BRANSTETTER *et al.*, 2017a) assim como, também, pelas características morfológicas que permitem reconhecer e diferenciar a Formicidae de outras famílias de himenópteros. Desta forma, consideram-se entre as principais sinapomorfias das formigas a presença de: glândula metapleurale, pecíolo nodoso ou cintura e antenas geniculadas, (BOLTON; PALACIO; FERNÁNDEZ, 2003; FERNÁNDEZ; GUERRERO; DELSINNE, 2019). Estas duas últimas características se apresentam também em alguns himenópteros próximos filogeneticamente às formigas, como vespas e abelhas, mas, no entanto, a presença da glândula metapleurale é considerada um caráter derivado e exclusivo (autapomorfia) da família Formicidae (BARONI URBANI, 1989; BARONI URBANI; BOLTON; WARD, 1992).

Estudos baseados em mirmecologia evolutiva estimaram diferentes idades para o ancestral comum mais recente das formigas existentes. Alguns estudos propõem que a origem foi entre 115–135 milhões de anos atrás (Ma) (BRADY *et al.*, 2006; SCHULTZ, 2000), outros obtiveram uma estimativa mais antiga, entre 139–148 Ma (MOREAU; BELL, 2013), e evidências mais recentes, baseadas em análise de genes nucleares, estimaram essa idade em 103–128 Ma (BOROWIEC *et al.*, 2019; BRANSTETTER *et al.*, 2017a). Apesar dessa diferença nas faixas de tempo, estes estudos coincidem em que a divergência das formigas teve sua origem no início do Cretáceo e provavelmente no hemisfério norte. Converteram-se em um grupo extremadamente abundante e que habita a maioria dos ecossistemas terrestres, com exceção dos polos (BRANDÃO, 1999), mas nem sempre foram considerados dominantes; estima-se que a maior concentração de eventos de especiação ocorreu junto a expansão das angiospermas há uns 60–80 Ma (MOREAU *et al.*, 2006). Assim, as formigas se adaptaram às

mais diversas funções ecológicas e se expandiram em milhares de espécies, colonizando com grande sucesso os diferentes ambientes terrestres (FOLGARAIT, 1998; WILSON; HÖLLDOBLER, 2005b).

As formigas constituem de 15 a 20 % da biomassa animal nas florestas tropicais e representam funções fundamentais nos ecossistemas que habitam (EGGLETON, 2020; WILSON, 1990; WILSON; HÖLLDOBLER, 2005b). Atualmente, a família Formicidae é composta por 17 subfamílias, 338 gêneros e quase 14.000 espécies descritas (BOLTON, 2021); as estimativas de vários mirmecologistas coincidem que um grande número de espécies ainda está por ser descoberto, especialmente em regiões tropicais (HÖLLDOBLER; WILSON, 1990; WARD, 2007, 2014). Além disso, dentre as espécies já conhecidas, muitas carecem de uma descrição correta e formal; isso ocorre porque várias das revisões taxonômicas são antigas, confusas e, às vezes, até contraditórias dentro do mesmo grupo (WARD, 2007), apresentando a necessidade de atualização.

Devido a sua grande biodiversidade e biomassa, as formigas desenvolveram uma ampla variedade de comportamentos, hábitos alimentares e de nidificação assim como o tipo de interação com o ambiente e outros organismos (BACCARO *et al.*, 2015; HÖLLDOBLER; WILSON, 1990; SCHULTZ; MCGLYNN, 2000). Estes insetos podem ser importantes predadores de invertebrados assim como herbívoros dominantes nas florestas tropicais, até, inclusive, se tornarem organismos pragas (DELLA LUCIA, 2003; PHILPOTT; ARMBRECHT, 2006; WIRTH *et al.*, 2003). Essa fascinante plasticidade biológica e ecológica lhes permite nidificar na serapilheira, no subsolo, embaixo de pedras, dentro de troncos caídos, sobre as árvores e nas construções urbanas (HÖLLDOBLER; WILSON, 1990; KASPARI, 2003). As espécies de formigas também desenvolveram interessantes especializações adaptativas que as colocam como protagonistas em diversas associações simbióticas, facultativas ou obrigatórias; desta forma, adquiriram a capacidade de colheita de sementes, cuidado de plantas hospedeiras contra possíveis herbívoros, domesticação de pulgões, parasitismo social, agricultura de fungos, entre outras (ARMBRECHT, *et al.*, 2019; MUELLER *et al.*, 2005; NESS; MOONEY; LACH, 2010; RABELING; BACCI, 2010; SCHULTZ; MCGLYNN, 2000).

Com tanta complexidade e particularidades, as formigas representam um dos grupos de insetos mais estudados e que continua alimentando a curiosidade de mirmecólogos e cientistas de outras áreas, bem como do público em geral.

1.2 Tribo Attini

A tribo Attini era conhecida como a tribo exclusiva das formigas cultivadoras de fungos. Recentemente, um estudo sobre a história evolutiva da subfamília Myrmicinae, baseado na análise de genes nucleares de um considerável número de espécies, revelou uma nova filogenia para a subfamília e consequentemente apoiou uma série de mudanças na sua classificação (WARD *et al.*, 2015). Duas destas alterações, entre as mais proeminentes, foram a redução de 25 tribos em apenas seis e a inclusão de gêneros de formigas não cultivadoras (ex: *Blepharidatta* Wheeler, *Cephalotes* Latreille, *Daceton* Perty, *Pheidole* Westwood, *Wasmannia* Forel, entre outros) dentro do grupo Attini (WARD *et al.*, 2015). A partir desse momento, o grupo que envolve exclusivamente formigas que cultivam fungos foi restrito à subtribo Attina [grupo de gêneros *Atta sensu* Ward *et al.* (2015)] ou grupo de formigas attíneas (*attine ants*), comumente chamado na bibliografia atual.

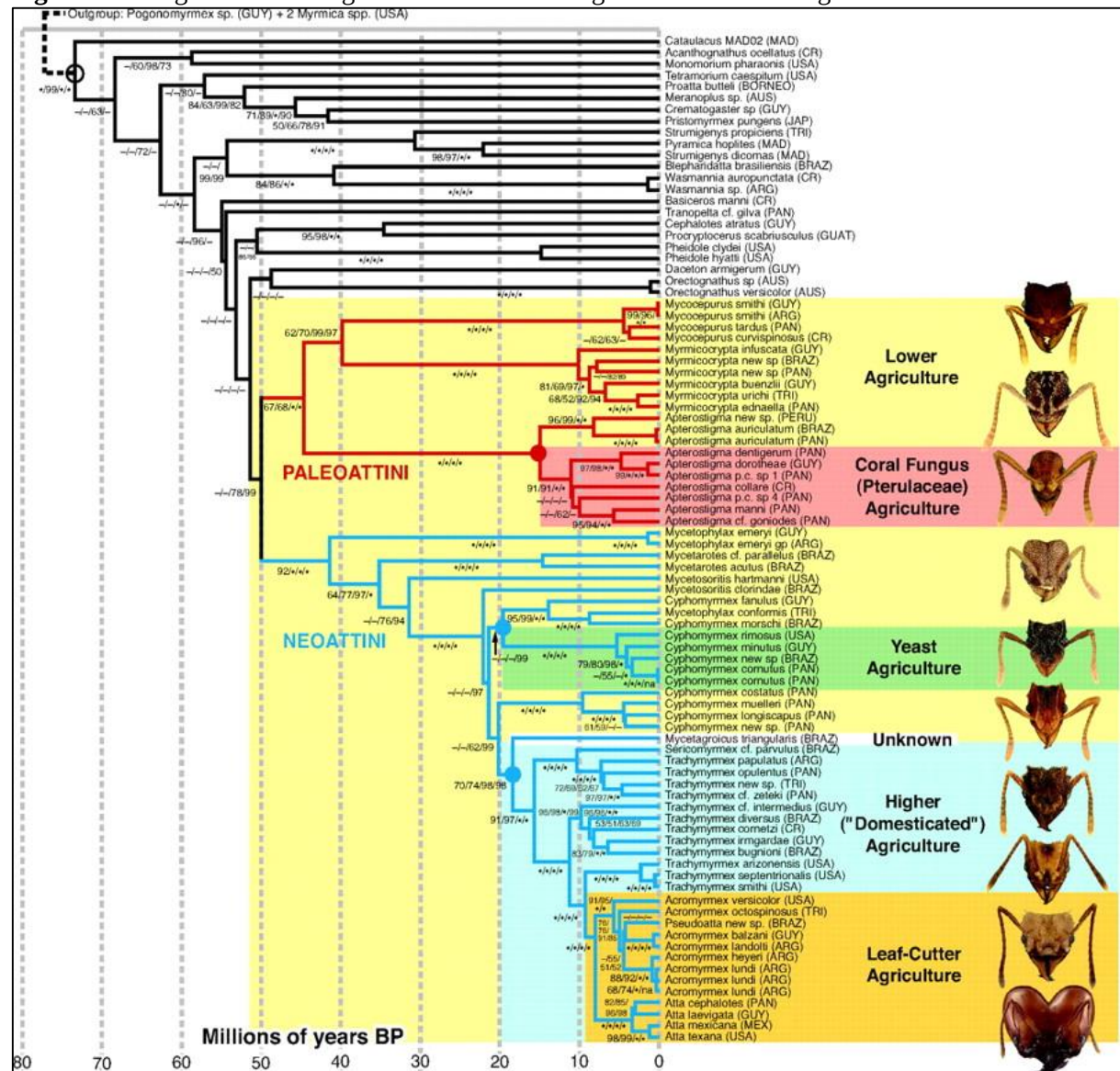
1.3 Attina: Formigas cultivadoras de fungos

O cultivo de fungos realizado por formigas é o sistema de agricultura não humana mais bem estudado. Esta associação das formigas attíneas e seus cultivares de fungo originou-se há 55–65 Ma na região Neotropical, durante o ótimo climático no início do Eoceno (BRANSTETTER *et al.*, 2017b; MUELLER; REHNER; SCHULTZ, 1998; NYGAARD *et al.*, 2016; SCHULTZ; BRADY, 2008). A partir do sistema agrícola original, três cultivares de fungos filogeneticamente distintos derivaram durante os últimos 30 Ma; e a partir de um destes últimos sistemas, foi originado o mais especializado sistema de cultivo, a agricultura de fungos de formigas cortadeiras (BANSTETTER *et al.*, 2017b; SCHULTZ; BRADY, 2008).

Assim são definidos cinco sistemas simbióticos das formigas attíneas e seus cultivares de fungos (BANSTETTER *et al.*, 2017b; SCHULTZ; BRADY, 2008) (ver Figura 1): (i) a agricultura inferior (*Lower Agriculture*) praticada por formigas Attina inferiores, com fungos pertencentes à tribo Leucocoprineae e caracterizados pela capacidade de sobreviver também de forma livre, ou seja, manter seu ciclo de vida fora da simbiose com attíneas (VO; MUELLER; MIKHEYEV, 2009); fazem parte deste sistema formigas dos gêneros *Apterostigma* Mayr, *Cyphomyrmex* Mayr, *Mycetagroicus* Brandão & Mayhé-Nunes e *Mycetophylax* Emery, entre outros; (ii) agricultura de fungos coral (*Coral fungus Agriculture*) cultivados exclusivamente por um clado de espécies de formigas do gênero *Apterostigma* (VILLESEN *et al.*, 2004); este grupo se especializou no cultivo de um fungo de coral (Pterulaceae) filogeneticamente diferente

e estreitamente relacionado com os gêneros *Pterula* Fr. e *Deflexula* Corner (MUNKASCSI *et al.*, 2004; VILLESEN *et al.*, 2004); (iii) agricultura de levedura (*Yeast Agriculture*) limitada às formigas do “grupo *rimosus*” do gênero *Cyphomyrmex* e também capazes de desenvolver vida livre e independente da simbiose com attíneas, no entanto em fase micelial; estes cultivares conseguem desenvolver a fase de levedura apenas quando associadas às formigas, por este motivo foi considerado um caso de adaptação mútua e/ou domesticação (SCHULTZ *et al.*, 2005); (iv) agricultura superior praticada por formigas *Attina* superiores (*Higher “domesticated” Agriculture*), um tipo de cultivares de fungos de simbiose obrigatória e capazes de desenvolver gongilídeos (pontas de hifas inchadas e nutritivas), cultivados principalmente por formigas dos gêneros *Mycetomoellerius* Solomon *et al.*, *Paratrachymyrmex* Solomon *et al.*, *Trachymyrmex* Forel e *Sericomyrmex* Mayr; e (v) agricultura especializada de formigas cortadeiras, derivada da agricultura *Attina* superior generalizada, onde uma diversidade de pouco mais do que 50 espécies de formigas se especializaram em cultivar uma única espécie de fungo, *Leucoagaricus gongylophorus* (Möller) Singer (MIKHEYEV; MUELLER; ABBOT, 2006; MIKHEYEV; MUELLER; BOOMSMA, 2007; SILVA-PINHATI *et al.*, 2004).

Figura 1 - Filogenia das formigas cultivadoras de fungos e seus sistemas agrícolas.



Fonte: SCHULTZ; BRADY, 2008.

Posteriormente, novas evidências revelaram que *L. gongylophorus* não se encontra associado exclusivamente a espécies de formigas cortadeiras e que algumas espécies de formigas cortadeiras são capazes também de cultivar espécies de fungos diferentes (MUELLER *et al.*, 2017; 2018; SOLOMON *et al.*, 2019). Assim, os cultivares de fungos de formigas *Attina* superiores foram divididos em Clado-A e Clado-B (ver Tabela 1). Fungos do Clado-A estão amplamente distribuídos e formam três grupos genotípicos diferentes (*clusters*) permitindo o intercâmbio genético dentro de uma única espécie, ou seja *L. gongylophorus*. E os fungos do Clado-B subdivididos em pelo menos seis linhagens bem suportadas, cada uma provavelmente representando uma espécie de cultivar distinta (MUELLER *et al.*, 2017).

Tabela 1. Classificação dos cultivares de fungo e as formigas Attina superiores que os cultivam.

Fungos de Attina superiores	Formigas Attina superiores
Cultivares Clado-A (<i>L. gongylophorus</i> , anteriormente <i>Attamyces</i>)	A maioria das espécies de formigas cortadeiras. Algumas espécies de formigas não cortadeiras. Exemplos: <i>Paratrachymyrmex diversus</i> (Mann), <i>Paratrachymyrmex intermedius</i> (Forel), <i>Trachymyrmex saussurei</i> (Forel).
Cultivares Clado-B (conjunto de espécies)	A maioria das espécies de formigas não cortadeiras. Algumas espécies de formigas cortadeiras, consumidoras de plantas monocotiledôneas e de ocorrência apenas na América do Sul. Exemplos: <i>Acromyrmex crassispinus</i> (Forel), <i>Atta laevigata</i> (Smith), <i>Atta vollenweideri</i> Forel].

1.4 Formigas cortadeiras

Estas formigas são chamadas de cortadeiras pelo hábito de cortar folhas, flores, galhos e demais partes das plantas as quais carregam e posteriormente usam dentro do seu ninho como substrato para o cultivo do fungo simbiote, que serve como fonte de alimento principalmente das larvas (HÖLLDOBLER; WILSON, 2011; WILSON, 1986). Quando comparado com a utilização de substratos em decomposição, como feito por outras formigas attíneas, o hábito de cortar e produzir o cultivar de fungo a partir de material vegetal fresco representa uma importante transição evolutiva, que caracteriza as formigas cortadeiras como as mais especializadas dentro do grupo de cultivadoras de fungo (MEHDIABADI; SCHULTZ, 2010; MUELLER; RABELING, 2008; WEBER, 1972).

As formigas cortadeiras tiveram sua origem há aproximadamente 17–19 Ma (BRANSTETTER *et al.*, 2017b; LI *et al.*, 2018), são endêmicas das Américas e consideradas os herbívoros dominantes dos trópicos do Novo Mundo (HÖLLDOBLER; WILSON, 2011; WILSON, 1986). Até agora, foram propostas duas hipóteses sobre a região geográfica onde surgiu o ancestral comum de todas as formigas cortadeiras. Por um lado, estudos mais antigos sustentaram uma origem sul-americana baseada na evidência de uma maior diversidade de espécies na América do Sul (FOWLER, 1983; KUSNEZOV, 1963; MUELLER *et al.*, 2017). Por outro lado, Branstetter *et al.* (2017b), a partir da reconstrução evolutiva de formigas attíneas, sugeriram que as formigas cortadeiras possivelmente se originaram em habitats secos

da América Central e subsequentemente tiveram sua dispersão pelas Américas do Sul e do Norte.

A distribuição geográfica atual das formigas cortadeiras é muito ampla. Esta abrange desde a Patagônia argentina no seu extremo sul, até o sul dos Estados Unidos no seu extremo norte, incluindo algumas ilhas do Caribe e com exceção do Chile, sendo o único país da América do Sul onde não ocorrem (FERNÁNDEZ; SENDOYA, 2004; HÖLLDOBLER; WILSON, 1990, 2011; KEMPF, 1972). Ademais, ocupam uma grande diversidade de ambientes como, por exemplo, a Floresta Amazônica tropical e úmida, assim como também habitats áridos como o Cerrado e a Caatinga brasileira (FORTI *et al.*, 2020; SIQUEIRA *et al.* 2018).

Pelo expressivo impacto que causam na vegetação e pela capacidade de se tornarem organismos pragas, principalmente nos sistemas agrícolas, em muitos casos, estas formigas são reconhecidas pela sociedade por um ponto de vista negativo (CHERRETT, 1986; DELLA LUCIA, 2003, 2011; MONTOYA-LERMA, *et al.*, 2012; WIRTH *et al.*, 2003). No entanto, por essa capacidade que elas têm de modificar o ambiente, não apenas com a remoção do material vegetal senão também por meio da construção dos seus enormes ninhos e sua influência sobre outros organismos com os quais têm diversas interações biológicas, estes insetos apresentam um importante valor econômico e principalmente ecológico atuando nos ambientes como engenheiros de ecossistemas (JONES; LAWTON; SHACHAK, 1994; LEAL; WIRTH; TABARELLI, 2014).

A capacidade de consumir uma grande quantidade e variedade de plantas é uma característica que contribui à popularidade destes insetos. No entanto, certos estudos demonstraram que também desenvolveram a habilidade de avaliar o tipo de planta que escolhem cortar (FARJI-BRENER, 2001; MONTOYA-LERMA, *et al.*, 2012; URBAS, 2005). Essa capacidade de seleção forma parte da complexidade comportamental das formigas cortadeiras, uma condição essencial para o seu sucesso nos diversos ambientes (FARJI-BRENER; PROTOMASTRO, 1992; FOWLER *et al.*, 1986).

Atualmente, este grupo de formigas compreende três gêneros (e um total de 53 espécies): *Atta* Fabricius (17 espécies), *Acromyrmex* Mayr (33 espécies) e *Amoimyrmex* Cristiano, Cardoso & Sandoval (3 espécies). Esta é a classificação taxonômica construída a partir de caracteres morfológicos dos táxons (BOLTON, 2021; BORGMEIER, 1959; CRISTIANO *et al.*, 2020; GONÇALVES, 1961). Desde o ponto de vista evolutivo, os estudos filogenéticos têm evidenciado as formigas cortadeiras como um grupo monofilético dentro do clado das Attina Superiores e o mais recentemente derivado de formigas cultivadoras de fungos

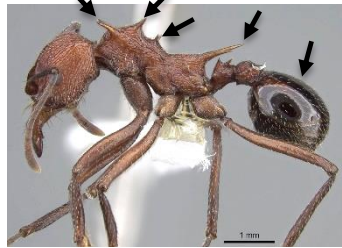
(BRANSTETTER *et al.*, 2017b; LI *et al.*, 2018; NYGAARD *et al.*, 2016;) (Figura 1). No entanto, a sistemática e filogenia das formigas cortadeiras se conhece principalmente a partir de evidências obtidas no estudo de grupos mais abrangentes de formigas e não de forma específica. Neste contexto, a maior parte da bibliografia conhecida, dedicada especificamente ao estudo da sistemática e classificação de formigas cortadeiras, provém exclusivamente de dados morfológicos (FERNÁNDEZ; CASTRO-HUERTAS; SERNA, 2015; GONÇALVES, 1986; HÖLLDOBLER; WILSON, 2011). Novos estudos sobre a evolução e reconstrução filogenética de formigas cortadeiras a partir de dados moleculares, proporcionam maiores amostragens de táxons e, por consequência, resultados mais robustos com uma alta resolução, se tornando importantes complementos aos estudos taxonômicos (BACCI *et al.*, 2009; CRISTIANO *et al.*, 2020; CRISTIANO; CARDOSO; FERNANDES-SALOMÃO, 2013; RABELING *et al.*, 2018; SÁNCHEZ-RESTREPO *et al.*, 2019). Assim, considera-se necessário mais pesquisas que tenham como objeto de estudo o grupo das formigas cortadeiras, em particular, e/ou focado em algum dos seus gêneros.

A seguir, apresenta-se uma sessão particular e detalhada sobre as formigas cortadeiras do gênero *Atta*, por ser este o principal objeto de estudo do presente trabalho.

1.5 O gênero *Atta*

As formigas do gênero *Atta* podem ser diferenciadas dos indivíduos dos outros dois gêneros de cortadeiras pela morfologia externa das operárias, principalmente as de maior tamanho (Tabela 2) (BRANDÃO; MAYHÉ-NUNES; SANHUDO, 2011; CRISTIANO *et al.*, 2020). As principais características diagnósticas de *Atta* são: três pares de espinhos presentes no dorso do mesossoma, o gáster liso, sem tubérculos, e a casta de operárias altamente polimórfica (BACCARO *et al.*, 2015). Também é possível reconhecer o gênero observando a casta de reprodutores, já que rainhas e machos de *Atta* são de tamanho consideravelmente maior. No entanto, esta é uma tarefa de maior dificuldade, primeiro porque indivíduos alados, no geral, emergem num período curto do ano e em segundo lugar são os menos representados nas coleções entomológicas (BORGMEIER, 1950; HÖLLDOBLER; WILSON, 1990, 2011).

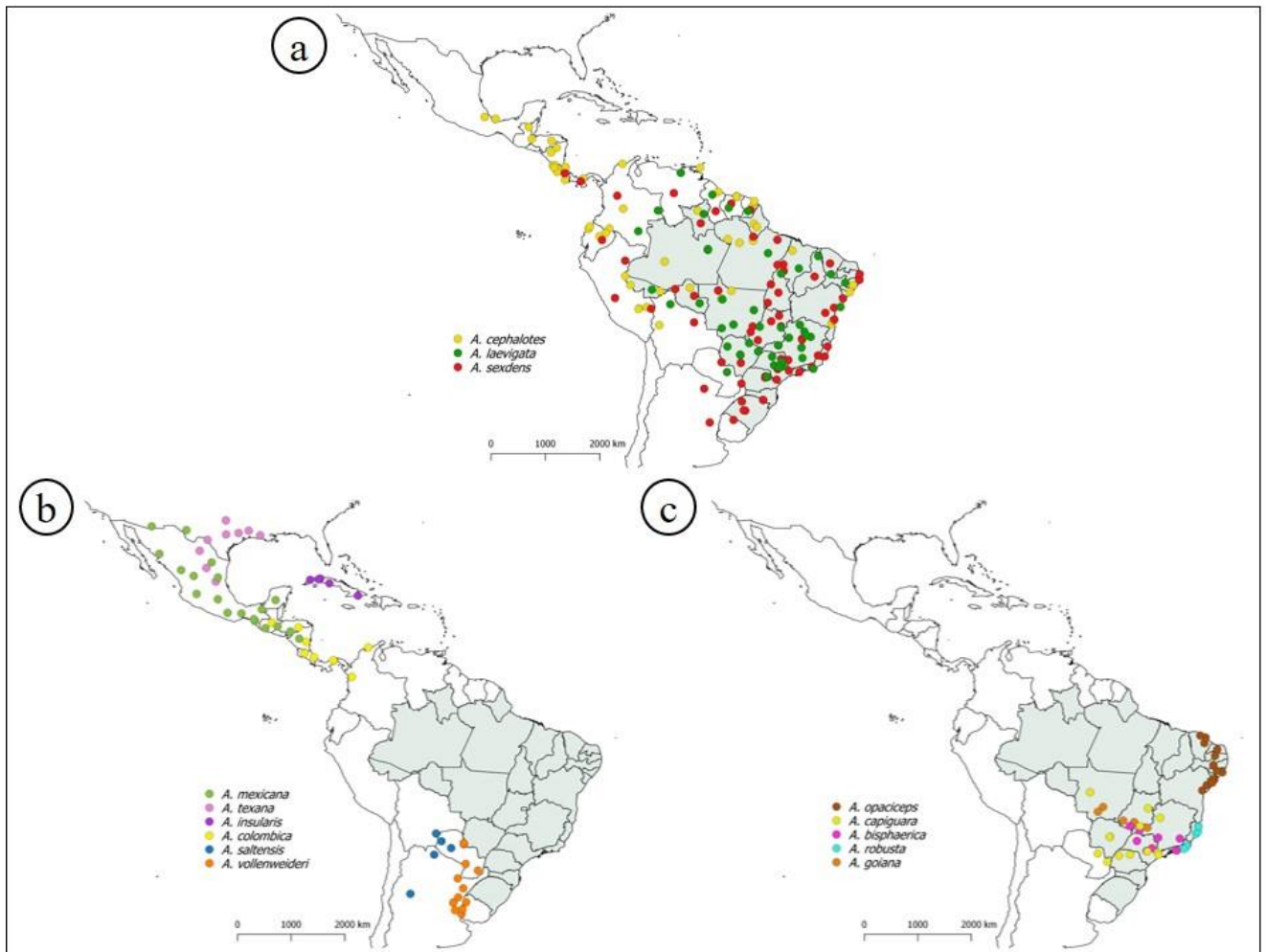
Tabela 2. Principais diferenças morfológicas entre os gêneros de formigas cortadeiras.

<i>Atta</i> - Três pares de espinhos no dorso do mesossoma. Primeiro par de espinhos pronotais ausente. - Gáster liso, sem tubérculos, muitas vezes brilhante.		<i>Atta saltensis</i> Forel
<i>Acromyrmex</i> - Quatro ou cinco pares de espinhos no dorso do mesossoma. Primeiro par de espinhos pronotais presente ou reduzido a tubérculos. - Gáster com presença de tubérculos, proeminentes ou reduzidos.		<i>Acromyrmex</i> <i>lundii</i> Guérin
<i>Amoimyrmex</i> - Quatro ou cinco pares de espinhos no dorso do mesossoma. Primeiro par de espinhos pronotais presente ou reduzido a tubérculos. - Gáster liso sem tubérculos, brilhante e em alguns casos com pequenas estrias.		<i>Amoimyrmex</i> <i>striatus</i> Roger

Fonte das fotos: AntWeb.org

Atta é um gênero de formigas de ampla distribuição geográfica no continente americano (BORGMEIER, 1959; GONÇALVES, 1960; JANICKI *et al.*, 2016). Apesar disso, só algumas das espécies se distribuem abrangendo grande parte da distribuição geográfica total do gênero. Por exemplo, enquanto espécies como *A. laevigata* e *Atta sexdens* Linnaeus se encontram amplamente distribuídas ao longo das Américas, principalmente América Central e do Sul (Figura 2a), outras possuem distribuição mais restrita, ocorrendo em alguns países dos extremos da distribuição geográfica do gênero, como *Atta texana* (Buckley, 1860) e *A. vollenweideri* (Figura 2b) ou apenas no Brasil, como é o caso de *Atta opaciceps* Borgmeier e *Atta robusta* Borgmeier (Figura 2c) (FORTI *et al.*, 2020; GONÇALVES, 1960).

Figura 2. Mapas da distribuição geográfica das espécies de *Atta*.



Fonte: Elaborado pela autora a partir dos dados obtidos para o presente estudo. Programa: Qgis v2.18.14.

Atualmente, o gênero *Atta* é composto por 15 espécies existentes (Tabela 3). São considerados outros dois táxons adicionais, *Atta pilosa* Buckley e *Atta tardigrada* Buckley (BOLTON, 2021); no entanto, estes são *incertae sedis*, ou seja, se encontram sem referência a espécimes depositados em coleções (o espécimen-tipo) e suas descrições são inadequadas. Quaisquer que sejam as verdadeiras identidades das duas espécies, certamente não correspondem a espécies de *Atta* como o gênero é atualmente conhecido.

Tabela 3. Caracterização das espécies de *Atta*: nome científico e autor, nome comum (quando conhecido), tipo de planta que consomem e distribuição geográfica.

Espécies	Nome comum	Substrato	Distribuição (países)
<i>A. bisphaerica</i> Forel, 1908	Saúva mata pasto	Monocotiledôneas	Brasil
<i>A. capiguara</i> Gonçalves, 1944	Saúva parda	Monocotiledôneas	Paraguai, Brasil
<i>A. cephalotes</i> (Linnaeus, 1758)	Saúva da mata	Dicotiledôneas	México, Belize, Honduras, Guatemala, El Salvador, Honduras, Nicarágua, Costa Rica, Ilha de Cocos, Panamá, Trinidad e Tobago, Antilhas Menores, Barbados, Guiana, Guiana Francesa, Suriname, Venezuela, Colômbia, Equador, Peru, Bolívia
<i>A. colombica</i> Guérin, 1844	-	Dicotiledôneas	Guatemala, Honduras, Nicarágua, Costa Rica, Panamá, Colômbia
<i>A. cubana</i> Fontela Rizo, 1995	-	Dicotiledôneas	Cuba
<i>A. goiana</i> Gonçalves, 1942	Saúva	Monocotiledôneas	Brasil
<i>A. insularis</i> Guérin, 1844	Bibijagua	Dicotiledôneas	Cuba
<i>A. laevigata</i> (Smith, 1858)	Saúva cabeça de vidro	Ambos, principalmente dicotiledôneas	Colômbia, Venezuela, Guiana Francesa, Guiana, Suriname, Brasil, Bolívia, Paraguai
<i>A. mexicana</i> (Smith, 1858)	-	Dicotiledôneas	Sul EUA, México, Guatemala, Belize, Honduras, El Salvador, Nicarágua
<i>A. opaciceps</i> Borgmeier, 1939	Saúva do sertão do nordeste	Dicotiledôneas	Nordeste do Brasil
<i>A. robusta</i> Borgmeier, 1939	Saúva preta	Dicotiledôneas	Sudeste do Brasil

<i>A. saltensis</i> Forel, 1913	-	Dicotiledôneas	Bolívia, Centro-Oeste e Norte da Argentina, Paraguai, Oeste do Brasil
<i>A. sexdens</i> (Linnaeus, 1758)	Saúva limão, Formiga da mandioca	Ambos, principalmente dicotiledôneas	Costa Rica, Panamá, Venezuela, Colômbia, Guiana Francesa, Guiana, Suriname, Equador, Peru, Brasil Bolívia, Paraguai, noroeste Argentina, Uruguai
<i>A. texana</i> (Buckley, 1860)	-	Dicotiledôneas	Sul dos EUA
<i>A. vollenweideri</i> Forel, 1893	-	Ambos, principalmente monocotiledôneas	Bolívia, Centro-Oeste do Paraguai, Oeste do Brasil, Centro-Norte e Nordeste da Argentina, Oeste do Uruguai
<i>A. pilosa</i> (Buckley, 1866) [unidentifiable taxa - <i>incertae sedis</i>]	-	-	EUA
<i>A. tardigrada</i> (Buckley, 1867) [unidentifiable taxa - <i>incertae sedis</i>]	-	-	EUA
<i>A. praecursor</i> Frič & Bayer, 1901 [<i>ichnotaxon</i>]	-	-	-

As espécies de *Atta* são polimórficas e o tamanho do corpo das operárias está diretamente relacionado com a função que cada uma desempenha. As de maior tamanho são especializadas na proteção da colônia e, por este motivo, são comumente chamadas de soldados. Operárias de tamanho médio, geralmente, realizam o forrageio e colheita do material vegetal e as menores desenvolvem tarefas, principalmente, dentro do ninho, como a manutenção do jardim de fungos e cuidado da rainha e da prole. Além disso, as dimensões que as colônias de *Atta* alcançam são gigantescas; os ninhos adultos podem viver em média 15 anos, atingir milhões de operárias e criar centenas de jardins de fungos simbiotes (FERNÁNDEZ;

CASTRO-HUERTAS; SERNA, 2015; FERNÁNDEZ; SERNA, 2019; HÖLLDOBLER; WILSON, 2011).

Na construção do seu ninho, as formigas cortadeiras do gênero *Atta* atuam como verdadeiras arquitetas. Um bom exemplo disso é o fantástico experimento que fizeram o professor Luiz Carlos Forti e a sua equipe de pesquisa da Universidade Estadual Paulista (UNESP-Botucatu). Durante três dias, os pesquisadores preencheram uma colônia adulta de *A. laevigata* com aproximadamente dez toneladas de cimento. Após um mês, procederam à escavação e obtiveram como resultado a estrutura representativa de uma colônia de oito metros de profundidade e mais de 300 metros de diâmetro, com até 8.000 câmaras internas e inúmeros túneis. A partir deste estudo, estimou-se que, para a construção de um formigueiro de dimensão e arquitetura semelhantes, as operárias precisam remover 40 toneladas de terra e andar uma distância equivalente a um quilômetro até a superfície do solo com cada uma das cargas (L. C. FORTI *et al.*, dados não publicados; MOREIRA *et al.*, 2004).

Como podemos perceber, este gênero de formigas alcança um nível de importância muito grande por várias razões. Por um lado, é um grupo bem destacado dentro de Formicidae no geral e, particularmente, dentro do grupo das formigas cultivadoras de fungos como um dos gêneros mais recentes e especializados. Além disso, essas formigas desempenham papéis fundamentais nos ecossistemas com a sua participação nas diversas interações simbióticas, como herbívoros dominantes, engenheiros de ecossistemas e de importância econômica como pragas agrícolas no Brasil e diversos outros países da Região Neotropical (BACCI *et al.*, 1995; CORRÊA *et al.*, 2016; HERZ; BEYSCHLAG; HÖLLDOBLER, 2007; LEAL; WIRTH; TABARELLI, 2014; MOUTINHO; NEPSTAD; DAVIDSON, 2003; OLIVEIRA *et al.*, 2018; STERNBERG *et al.*, 2007).

Apesar de *Atta* ser um gênero muito bem estudado na sua biologia e ecologia, vários aspectos na sua evolução, biogeografia e taxonomia ainda permanecem sem resolução. Estudos que abordem estes assuntos são relevantes no preenchimento de lacunas no conhecimento sobre este tão característico e importante grupo.

1.6 A filogenômica como ferramenta para estudos em sistemática e evolução de formigas

Na ciência moderna, os estudos filogenéticos nos grupos de formigas têm avançado muito graças às técnicas que utilizam dados genômicos (BLAIMER *et al.*, 2015; NYGAARD *et al.*, 2016; WARD *et al.*, 2016). Durante a última década, a captura e sequenciamento de Elementos Ultra-conservados ou UCEs, tem sido um dos recursos mais eficientes nos estudos

de sistemática animal e biogeografia (DO AMARAL *et al.*, 2015; FAIRCLOTH *et al.*, 2015; GUEUNING; FREY; PRAZ, 2020; MCCORMACK *et al.*, 2012).

Os UCEs são regiões genômicas fortemente conservadas ao longo da evolução (BEJERANO *et al.*, 2004) que, juntamente com suas regiões vizinhas variáveis, são usados como marcadores moleculares para estudos filogenéticos e análises de datação por divergência (CRAWFORD *et al.*, 2012; FAIRCLOTH *et al.*, 2012; SMITH *et al.*, 2014). Na mirmecologia, a utilização de UCEs permitiu a obtenção de evidências com alto suporte sobre as relações filogenéticas em vários níveis. Por um lado, aquelas entre as formigas e seus grupos irmãos mais recentes, vespas (Apoidea) e abelhas (BRANSTETTER *et al.*, 2017a; FAIRCLOTH *et al.*, 2015). Por outro lado, permitiu elucidar diversificações em subfamílias e tribos de Formicidae (BOROWIEC, 2019; PREBUS, 2017, 2020; WILLIAMS *et al.*, 2020), até com uma resolução superior à fornecida por dados de sequência multilocus tradicionalmente usados em reconstruções filogenéticas (BLAIMER *et al.*, 2015). Dentro do grupo de formigas cultivadoras de fungos, graças aos UCEs, também houve progresso no conhecimento de relações filogenéticas que eram consideradas taxonomicamente conflitantes (gênero *Sericomyrmex*, JEŠOVNIK *et al.*, 2017).

Assim, consideramos que gerar dados de UCEs é uma estratégia muito promissora para caracterizar a biogeografia de *Atta* e estudar a história evolutiva do gênero. Além disso, baseado no estudo destes marcadores moleculares, também está em andamento a revisão filogenética de outros dois gêneros de formigas cultivadoras de fungos, *Cyphomyrmex* (por E. Z. ALBUQUERQUE *et al.*) e *Acromyrmex* (por C. RABELING *et al.*). Estas serão, sem dúvida, peças chaves do quebra-cabeça nos estudos filogenéticos do grupo de formigas attíneas que, em conjunto com os resultados obtidos a partir do presente estudo, nos permitirão fortalecer o conhecimento sobre o grupo Attina.

1.7 Objetivo Geral

A partir do presente estudo filogenético molecular, nos propomos gerar um grande conjunto de dados genômicos de *Atta* que permita resolver as relações filogenéticas ainda indeterminadas de seus clados e reconstruir a história evolutiva do gênero fornecendo novas evidências sobre sua origem, datas de divergência e padrões biogeográficos. Esperamos que nossos resultados forneçam informações adicionais que possam contribuir nos estudos evolutivos e taxonômicos de formigas cortadeiras e outras formigas attíneas.

COLABORAÇÃO EXTERNA

Para a execução desta pesquisa de doutorado contamos com a colaboração do Dr. Christian Rabeling, como co-orientador do estudo, e da sua equipe de pesquisa na *School of Life Sciences* da *Arizona State University* (ASU) em Tempe, AZ, EUA. No *Rabeling Lab*, os estudos são especializados em mecanismos de especiação e diversidade biológica de formigas, bem como na ecologia evolutiva de interações simbióticas entre formigas e outros organismos. As pesquisas do Dr. Rabeling envolvem história natural, comportamento, taxonomia, bem como filogenética, genética populacional e genômica de formigas. Esta colaboração e compromisso com nosso estudo envolveu assistência nos trabalhos de campo, financiamento econômico, fornecimento de infraestrutura, materiais e insumos de laboratório, assim como o acesso e utilização da própria coleção entomológica que faz parte do laboratório do Dr. Rabeling na ASU.

Além disso, contamos com a colaboração do Dr. Jeffrey Sosa-Calvo no treinamento da aluna nos métodos de laboratório (procedimentos de coleta e tratamento de UCEs) e nas análises dos dados; e do Dr. Ted R. Schultz no planejamento e organização do projeto, assim como também com contribuição acadêmica na elaboração do manuscrito produzido para sua publicação científica. Os Drs. Sosa-Calvo e Schultz são pesquisadores do *National Museum of Natural History, Smithsonian Institution*, em Washington, DC, EUA e, assim como também o Dr. Rabeling, há vários anos formam parte de uma equipe de trabalho em parceria e colaboração com o diretor e orientador deste estudo. No *Smithsonian Institution*, estes cientistas, dirigem e acompanham importantes projetos de pesquisa sobre evolução e sistemática de formigas, especialmente as formigas cultivadoras de fungos, ecologia histórica e evolução do comportamento de cultivo de fungos, teoria e método de análise filogenética, métodos quantitativos para avaliar a biodiversidade de formigas, entre outros.

REFERÊNCIAS

- ARMBRECHT, P. *et al.* Ecologia. In: FERNÁNDEZ, F.; GUERRERO, R. J.; DELSINNE, T. (eds.). **Hormigas de Colombia**. Bogotá: Universidad Nacional de Colombia. Facultad de Ciencias. Instituto de Ciencias Naturales, 2019. p. 175–201.
- ANTWEB. **Versão 8.56. California Academy of Science**. 2021. Disponível em: <https://www.antweb.org>. Acesso em: 27 jan. 2021.
- BACCARO, F. B. *et al.* **Guia para os gêneros de formigas do Brasil**. Manaus: Editora INPA, 2015.
- BACCI, M. *et al.* Biopolymer-degrading bacteria from nests of the leaf-cutting ant *Atta sexdens rubropilosa*. **Brazilian Journal of Medical and Biological Research**, v. 28, n. 1, p. 79–82, 1995.
- BACCI, M. *et al.* Phylogeny of leafcutter ants in the genus *Atta* Fabricius (Formicidae: Attini) based on mitochondrial and nuclear DNA sequences. **Molecular Phylogenetics and Evolution**, v. 51, n. 3, p. 427–437, 2009.
- BARONI URBANI, C. Phylogeny and behavioural evolution in ants, with a discussion of the role of behaviour in evolutionary processes. **Ethology Ecology & Evolution**, v. 1, n. 2, p. 137–168, 1989.
- BARONI URBANI, C.; BOLTON, B.; WARD, P. S. The internal phylogeny of ants (Hymenoptera: Formicidae). **Systematic Entomology**, v. 17, n. 4, p. 301–329, 1992.
- BLAIMER, B. B. *et al.* Phylogenomic methods outperform traditional multi-locus approaches in resolving deep evolutionary history: a case study of formicine ants. **BMC Evolutionary Biology**, v. 15, n. 1, p. 1, 2015. DOI: 10.1186/s12862-015-0552-5
- BOLTON, B. **An online catalog of the ants of the world**. 2021. Disponível em: <https://antcat.org>. Acesso em: 15 fev. 2021.
- BOLTON, B.; PALACIO, E. E.; FERNÁNDEZ, F. Morfología y glosario. In: FERNÁNDEZ, F. (ed.). **Introducción a las hormigas de la región Neotropical**. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, 2003. p. 221–231.
- BORGMEIER, T. Estudos sobre *Atta* (Hym. Formicidae). **Memórias do Instituto Oswaldo Cruz**, v. 48, p. 239–263, 1950.
- BORGMEIER, T. Nova contribuição para o conhecimento das formigas neotropicas (Hym. Formicidae). **Revista de Entomologia (Rio de Janeiro)**, v. 10, p. 403–428, 1939.
- BORGMEIER, T. Revision der Gattung *Atta* Fabricius (Hymenoptera, Formicidae). **Studia**, v. 2, n. 1–4, p. 321–390, 1959.
- BOROWIEC, M. L. Convergent evolution of the army ant syndrome and congruence in big-data phylogenetics. **Systematic Biology**, v. 68, n. 4, p. 642–656, 2019.

BOROWIEC, M. L. *et al.* Compositional heterogeneity and outgroup choice influence the internal phylogeny of the ants. **Molecular Phylogenetics and Evolution**, v. 134, p. 111–121, 2019.

BRADY, S. G. *et al.* Evaluating alternative hypotheses for the early evolution and diversification of ants. **Proceedings of the National Academy of Sciences**, v. 103, n. 48, p. 18172–18177, 2006.

BRANDÃO, C. R. F. Reino Animalia: Formicidae. In: JOLY, C. A.; CANCELLO, E. M. (eds.). **Invertebrados terrestres. Biodiversidade do Estado de São Paulo: síntese do conhecimento ao final do século XX**. São Paulo: FAPESP, 1999. p. 58–63.

BRANDÃO, C. R. F.; MAYHÉ-NUNES, A. J. A new fungus-growing ant genus, *Mycetagroicus* gen. with the description of three new species and comment on the monophyly of the Attini (Hymenoptera: Formicidae). **Sociobiology**, v. 38, n. 3B, 2001.

BRANDÃO, C. R. F.; MAYHÉ-NUNES, A. J.; SANHUDO, C. E. D. Taxonomia e filogenia das formigas-cortadeiras. In: DELLA LUCIA, T. M. C. (ed.). **Formigas-cortadeiras: da bioecologia ao manejo**. Viçosa: Universidade Federal de Viçosa, 2011. p. 27–48.

BRANSTETTER, M. G. *et al.* Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. **Current Biology**, v. 27, n. 7, p. 1019–1025, 2017. a.

BRANSTETTER, M. G. *et al.* Dry habitats were crucibles of domestication in the evolution of agriculture in ants. **Proceedings of the Royal Society B: Biological Sciences**, v. 284, n. 1852, p. 20170095, 2017. b. DOI: 10.1098/rspb.2017.0095

BUCKLEY, S. B. Descriptions of new species of North American Formicidae (continued from page 172.). **Proceedings of the Entomological Society of Philadelphia**, v. 6, p. 335–350, 1867.

BUCKLEY, S. B. The cutting ant of Texas. **Proceedings of the Academy of Natural Sciences of Philadelphia**, v. 12, p. 233–236, 1860.

CHERRETT, J. M. The biology, pest status and control of leaf-cutting ants. **Agricultural Zoology Reviews**, v. 1, p. 1–37, 1986.

CORNER, E. J. H. **A monograph of Clavaria and allied genera**. Oxford University Press. 1950.

CORREIA, M. M. *et al.* Foraging activity of leaf-cutting ants changes light availability and plant assemblage in Atlantic forest. **Ecological Entomology**, v. 41, n. 4, p. 442–450, 2016.

CRAWFORD, N. G. *et al.* More than 1000 ultraconserved elements provide evidence that turtles are the sister group of archosaurs. **Biology Letters**, v. 8, n. 5, p. 783–786, 2012.

CRISTIANO, M. P. *et al.* *Amoimymex* Cristiano, Cardoso & Sandoval, gen. nov. (Hymenoptera: Formicidae): a new genus of leaf-cutting ants revealed by multilocus molecular phylogenetic and morphological analyses. **Austral Entomology**, v. 59, n. 4, p. 643–676, 2020.

CRISTIANO, M. P.; CARDOSO, D. C.; FERNANDES-SALOMÃO, T. M. Cytogenetic and molecular analyses reveal a divergence between *Acromyrmex striatus* (Roger, 1863) and other congeneric species: taxonomic implications. **PLoS One**, v. 8, n. 3, 2013.

DELLA LUCIA, T. M. C. Hormigas de importancia económica en la región Neotropical. In: FERNÁNDEZ, F. (ed.). **Introducción a las hormigas de la región Neotropical**. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, 2003. p. 337–349.

DELLA LUCIA, T. M. C.; SOUZA, D. J. Importância e história de vida das formigas-cortadeiras. In: DELLA LUCIA, T. M. C. (ed.). **Formigas-cortadeiras: da bioecologia ao manejo**. Viçosa: Universidade Federal de Viçosa, 2011. p. 13–26.

DO AMARAL, F. R. *et al.* Ultraconserved elements sequencing as a low-cost source of complete mitochondrial genomes and microsatellite markers in non-model amniotes. **PLoS One**, v. 10, n. 9, p. e0138446, 2015.

EGGLETON, P. The state of the world's insects. **Annual Review of Environment and Resources**, v. 5, p. 61–82, 2020.

EMERY, C. Études sur les Myrmicinae. [V-VII.]. **Annales de la Société Entomologique de Belgique**, v. 57, p. 250–262, 1913.

FABRICIUS, J. C. **Systema Piezatorum secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus**. Brunswick: C. Reichard, 1804.

FAIRCLOTH, B. C. *et al.* Target enrichment of ultraconserved elements from arthropods provides a genomic perspective on relationships among Hymenoptera. **Molecular Ecology Resources**, v. 15, n. 3, p. 489–501, 2015.

FAIRCLOTH, B. C. *et al.* Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. **Systematic Biology**, v. 61, p. 717–726, 2012.

FARJI-BRENER, A. G. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. **Oikos**, v. 92, n. 1, p. 169–177, 2001.

FARJI-BRENER, A. G.; PROTOMASTRO, J. J. Patrones forrajeros de dos especies simpátricas de hormigas cortadoras de hojas (Attini, *Acromyrmex*) en un bosque subtropical seco. **Ecotrópicos**, v. 5, n. 1, p. 32–43, 1992.

FERNÁNDEZ, F.; CASTRO-HUERTAS, V.; SERNA, F. **Hormigas cortadoras de hojas de Colombia: *Acromyrmex* & *Atta* (Hymenoptera: Formicidae)**. Fauna de Colombia, Monografía No. 5, Bogotá: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, 2015.

FERNÁNDEZ, F.; GUERRERO, R. J.; DELSINNE, T. Filogenia y sistemática de las hormigas neotropicales. *In*: FERNÁNDEZ, F.; GUERRERO, R. J.; DELSINNE, T. (eds.). **Hormigas de Colombia**. Bogotá: Universidad Nacional de Colombia. Facultad de Ciencias. Instituto de Ciencias Naturales, 2019. p. 57–89.

FERNÁNDEZ, F.; SENDOYA, S. Synonymic list of neotropical ants (Hymenoptera: Formicidae). **Biota Colombiana**, v. 5, n. 1, 2004.

FERNÁNDEZ, F.; SERNA, F. J. Subfamilia Myrmicinae. *In*: FERNÁNDEZ, F.; GUERRERO, R. J.; DELSINNE, T. (eds.). **Hormigas de Colombia**. Bogotá: Universidad Nacional de Colombia. Facultad de Ciencias. Instituto de Ciencias Naturales, 2019. p. 791–888.

FOLGARAIT, P. J. Ant biodiversity and its relationship to ecosystem functioning: a review. **Biodiversity & Conservation**, v. 7, n. 9, p. 1221–1244, 1998.

FONTENLA RIZO, J. L. Nueva especie de *Atta* (Hymenoptera: Formicidae) del archipiélago cubano. **Avicennia**, v. 3, p. 77–86, 1995.

FOREL, A. Ameisen aus Guatemala usw., Paraguay und Argentinien (Hym.). **Deutsche Entomologische Zeitschrift**, p. 239–269, 1909.

FOREL, A. Ameisen aus Sao Paulo (Brasilien), Paraguay etc. gesammelt von Prof. Herm. v. Ihering, Dr. Lutz, Dr. Fiebrig, etc. **Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien**, v. 58, p. 340–418, 1908.

FOREL, A. Études myrmécologiques en 1884 avec une description des organes sensoriels des antennes. **Bulletin de la Société Vaudoise des Sciences Naturelles**, v. 20, p. 316–380, 1885 ("1884").

FOREL, A. Formicides de l'Antille St. Vincent, récoltées par Mons. H. H. Smith. **Transactions of the Entomological Society of London**, p. 333–418, 1893.

FOREL, A. Fourmis d'Argentine, du Brésil, du Guatemala & de Cuba reçues de M. M. Bruch, Prof. v. Ihering, Mlle Baez, M. Peper et M. Rovereto. **Bulletin de la Société Vaudoise des Sciences Naturelles**, v. 49, p. 203–250, 1913.

FOREL, A. Note sur les Attini. **Annales de la Société Entomologique de Belgique**, v. 37, p. 586–607, 1893.

FORTI, L. C. *et al.* Occurrence of Leaf-Cutting and Grass-Cutting Ants of the Genus *Atta* (Hymenoptera: Formicidae) in Geographic Regions of Brazil. **Sociobiology**, v. 67, n. 4, p. 514–525, 2020.

FOWLER, H. G. Latitudinal gradients and diversity of the leaf-cutting ants (*Atta* and *Acromyrmex*) (Hymenoptera: Formicidae). **Revista de Biología Tropical**, v. 31, n. 2, p. 213–216, 1983.

FOWLER, H. G. *et al.* Economics of grass-cutting ants. *In*: LOFGREN, C. S.; VANDERMEER, R. K. (eds.). **Fire ants and leaf-cutting ants**. Boulder: Westview Press, 1986. p.18–35.

FRIES, E. **Systema orbis vegetabilis**. Lunde, e Typographia academica, 1825.

GONÇALVES, C. R. Contribuição para o conhecimento do gênero *Atta* Fabr., das formigas saúvas. **Boletim da Sociedade Brasileira de Agronomia**, v. 5, p. 333–358, 1942.

GONÇALVES, C. R. Descrição de uma nova saúva brasileira (Hym., Form.). **Revista Brasileira de Biologia**, v. 4, p. 233–238, 1944.

GONÇALVES, C. R. Distribuição, biologia e ecologia das saúvas. **Divulgação Agrônômica**, v. 1, p. 2–10, 1960.

GONÇALVES, C. R. Filogenia do gênero *Atta* Fabricius (Hymenoptera, Formicidae). Anais do VI Congresso Brasileiro de Zoologia. **Publicações Avulsas do Museu Nacional, Rio de Janeiro**, v. 65, p. 13–17, 1986.

GONÇALVES, C. R. O gênero *Acromyrmex* no Brasil (Hym. Formicidae). **Studia Entomologica**, v. 4, n. 1-4, p. 113–180, 1961.

GUÉRIN-MÉNEVILLE, F. E. **Iconographie du règne animal de G. Cuvier, ou représentation d'après nature de l'une des espèces les plus remarquables, et souvent non encore figurées, de chaque genre d'animaux**. Insectes. Paris: J. B. Baillière, 1844.

GUEUNING, M.; FREY, J. E.; PRAZ, C. Ultraconserved yet informative for species delimitation: Ultraconserved elements resolve long-standing systematic enigma in Central European bees. **Molecular Ecology**, v. 29, n. 21, p. 4203–4220, 2020.

HERZ, H.; BEYSCHLAG, W.; HÖLLDOBLER, B. Herbivory rate of leaf-cutting ants in a tropical moist forest in Panama at the population and ecosystem scales. **Biotropica**, v. 39, n. 4, p. 482–488, 2007.

HÖLLDOBLER, B.; WILSON, E. O. **The ants**. Cambridge,: Harvard University Press, 1990.

HÖLLDOBLER, B.; WILSON, E. O. **The leafcutter ants: civilization by instinct**. London and New York: W. W. Norton & Company, 2011.

JANICKI, J. *et al.* Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. **Ecological Informatics**, v. 32, 185–193. 2016.

JEŠOVNIK, A. *et al.* Phylogenomic species delimitation and host-symbiont coevolution in the fungus-farming ant genus *Sericomyrmex* Mayr (Hymenoptera: Formicidae): ultraconserved elements (UCEs) resolve a recent radiation. **Systematic Entomology**, v. 42, n. 3, p. 523–542, 2017.

JONES, C. G.; LAWTON, J. H.; SHACHAK, M. Organisms as ecosystem engineers. In: SAMSON, F. B.; KNOPE, F. L. (eds.). **Ecosystem management**. New York: Springer, 1994. p. 130–147.

- KASPARI, M. Introducción a la ecología de las hormigas. *In*: FERNÁNDEZ, F. (ed.). **Introducción a las hormigas de la región Neotropical**. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, 2003. p. 97–112.
- KEMPF, W. W. Catálogo abreviado das formigas da Região Neotropical. **Studia Entomologica**, v. 15, p. 3–344, 1972.
- KUSNEZOV, N. Zoogeografía de las hormigas en Sudamérica. **Acta Zoologica Lilloana**, v. 19, p. 25–186, 1963.
- LATREILLE, P. A. **Histoire naturelle, générale et particulière des crustacés et des insectes**, v. 3, Paris: F. Dufart, 1802.
- LEAL, I. R.; WIRTH, R.; TABARELLI, M. The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified Neotropical forests. **Biotropica**, v. 46, n. 5, p. 516–528, 2014.
- LI, H. *et al.* Convergent evolution of complex structures for ant–bacterial defensive symbiosis in fungus-farming ants. **Proceedings of the National Academy of Sciences**, v. 115, n. 42, p. 10720–10725, 2018.
- LINNAEUS, C. **Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis**. Tomus I. Editio decima, reformata. Holmiae [= Stockholm]: L. Salvii, 1758.
- MANN, W. M. The Stanford Expedition to Brazil, 1911, John C. Branner, Director. The ants of Brazil. **Bulletin of the Museum of Comparative Zoology**, v. 60, p. 399–490, 1916.
- MAYR, G. **Myrmecologische Studien**. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, v. 12, p. 649–776, 1862.
- MAYR, G. Formicidae. *In*: **Novara Expedition 1865**. Reise der Österreichischen Fregatte "Novara" um die Erde in den Jahren 1857, 1858, 1859. Zoologischer Theil. Bd. II. Abt. 1. Wien: K. Gerold's Sohn, 1865.
- MCCORMACK, J. E. *et al.* Ultraconserved elements are novel phylogenomic markers that resolve placental mammal phylogeny when combined with species-tree analysis. **Genome Research**, v. 22, n. 4, p. 746–754, 2012.
- MEHDIABADI, N. J.; SCHULTZ, T. R. Natural history and phylogeny of the fungus-farming ants (Hymenoptera: Formicidae: Myrmicinae: Attini). **Myrmecological News**, v. 13, p. 37–55, 2010.
- MIKHEYEV, A. S.; MUELLER, U. G.; ABBOT, P. Cryptic sex and many-to-one coevolution in the fungus-growing ant symbiosis. **Proceedings of the National Academy of Sciences**, v. 103, n. 28, p. 10702–10706, 2006.
- MIKHEYEV, A. S.; MUELLER, U. G.; BOOMSMA, J. J. Population genetic signatures of diffuse co-evolution between leaf-cutting ants and their cultivar fungi. **Molecular Ecology**, v. 16, n. 1, p. 209–216, 2007.

- MONTOYA-LERMA, J. *et al.* Leaf-cutting ants revisited: towards rational management and control. **International Journal of Pest Management**, v. 58, n. 3, p. 225–247, 2012.
- MOUTINHO, P.; NEPSTAD, D. C.; DAVIDSON, E. A. Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. **Ecology**, v. 84, n. 5, p. 1265–1276, 2003.
- MOREAU, C. S. *et al.* Phylogeny of the ants: diversification in the age of angiosperms. **Science**, v. 312, n. 5770, p. 101–104, 2006.
- MOREAU, C. S.; BELL, C. D. Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. **Evolution**, v. 67, n. 8, p. 2240–2257, 2013.
- MOREIRA, A. *et al.* Nest architecture of *Atta laevigata* (F. Smith, 1858) (Hymenoptera: Formicidae). **Studies on Neotropical Fauna and Environment**, v. 39, n. 2, p. 109–116, 2004.
- MUELLER, U. G. *et al.* Biogeography of mutualistic fungi cultivated by leafcutter ants. **Molecular Ecology**, v. 26, n. 24, p. 6921–6937, 2017.
- MUELLER, U. G. *et al.* The evolution of agriculture in insects. **Annual Review of Ecology, Evolution, and Systematics**, v. 36, p. 563–595, 2005.
- MUELLER, U. G.; RABELING, C. A breakthrough innovation in animal evolution. **Proceedings of the National Academy of Sciences**, v. 105, n. 14, p. 5287–5288, 2008.
- MUELLER, U. G.; REHNER, S. A.; SCHULTZ, T. R. The evolution of agriculture in ants. **Science**, v. 281, n. 5385, p. 2034–2038, 1998.
- MUNKACSI, A. B. *et al.* Convergent coevolution in the domestication of coral mushrooms by fungus-growing ants. **Proceedings of the Royal Society of London. Series B: Biological Sciences**, v. 271, n. 1550, p. 1777–1782, 2004.
- NESS, J.; MOONEY, K.; LACH, L. Ants as mutualists. *In*: LACH, L., PARR, C. L.; ABBOTT, K. L. (eds.). **Ant ecology**. New York: Oxford University Press Inc., 2010. p. 97–114.
- NYGAARD, S. *et al.* Reciprocal genomic evolution in the ant–fungus agricultural symbiosis. **Nature Communications**, v. 7, n. 1, p. 1–9, 2016.
- OLIVEIRA, M. V. *et al.* Ninhos de *Atta sexdens* (Hymenoptera: Formicidae) podem afetar a estrutura da assembleia de artrópodes do solo na Mata Atlântica? **Iheringia. Série Zoologia**, v. 108, 2018.
- PERTY, M. **Delectus animalium articulorum, quae in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae regis augustissimi peracto, collegerunt Dr. J. B. Spix et Dr. C. F. Ph. de Martius. Fasc. 3. Monachii** [= Munich]: published by the author, p. 125–224, 1833.

PHILPOTT, S. M.; ARMBRECHT, I. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. **Ecological Entomology**, v. 31, n. 4, p. 369–377, 2006.

PREBUS, M. M. Insights into the evolution, biogeography and natural history of the acorn ants, genus *Temnothorax* Mayr (Hymenoptera: Formicidae). **BMC Evolutionary Biology**, v. 17, n. 1, p. 1–22, 2017.

PREBUS, M. M. Phylogenomic species delimitation in the ants of the *Temnothorax salvini* group (Hymenoptera: Formicidae): an integrative approach. **Systematic Entomology**, 2020. DOI: 10.1111/syen.12463

RABELING, C. *et al.* Reconstructing the evolutionary history of leaf-cutting ants reveal multiple origins of inquiline social parasitism via sympatric speciation. *In*: INTERNATIONAL CONFERENCE OF THE UNION FOR THE STUDY OF SOCIAL INSECTS, 18., 2018, Guarujá. **Anais [...]**. Guarujá, São Paulo, Brasil: IUSSI, 2018.

RABELING, C.; BACCI, M. A new workerless inquiline in the Lower Attini (Hymenoptera: Formicidae), with a discussion of social parasitism in fungus-growing ants. **Systematic Entomology**, v. 35, n. 3, p. 379–392, 2010.

SÁNCHEZ-RESTREPO, A. F. *et al.* Distribution and diversity of leaf-cutting ants in Northeastern Argentina: species most associated with forest plantations. **International Journal of Pest Management**, v. 65, n. 3, p. 244–257, 2019.

SCHULTZ, T. R. In search of ant ancestors. **Proceedings of the National Academy of Sciences**, v. 97, n. 26, p. 14028–14029, 2000.

SCHULTZ, T. R. *et al.* Reciprocal illumination: a comparison of agriculture in humans. *In*: VEGA, F.; BLACKWELL, M. (eds.). **Ecological and evolutionary advances in insect-fungal associations**. New York: Oxford University Press, 2005. p 149–190.

SCHULTZ, T. R.; BRADY, S. G. Major evolutionary transitions in ant agriculture. **Proceedings of the National Academy of Sciences**, v. 105, n. 14, p. 5435–5440, 2008.

SCHULTZ T. R.; MCGLYNN, T. P. The interactions of ants with other organisms. *In*: AGOSTI, D.; MAJER, J. D.; ALONSO, L. E.; SCHULTZ, T. R. (eds.). **Ants: measuring and monitoring biological diversity**. Washington and London: Smithsonian Institution Press, 2000. p. 35–44.

SILVA-PINHATI, A. C. O. *et al.* Low variation in ribosomal DNA and internal transcribed spacers of the symbiotic fungi of leaf-cutting ants (Attini: Formicidae). **Brazilian Journal of Medical and Biological Research**, v. 37, n. 10, p. 1463–1472, 2004.

SINGER, R. The Agaricales in modern taxonomy 4th edn. **Dehradun: Bishen Singh and Mahendra Pal Singh**, p. 477, 1986.

SIQUEIRA, F. F. S. *et al.* Human disturbance promotes herbivory by leaf-cutting ants in the Caatinga dry forest. **Biotropica**, v. 50, n. 5, p. 779–788, 2018.

SMITH, B. T. *et al.* Target capture and massively parallel sequencing of ultraconserved elements for comparative studies at shallow evolutionary time scales. **Systematic Biology**, v. 63, n. 1, p. 83–95, 2014.

SMITH, F. **Catalogue of hymenopterous insects in the collection of the British Museum.** Part VI. Formicidae. London: British Museum, 1858.

SOLOMON, S. E. *et al.* The molecular phylogenetics of *Trachymyrmex* Forel ants and their fungal cultivars provide insights into the origin and coevolutionary history of ‘higher-attine’ ant agriculture. **Systematic Entomology**, v. 44, n. 4, p. 939–956, 2019.

STERNBERG, L. D. *et al.* Plants use macronutrients accumulated in leaf-cutting ant nests. **Proceedings of the Royal Society B: Biological Sciences**, v. 274, n. 1608, p. 315–321, 2007.

URBAS, P. **Effects of forest fragmentation on bottom-up control in leaf-cuttings ants.** 2005. Tese (Doutorado em Ciências) - Department of Biology Technical University of Kaiserslautern, Kaiserslautern, 2005.

VILLESEN, P. *et al.* Evolution of ant-cultivar specialization and cultivar switching in *Apterostigma* fungus-growing ants. **Evolution**, v. 58, n. 10, p. 2252–2265, 2004.

VO, T. L.; MUELLER, U. G.; MIKHEYEV, A. S. Free-living fungal symbionts (Lepiotaceae) of fungus-growing ants (Attini: Formicidae). **Mycologia**, v. 101, n. 2, p. 206–210, 2009.

WARD, P. S. Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae). **Zootaxa**, v. 1668, n. 1, p. 549–563, 2007.

WARD, P. S. The phylogeny and evolution of ants. **Annual Review of Ecology, Evolution, and Systematics**, v. 45, p. 23–43, 2014.

WARD, P. S. *et al.* Phylogenetic classifications are informative, stable, and pragmatic: the case for monophyletic taxa. **Insectes Sociaux**, v. 63, n. 4, p. 489–492, 2016.

WARD, P. S. *et al.* The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). **Systematic Entomology**, v. 40, n. 1, p. 61–81, 2015.

WEBER, N. A. **Gardening ants, the Attines.** Philadelphia: The American Philosophical Society, 1972.

WESTWOOD, J. O. **An introduction to the modern classification of insects; founded on the natural habits and corresponding organisation of the different families.** v. 2. Part XI. London: Longman, Orme, Brown, Green and Longmans, p. 193–224, 1839.

WHEELER, W. M. Two new genera of myrmicine ants from Brazil. **Bulletin of the Museum of Comparative Zoology**, v. 59, p. 483–491, 1915.

WILLIAMS, J. L. *et al.* Global domination by crazy ants: phylogenomics reveals biogeographical history and invasive species relationships in the genus *Nylanderia* (Hymenoptera: Formicidae). **Systematic Entomology**, v. 45, n. 4, p. 730–744, 2020.

WILSON, E. O. **Success and dominance in ecosystems: the case of the social insects**. Germany: Oldendorf/Luhe, Ecology Institute, 1990.

WILSON, E. O. The defining traits of fire ants and leaf-cutting ants. *In*: LOFGREN, C. S., VANDER MEER, R. K. (eds.). **Fire ants and leaf-cutting ants**. Boulder: Westview Press, 1986. p. 1–9.

WILSON, E. O. **The insect societies**. Cambridge, Massachusetts: Harvard University Press, 1971.

WILSON, E. O.; HÖLLDOBLER, B. Eusociality: origin and consequences. **Proceedings of the National Academy of Sciences**, v. 102, n. 38, p. 13367–13371, 2005. a.

WILSON, E. O.; HÖLLDOBLER, B. The rise of the ants: a phylogenetic and ecological explanation. **Proceedings of the National Academy of Sciences**, v. 102, n. 21, p. 7411–7414, 2005. b.

WIRTH, R. *et al.* **Herbivory of leaf-cutting ants: a case study on *Atta colombica* in the tropical rainforest of Panama**. New York: Springer-Verlag Berlin Heidelberg, 2003.

Capítulo 1

2. CAPÍTULO 1

Phylogenomic reconstruction reveals new insights into the evolution and biogeography of *Atta* leaf-cutting ants (Hymenoptera: Formicidae)

*Corina A. Barrera^{1,2}, Jeffrey Sosa-Calvo^{2,3}, Ted R. Schultz³, #Christian Rabeling²,
 #*Maurício Bacci Jr.¹

¹Universidade Estadual Paulista (UNESP), Instituto de Biociências, Centro de Estudos de Insetos Sociais (CEIS), Rio Claro, SP, Brazil.

²School of Life Sciences, Arizona State University, Tempe, AZ, U.S.A.

³Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

***Corresponding Authors**

#Authors contributed equally to this study

Email addresses: Corina A. Barrera – corinabarrera@gmail.com
 Jeffrey Sosa-Calvo – sossajef@si.edu
 Ted R. Schultz – schultzt@si.edu
 Christian Rabeling – crabeling@gmail.com
 Maurício Bacci Jr. – mauricio.bacci@unesp.br

Status: Minor revision in “*Systematic Entomology*”

RESUMO

As formigas cortadeiras são herbívoros dominantes na Região Neotropical. Elas são importantes engenheiros de ecossistemas e muitas espécies são pragas agrícolas de grande importância ecológica e econômica. As formigas cortadeiras do gênero *Atta* Fabricius estão amplamente distribuídas nas Américas. As relações filogenéticas dentro do gênero permanecem incertas e a delimitação e identificação de algumas espécies de *Atta* são problemáticas. Aqui, abordamos essas incertezas empregando marcadores filogenômicos (Elementos Ultraconservados ou UCEs) em uma análise que inclui 2340 loci de UCE de 224 espécimes *Atta* de toda a distribuição geográfica do gênero e 49 espécimes como grupos externos. Nossos resultados indicaram a monofilia do gênero *Atta* e das 14 espécies estudadas (das 15 espécies conhecidas e identificáveis) com alto suporte, representando a estimativa filogenética mais abrangente até o momento para este gênero de formigas cortadeiras. Dentro do gênero *Atta*, recuperamos quatro clados bem sustentados que coincidem com os grupos de espécies previamente recuperados e correlacionados com os subgêneros anteriormente descritos, *Archeatta* Gonçalves, *Atta* s.s. Emery, *Epiatta* Borgmeier e *Neoatta* Gonçalves. O clado *Archeatta* contém três espécies que ocorrem na América do Norte, Central e no Caribe e é o grupo irmão de todas as outras espécies de *Atta*. O clado *Atta* s.s. é composto por duas espécies que ocupam as América do Norte, Central e do Sul. O clado *Epiatta* contém sete espécies exclusivamente sul-americanas, e as duas espécies do clado *Neoatta* ocorrem na América Central e do Sul. Nossas análises identificaram uma série de eventos importantes no Mioceno, como a origem das formigas cortadeiras há 18.9 milhões de anos (Ma), a divergência de *Acromyrmex* Mayr e *Atta* por volta de 16.7 Ma e a origem do grupo *crown* de *Atta* por volta de 8.5 Ma. As espécies de *Atta* existentes evoluíram muito recentemente, originando-se no início do Pleistoceno, aproximadamente entre 1.8 e 0.3 Ma (idade do grupo *crown*). O clado *Neoatta* inclui *Atta robusta* Borgmeier, a espécie do grupo *crown* mais jovem do gênero, com idade de 0.3 Ma. Nossa filogenia forneceu a primeira evidência de que *Atta goiana* Gonçalves pertence ao clado *Epiatta* e indica, para ambos os clados, *Epiatta* e *Neoatta*, um padrão interessante no qual espécies intimamente relacionadas apresentam ecologias diferentes. As idades muito jovens do gênero *Atta* e suas espécies representam uma radiação recente e rápida. Nossas análises biogeográficas sugerem que o ancestral comum do gênero *Atta* se originou na América do Norte e que uma linhagem filha, que posteriormente se dispersou na América do Sul, rapidamente se diversificou no bioma Cerrado recém-formado.

Palavras-chave: Attina. Attini. Attíneas Superiores. Especiação. Filogenética. Formigas cortadeiras. Sequenciamento DNA. Sistemática.

ABSTRACT

Leaf-cutting ants are dominant herbivores in the Neotropical region. They are important ecosystem engineers and many species are agricultural pests of great ecological and economic importance. Leaf-cutting ants in the genus *Atta* Fabricius are widely distributed throughout the Americas. Phylogenetic relationships within the genus remain uncertain, and the delimitation and identification of some *Atta* species are problematic. Here, we address these uncertainties by employing phylogenomic markers (ultraconserved elements, UCEs) in an analysis that includes 2340 UCE loci from 224 *Atta* specimens from across the geographic distribution of the genus and 49 outgroup specimens. Our results inferred the monophyly of *Atta* and its 14 studied species (out of the 15 known and identifiable species) with high support, representing the most comprehensive phylogenetic estimate to date for this leaf-cutting ant genus. Within the genus *Atta*, we recovered four well-supported clades that correspond to the previously recognized subgenera, *Archeatta* Gonçalves, *Atta* s.s. Emery, *Epiatta* Borgmeier, and *Neoatta* Gonçalves. The *Archeatta* clade contains three species occurring in North and Central America and the Caribbean and is the sister group of the remainder of all other *Atta* species. The *Atta* s.s. clade is composed of two species occupying North, Central, and South America. The *Epiatta* clade contains seven entirely South American species and the two species of the *Neoatta* clade occur in Central and South America. Our analyses identified a series of major events in the Miocene, such as the origin of leaf-cutting ants 18.9 million years ago (Ma), the divergence of *Acromyrmex* Mayr and *Atta* around 16.7 Ma, and crown-group origin of *Atta* around 8.5 Ma. Extant *Atta* species evolved very recently, originating in the early Pleistocene, approximately 1.8 to 0.3 Ma (crown-group ages). The *Neoatta* clade includes *Atta robusta* Borgmeier, the species with the youngest crown-group age in the genus of 0.3 Ma. Our phylogeny provides the first evidence that *Atta goiana* Gonçalves belongs to the *Epiatta* clade and indicates, for both the *Epiatta* and *Neoatta* clades, an interesting pattern in which closely related species exhibit distinct ecologies. The very young ages of the genus *Atta* and its component species indicate a recent, rapid radiation. Our biogeographic analyses suggest that the common ancestor of the genus *Atta* originated in North America and that a daughter lineage, which subsequently dispersed to South America, rapidly diversifying in the newly formed Cerrado biome.

Keywords: Attina. Attini. DNA sequencing. Higher-Attine ants. Leaf-cutter ants. Phylogenetics. Speciation. Systematics.

2.1 Introduction

The fungus-growing ants are perhaps the most conspicuous and charismatic ants in the Neotropics. Their association with fungal cultivars originated approximately 55–65 Million years ago (Ma) and has become one of the most successful symbiotic systems in nature (BRANSTETTER *et al.*, 2017a; HÖLLDOBLER; WILSON, 1990; MUELLER; REHNER; SCHULTZ, 1998; NYGAARD *et al.*, 2016; SCHULTZ; BRADY, 2008; WEBER, 1972). Leaf-cutting ants, a monophyletic group composed of four valid genera [*Atta* Fabricius, *Acromyrmex* Mayr, *Amoimyrmex* Cristiano, Cardoso & Sandoval, and *Pseudoatta* Gallardo, a workerless social parasite of *Acromyrmex heyeri* (Forel)], constitute what is arguably the most highly specialized subset (~15%) of the larger group of fungus-growing ants (tribe Attini, subtribe Attina; the *Atta* genus-group *sensu* Ward *et al.*, 2015, hereafter referred to as "attine" ants). Leaf-cutting ants are thought to have originated around 17–19 Ma (BRANSTETTER *et al.*, 2017b; JEŠOVNIK; GONZÁLEZ; SCHULTZ, 2016; LI *et al.*, 2018; NYGAARD *et al.*, 2016), and belong to the "higher-attine" ants, which also include five genera of non-leaf-cutting ants (MUELLER *et al.*, 2017, 2018; SCHULTZ; BRADY, 2008; SOLOMON *et al.*, 2019). Compared with fungi cultivated by the ancestral attine ant and still cultivated by the so-called "lower-attine" ants, which are facultative symbionts, fungi cultivated by leaf-cutting ants are obligate mutualists that may have originated more recently, around 22–30 Ma, coincident with or subsequent to the origin of the higher-attine ants (BRANSTETTER *et al.*, 2017b; MIKHEYEV; MUELLER; ABBOT, 2010; MUELLER *et al.*, 2017; NYGAARD *et al.*, 2016; SCHULTZ; BRADY, 2008). Further derived within higher-attine agriculture, the mutualistic symbiotic system of leaf-cutting ants is extremely specialized, consisting of approximately 50 species that mostly cultivate a single species of fungus, *Leucoagaricus gongylophorus* Möller (also referred to as "Clade-A" or *Attamyces* fungi) (MIKHEYEV; MUELLER; ABBOT, 2006; MUELLER *et al.*, 2017, 2018; SILVA-PINHATI *et al.*, 2004); although a few leaf-cutting ant species were recently shown to cultivate fungal species arising in the sister clade of *L. gongylophorus*, sometimes referred to as "Clade-B" (MUELLER *et al.*, 2018; SOLOMON *et al.*, 2019), which are also cultivated by non-leaf-cutting higher-attine ants. In addition to being obligate symbionts, higher-attine fungi, including *L. gongylophorus*, are polyploid, consistently produce nutritious swollen hyphal tips (gongylidia), and express significantly elevated enzyme profiles mostly associated with the degradation of fresh plant material (DE FINE LICHT *et al.*, 2013; MASIULIONIS *et al.*, 2014; MÖLLER, 1893; MUELLER *et al.*, 2018; SCHULTZ; BRADY, 2008).

Like the other fungus-growing ants, leaf-cutting ants depend on their fungus for food (BELT, 1874; SIQUEIRA *et al.*, 1998; WEBER, 1982). They differ from other fungus-growing ants, however, by cutting and using fresh plant material as the substrate on which they grow their gardens (HÖLLDOBLER; WILSON, 2011; WEBER, 1966). Because of this behavior and the large quantities of vegetal material that they harvest, several species have become pests of human agriculture, with significant economic impact (CHERRETT, 1989; DELLA LUCIA, 2003, 2011; FISCHER, 2015; FOWLER *et al.*, 1989; HÖLLDOBLER; WILSON, 1990; LEAL; WIRTH; TABARELLI, 2014; MOSER, 1986; SCHOWALTER; RING, 2017; WIRTH *et al.*, 2003). Many species have large underground colonies, particularly those of *Atta* with up to eight million workers (FERNÁNDEZ; CASTRO-HUERTAS; SERNA, 2015), and have been characterized as ecosystem engineers due to their high capacity to modify the environment (JONES; LAWTON; SHACHAK, 1994; LEAL; WIRTH; TABARELLI, 2014). The population densities of some leaf-cutting species are enhanced by anthropic activities (FOWLER *et al.*, 1986) such as deforestation and agricultural land use (FORTI *et al.*, 2006; URBAS *et al.*, 2007; WIRTH *et al.*, 2007). In addition, leaf-cutting ants are characterized by colony longevity (queens of *Atta* can live 15 or more years; FERNÁNDEZ; SERNA, 2019), multiple interactions with other organisms, multiple queen mating frequencies, and, in *Atta*, claustral nest founding (HÖLLDOBLER; WILSON, 1990, 2011; MEHDIABADI; SCHULTZ, 2009).

In addition to their biological and ecological importance, the long-lived colonies of *Atta* leaf-cutting ants represent a consistently dependable nutritional resource for diverse organisms, and several Native Amerindian groups used them as food. Their gigantic subterranean nests significantly contribute to nutrients in the soil (DUFOUR, 1987; WEBER, 1966). Leaf-cutting nests host many underground microorganisms and insects, which derive nutrition from the large quantity of organic matter provided by the ants (BACCI *et al.*, 1995; MOUNTINHO; NEPSTAD; DAVIDSON *et al.*, 2003; RODRIGUES *et al.*, 2005). Fifteen species are currently recognized in the genus *Atta* (BACCI *et al.*, 2009; BOLTON, 2021; FERNÁNDEZ; CASTRO-HUERTAS; SERNA, 2015; HÖLLDOBLER; WILSON, 2011), and their biogeographic distributions extend from the southern United States in the north, to northeastern Argentina and western Uruguay in South America (BORGMEIER, 1959; FERNÁNDEZ; SENDOYA, 2004; HÖLLDOBLER; WILSON, 1990, 2011; JANICKI *et al.*, 2016; KEMPF, 1972), and to some islands in the Caribbean (Cuba, Trinidad & Tobago, and the Lesser Antilles; FONTENLA RIZO, 1995; WEBER, 1968; WILSON, 1986). Due to its high ecological and economic importance, the biology, behavior, and control of the genus *Atta* is relatively well studied

compared to that of most other tropical insects (DELLA LUCIA, 2003, 2011; HÖLLDOBLER; WILSON, 2011; MUELLER; RABELING, 2008). However, the delimitation of species and their taxonomic identification remain problematic (BACCI *et al.*, 2009; BORGMEIER, 1959; SCHULTZ; BRADY, 2008; SOLOMON *et al.*, 2019).

Early studies on the phylogeny and systematics of the genus *Atta* were largely based on morphological characters. Emery (1913, 1922) was the first entomologist to differentiate species using characters of the male genitalia. These characters of the males and those of large-sized workers were combined with biological information and nest architecture to produce the first complete revision of the genus, including the grouping of species into subgenera (GONÇALVES, 1942). Later, Borgmeier, (1950, 1959) added information to Gonçalves' (1942) study, analyzing 14 of the species recognized at that time, and constructing the identification key still currently in use. These studies require updating for a number of reasons, including the use of subspecific names, a category disfavored by modern ant taxonomists (BOLTON *et al.*, 2006; WILSON; BROWN, 1953), as well as taxonomic changes that have occurred in the last decades (e.g., DELABIE, 1998; FONTENLA RIZO, 1995) but have not yet been included in a general taxonomic review.

Studies of morphology, nesting behavior, ecology, biogeography, and pest control, among other topics, can provide information about the classification, taxonomy, and identification of *Atta* species as well as of leaf-cutting ants in general (FERNÁNDEZ; CASTRO-HUERTAS; SERNA, 2015; HÖLLDOBLER; WILSON, 2011). However, the sole use of morphological characters for species identification is problematic because large-sized workers have a high level of within-species polymorphism (BORGMEIER, 1950, 1959) and small-sized workers from different species are very similar to each other. Male genitalic morphology is informative for taxonomy (GONÇALVES, 1942, 1986), but males only emerge once each year during the mating season and are therefore underrepresented in collections. Very few collections have complete series representing all sexes and female castes from the same nest for all or most of the species (S. E. SOLOMON, personal communication; C. A. BARRERA, personal observation), providing fragmented information for systematic studies. In addition, to date, there have been only a few studies, mainly molecular, that have focused on leaf-cutting ants in general or on particular leaf-cutting ant genera (BACCI *et al.*, 2009; CRISTIANO *et al.*, 2020; CRISTIANO; CARDOSO; FERNANDES-SALOMÃO, 2013; PEREIRA *et al.*, 2018; RABELING *et al.*, 2018; SÁNCHEZ-RESTREPO *et al.*, 2019; SUMNER *et al.*, 2004). These challenges, particularly in *Atta* taxonomy and phylogenetics, motivated this present study, which contributes to a better understanding of the evolutionary

history and phylogenetic relationships of the leaf-cutting ants and which will serve as a reference for taxonomic studies of the genus *Atta*.

During the past four decades, phylogenetic systematics has progressed rapidly due to the use of molecular genetic markers. Most recently, during the past decade, progress in understanding evolutionary relationships in ants has accelerated due to techniques employing massive sequencing of genomic data (BRANSTETTER *et al.*, 2017b; JEŠOVNIK; GONZÁLEZ; SCHULTZ, 2016; NYGAARD *et al.*, 2016; WARD; BLAIMER; FISHER, 2016). Techniques involving selective enrichment and next-generation sequencing (NGS) have allowed the efficient processing of large numbers of taxa for a large number of independent loci in a short time frame (DO AMARAL *et al.*, 2015; FAIRCLOTH *et al.*, 2012a, 2015; LEMMON; LEMMON, 2013). In particular, ant phylogenetics has benefited most from the sequencing of so-called ultraconserved elements (UCEs). UCEs are genomic regions that have been highly conserved in genomic evolution (BEJERANO *et al.*, 2004) and, together with more variable flanking regions, provide valuable data for phylogenetic studies at a broad range of phylogenetic levels (BLAIMER *et al.*, 2015; CRAWFORD *et al.*, 2012; FAIRCLOTH *et al.*, 2012a; SMITH *et al.*, 2014).

Technological advances have also greatly improved the ability to reconstruct the evolutionary history of fungus-growing ants. Molecular data have provided critical information for reconstructing evolutionary relationships in the tribe Attini, the larger group that includes the fungus-growing ants (WARD *et al.*, 2015), thereby revealing the major transitions in ant-fungus co-evolution (BRANSTETTER *et al.*, 2017b; MEHDIABADI *et al.*, 2012; NYGAARD *et al.*, 2016; SCHULTZ; BRADY, 2008; SOSA-CALVO *et al.*, 2017), the history of ant-Actinobacteria co-evolutionary associations (CURRIE *et al.*, 2003; LI *et al.*, 2018; MEIRELLES *et al.*, 2015), the evolution of asexual reproduction and social parasitism (RABELING *et al.*, 2011, 2014; SCHRADER *et al.*, 2021; SUMNER *et al.*, 2004), as well as the revision, recognition, and description of new genera and species (CRISTIANO *et al.*, 2020; CRISTIANO; CARDOSO; FERNANDES-SALOMÃO, 2013; JESOVNIK *et al.*, 2017; RABELING *et al.*, 2015, 2019; SOLOMON *et al.*, 2019; SOSA-CALVO *et al.*, 2013, 2018). Molecular data have likewise proven useful in studies of systematics and, in particular, the phylogenetic relationships of leaf-cutting ants. Prior such studies (BRANSTETTER *et al.*, 2017a; CRISTIANO *et al.*, 2020; NYGAARD *et al.*, 2016; RABELING *et al.*, 2018; SÁNCHEZ-RESTREPO *et al.*, 2019) revealed that *Atta* is the sister genus to *Acromyrmex*, and that both are sister to *Amoimyrmex*. They also indicate that the genus *Atta* is remarkably young.

Prior studies of *Atta* utilizing mitochondrial and nuclear DNA sequence data produced important discoveries about the ecology and evolution of the genus. For example, SOLOMON *et al.* (2008) examined the phylogeography of a subset of *Atta* species with broad distributions in order to test three hypotheses about the causes underlying those distributions. A subsequent phylogenetic study produced the first nearly complete phylogeny of the genus based on molecular data (BACCI *et al.*, 2009), supporting the monophyly of the genus and placing, with strong support, the 13 studied species into four clades representing the four previously recognized but subsequently synonymized (BOLTON *et al.*, 2006) subgenera *Archeatta* Gonçalves, *Atta* s.s. Emery, *Epiatta* Borgmeier, and *Neoatta* Gonçalves. Bacci *et al.* (2009) cautioned, however, that their data were unable to resolve a number of important phylogenetic relationships, which were reconstructed as polytomies. More recently, a phylogeny of six *Atta* species was reconstructed based on mitogenomes (BARBOSA *et al.*, 2019).

Here, we provide the results of a phylogenomic analysis of the leaf-cutting ant genus *Atta* based on UCE data and comprehensive taxon sampling. By reconstructing a robust phylogeny, we aimed to infer: (i) the phylogenetic relationship of the genus *Atta* with other higher-attine ants, (ii) the phylogenetic relationships of species and species groups within *Atta*, (iii) the evolutionary history and divergence times of *Atta* from other higher-attine ant groups, as well as (iv) the historical biogeography and the current biogeographic distributions of *Atta*. It is our goal that the reconstruction of *Atta* internal relationships, divergence times, and biogeography will inform further evolutionary and taxonomic studies of leaf-cutting and other attine ants.

2.2 Materials and Methods

2.2.1 Taxon sampling

We assembled a total of 865 samples (i.e., sets of specimens from the same nest) from 19 countries and from 25 out of 26 Brazilian states (Fig. 1). Our samples include 14 out of the 15 recognized, extant species currently assigned to the genus *Atta*. We do not include the species *Atta cubana* Fontenla Rizo because specimens were not available for our study. Two additional North American taxa, *Atta pilosa* Buckley and *Atta tardigrada* Buckley, are *incertae sedis* (BOLTON, 2021), i.e., they were inadequately described in the 19th century without reference to voucher or type specimens and, whatever the true identities of the two species, they were certainly not species of *Atta* as the genus is currently understood. We identified *Atta*

specimens using the keys and descriptions in the currently available literature (BORGMEIER, 1959; GONÇALVES, 1963, 1967, 1971; KUSNEZOV, 1978). Wherever possible, we densely sampled specimens of *Atta* to represent the entire geographic distributions of the species (Fig. 2a). Most of the samples used in this study belong to the Bacci (UNESP) and Rabeling (ASU) collections. We complemented our sampling with specimens either donated or loaned by colleagues, borrowed from major entomological collections in Brazil and the United States (Table 1), and collected during various field trips. We thoroughly sampled the known widely distributed species to account for potential cryptic species (Fig. 1 and Supplementary Table S1).

Table 1. Entomological collections, listing institutions from which specimens were donated or borrowed, where specimens were studied during visits, and/or where vouchers are deposited.

CEIS	Centro de Estudos de Insetos Sociais (UNESP), André Rodrigues, personal collection, Rio Claro, SP, Brazil
CPDC	Centro de Pesquisas do Cacau, Comissão Executiva do Plano de Lavoura Cacaueira (CEPLAC), Jacques Delabie, Itabuna, BA, Brazil
CU	Cornell University, Corrie Moreau, personal collection, Ithaca, NY, U.S.A.
DZUP	Coleção Entomológica ‘Padre Jesus Santiago Moure’, Universidade Federal do Paraná (UFPR), Curitiba, PR, Brazil
EMBRAPA	Embrapa Florestas, Laboratório de Entomologia, Colombo, PR, Brazil
ICBS	Instituto de Ciências Biológicas e da Saúde, Coleção Entomológica Ângelo Moreira da Costa Lima, Universidade Federal Rural do Rio de Janeiro (UFRRJ), Seropédica, RJ, Brazil
INPA	Instituto Nacional de Pesquisas da Amazônia, Coleção Zoológica de Invertebrados, Manaus, AM, Brazil
JTLC	John T. Longino Collection, University of Utah, Salt Lake City, UT, U.S.A.
MPEG	Museu Paraense ‘Emílio Goeldi’, Coleção de Entomologia, Belém, PA, Brazil
MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil
UFU	Universidade Federal de Uberlândia, Coleção Zoológica do Museu de Biodiversidade do Cerrado, Uberlândia, MG, Brazil
UFV	Universidade Federal de Viçosa, Museu Regional de Entomologia, Viçosa, MG, Brazil
SIBR	Social Insect Biodiversity Repository, School of Life Sciences, Arizona State University, Tempe, AZ, U.S.A.
UCDC	Bohart Museum of Entomology, University of California, Davis, CA, U.S.A.

During field work, at each collection site we collected at least ten individuals per nest from at least three nests, including workers of different sizes, preferentially large workers. We collected the individuals into Eppendorf® vials and Falcon centrifuge tubes filled with 95–100% ethanol. We stored these collections in a -20 °C freezer in the *Laboratório de Evolução Molecular (LEM)* at the *Centro de Estudos de Insetos Sociais (CEIS)* at UNESP in Rio Claro, São Paulo, Brazil. Borrowed specimen series were both point-mounted and preserved in ethanol. The list of all taxa used in this study is presented in Supplementary Table S1, and includes sampling information, DNA extraction code, voucher specimen code, and Sequence Read Archive (SRA) accession numbers (numbers available upon acceptance of manuscript). The voucher specimens are deposited in the Social Insect Biodiversity Repository (SIBR) in the School of Life Sciences at Arizona State University in Tempe, Arizona, U.S.A. Replicate vouchers (individuals from the same nest) are deposited to the *Museu de Zoologia da Universidade de São Paulo (MZUSP)* in São Paulo, Brazil. Borrowed voucher specimens are deposited in the corresponding insect collections listed in Table 1 (for more details see Supplementary Table S1). We plotted our samples on a map using SimpleMapp (SHORTHOUSE, 2010) (Fig. 1) and the map for bioregions using Qgis v2.18.14 software (Esri, Redlands, CA) (Fig. 2).

2.2.2 UCE data collection

We carried out the UCE laboratory methods at Arizona State University, Tempe, AZ, U. S. A. following protocols based on Blaimer *et al.* (2015), and Borowiec (2019a), as described below.

2.2.2.1 Taxon selection and specimen conditioning

We selected 224 specimens (165 workers, 50 soldiers, five males, and four queens) for DNA extraction and UCE sequencing to represent as fully as possible both the morphospace and geographic distributions of the species within *Atta*. We also chose 49 outgroup specimens that we had already sequenced, which included species in the leaf-cutting genera *Amoimyrmex* and *Acromyrmex*, other higher attines in the genera *Mycetomoellerius* Solomon *et al.*, *Paratrachymyrmex* Solomon *et al.*, *Sericomyrmex* Mayr, *Trachymyrmex* Forel, and *Xerolitor* Sosa-Calvo *et al.*, and a more distantly related lower-attine genus, *Mycetagroicus* Brandão & Mayhé-Nunes (for more detailed information on sample numbers per genus and species see

Supplementary Table S1). This selection was based on results from previously published phylogenetic analyses employing multi-locus and genomic data (BRANSTETTER *et al.*, 2017a; CRISTIANO *et al.*, 2020; CRISTIANO; CARDOSO; FERNANDES-SALOMÃO, 2013; JESOVNIK *et al.*, 2017; LI *et al.*, 2018; RABELING *et al.*, 2018; SCHULTZ *et al.*, 2015; SCHULTZ; BRADY, 2008; SOLOMON *et al.*, 2019; SOSA-CALVO *et al.*, 2017, 2018).

We extracted DNA from specimens with minimum morphological damage (non-destructive extraction) or with partial damage (removing and pulverizing three legs per individual). For point-mounted specimens, we removed the individuals from their points and placed them in 95% ethanol to decrease cuticle stiffness and to prevent excessive damage. For non-destructive extractions, we poked small holes with a sterilized entomological pin on the right side of the pronotum, propodeum, and metasoma to facilitate the lysis process. For partially invasive extractions, we removed the right three legs of large specimens (large-sized workers, queens, and males), placed them in a 2.0 ml tube with a previously sterilized glass bead, and then disrupted the sample by using a vortexer. After extraction, we retained all specimens (voucher collection, see Table 1).

2.2.2.2 DNA extraction and library preparation

We extracted DNA using either the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, U.S.A.) for samples that were recently collected (<30 years old), or the QIAmp DNA Micro Kit (Qiagen, Valencia, CA, U.S.A.) for samples that were older than 30 years or for which we suspected DNA had degraded due to poor preservation conditions. For both kits we followed the recommendations of the manufacturer, with the following modifications to the protocols: overnight cell lysis with 20 μ L of Proteinase-K in a dry bath shaker at 56 °C and at 500 rpm, and eluting the extracted DNA from the spin-collection columns in two steps, each using 65 μ L of nuclease-free water (manufacturer's protocol calls for 1–8 hours cell lysis and 200 μ L of AE buffer for DNA elution). After extraction, we cleaned the specimen (voucher) with ethyl acetate (5–10 minutes), rinsed it, and preserved it in 95–100% ethanol. Later, we point-mounted the vouchers, labeled them, and deposited them in the insect collections mentioned above for future taxonomic study.

We quantified each DNA extraction by using 2 μ L of DNA template with a Qubit 3.0 Fluorometer employing the High Sensitivity Kit (Thermo Fisher Scientific, Inc.). Prior to library preparation, we sheared <5–50 ng of DNA template to an average fragment length of 300–600 bp using a Qsonica Q800R3 Sonicator (Qsonica LLC, Newton, CT, U.S.A.) generally

for 60 s. However, we adjusted the shearing time in relation to the preservation of the sample and the concentration of the DNA extracted, varying the shearing time to 30 or 15 s. Library preparations were carried out on 96-well plates using the Kapa Hyper Prep Library Kit (Kapa Biosystems, Inc., Wilmington, MA, U.S.A.) as described in Faircloth *et al.* (2015) with the iTru Adapters protocol. We implemented all magnetic bead clean-up steps (FISHER *et al.*, 2011) using a SPRI substitute (ROHLAND; REICH, 2012) as described in Faircloth *et al.* (2015). We used dual-indexing TruSeq adapters (FAIRCLOTH; GLENN, 2012; GLENN *et al.*, 2019) for ligation. We followed the ligation step by PCR-amplification of 15 μ L of the library using the KAPA HiFi Ready Mix (Kapa Biosystems, Inc., Wilmington, MA, U.S.A.) with 25 μ L of HiFi mix, 2.5 μ L of each of Illumina TruSeq i5 and i7 primers, and 5 μ L nuclease-free ddH₂O. For the PCR we employed the following thermal cycler program: 98 °C for 45 s; 14 cycles of 98 °C for 15 s, 60 °C for 30 s, 72 °C for 60 s; and final extension at 72 °C for 5 m. Following PCR, we purified DNA products using 1.2x speedbeads and rehydrated the purified product in 22 μ L of Elution Buffer (EB, pH= 8). We quantified individual libraries using 2 μ L of library products in a Qubit 3.0 Fluorometer using the Broad Range Kit.

2.2.2.3 Sample pooling and target enrichment of libraries

We pooled post-PCR libraries (eight to 12 libraries together) at equimolar concentrations into 22 pools. We adjusted pool concentrations to 147 ng/ μ L by drying samples in a vacuum centrifuge for 45-60 m (or until all liquid was evaporated) at 60 °C, and then resuspending them in nuclease-free water at volumes estimated for each pool. We used 2 μ L of the resuspended product to measure each pool concentration in a Qubit 3.0 Fluorometer with the Broad Range Kit. Final concentrations of pre-enrichment pools were 37.8–149 ng/ μ L.

We enriched each pool using 9446 baits (myBaits®; Arbor BioSciences) targeting 2524 conserved loci in Hymenoptera (BRANSTETTER *et al.*, 2017b) for 24 h at an incubation temperature of 65 °C. Enrichment, bead-cleaning, and PCR reaction procedures followed (BOROWIEC, 2019a). The resulting reactions were purified using 1.0X speedbeads and the enriched pools were then rehydrated in 22 μ L EB. Following this step, we quantified 2 μ L of each enriched pool using the Qubit 3.0 Fluorometer and the Broad Range Kit. To obtain reliable estimates of DNA concentration for each enriched pool, we performed a quantitative qPCR on an Applied Biosystems 7500 Real-Time PCR System (Applied Biosystems™, Thermo Fisher Scientific, Inc.) using the KAPA Library Quantification Kit (Kapa Biosystems, Inc.) with the KAPA SYBR® FAST qPCR Master Mix, universal Illumina primers, and dilutions of

1:1,000,000 and 1:2,000,000 for each pool. We then used the resulting concentration estimates to pool the libraries at equimolar concentrations in a single final pool, with a final volume of 200 μ L. We sent two final enriched pools, containing libraries for 128 and 120 samples, respectively, to the University of Utah High Throughput Genomics Core Facility for quality control and sequencing of two full lanes of a HiSeq 2500 (125 Cycle Paired-End Sequencing v4) run. Raw sequences generated as part of this study are deposited at the NCBI Sequence Read Archive (SRA). Raw sequences generated as part of this study will be deposited at the NCBI Sequence Read Archive (SRA).

2.2.2.4 Processing of UCE sequence data

The raw sequence data was demultiplexed and converted to FASTQ format at the University of Utah High Throughput Genomics Core Facility. We cleaned, assembled, and aligned the output from the demultiplexed FASTQ data using the PHYLUCE package v1.6.7 (FAIRCLOTH, 2016) and following the recommendations in Branstetter *et al.* (2017b). Within the PHYLUCE package, we took advantage of wrapper scripts designed to facilitate batch processing of large amounts of data. We trimmed raw reads for adapter contamination and low-quality bases using Illumiprocessor v.2.0.6 (FAIRCLOTH, 2013), which includes Trimmomatic v0.39 (BOLGER; LOHSE; USADEL, 2014). We used Trinity v.r2013_2_25 (GRABHERR *et al.*, 2011) for assembly of reads into contigs and Lastz v1.0 (HARRIS, 2007) to match the assembled contigs to the input probe set (ant-specific-hym-v2 bait file) with the script *phyluce_assembly_match_contigs_to_probes* with default settings.

Following UCE contig extraction, we aligned each UCE locus using MAFFT v7.407 (KATO; STANDLEY, 2013) with the L-INS-i option. We trimmed the resulting alignments with GBLOCKS v.091b (TALAVERA; CASTRESANA, 2007) using relaxed settings (-b1 = 0.5 -b2 = 0.5 -b3 = 12 -b4 = 7). We concatenated the trimmed single-locus UCE alignments using the scripts *phyluce_align_get_only_loci_with_min_taxa* and *phyluce_align_format_nexus_files_for_raxml* to generate the datasets or alignments. Most of the ingroup taxa involved in our study had over 2000 UCE loci. We identified long branches associated with sequences from older specimens or from specimens with low-quality DNA and less than 1000 loci, probably caused by problems in the alignment of sequence fragments with large length differences. If we determined that such long-branched sequences could negatively affect the analyses, we removed them using manual cutoff. We did not use the program Spruceup (BOROWIEC, 2019b) to address these sequences, because it would have removed

even more characters from those taxa and potentially eroded phylogenetic signal, leading to inaccurate phylogenetic estimates for those taxa (WIENS; MORRILL, 2011). We ultimately generated three final alignments, a dataset including loci in which 70% of the taxa were present (Atta273t_70per), a more ‘complete’ dataset that included loci in which 90% of the taxa were present (Atta273t_90per), and a reduced dataset for the divergence-dating analysis (Atta73t_div). We calculated summary statistics for the final data matrices using the script *phyluce_align_get_align_summary_data* in the Phyluce package. For the construction and analysis of the phylogeny presented in our results, we used the dataset from Atta273t_70per matrix, which resulted in a final dataset of 2340 UCE loci and 2,308,679 bp of sequence data; for the divergence-dating analysis we used the reduced dataset from Atta73t_div matrix (Table 2; for more details on alignment matrices statistics see Supplementary Table S2).

Table 2. Datasets consisting of partitioned alignments (SWSC-EN) used in the phylogenetic and divergence-dating analyses, with summary statistics for the aligned and concatenated matrices.

Matrix	Data matrix	Number of taxa	UCE loci	Alignment length (pb)	Partitions	Distinct alignment patterns	UCE mean loci length	% missing data
Atta273t_70per	70%	273	2340	2308679	1520	1386996	986.61	4.54
Atta273t_90per	90%	273	1038	1064781	774	648340	1025.8	2.45
Atta73t_div	70%	73	2274	2168673	1039	848122	953.68	7.09

2.2.2.5 UCE phylogenomic analysis

We ran preliminary, unpartitioned, analyses using IQ-TREE multicore v.1.6.12 (NGUYEN *et al.*, 2015). Branch support was calculated with 1000 ultrafast bootstraps (HOANG *et al.*, 2018), using -m GTR+G, and estimating a Neighbor Joining tree (-t BioNJ) for the three datasets (CHERNOMOR; HAESELER; MINH, 2016). We then partitioned the datasets using the Sliding-Window Site Characteristics based on Entropy (SWSC-EN, TAGLIACOLLO; LANFEAR, 2018) program, which uses a sliding window method to partition UCE loci into three regions (the core and its right and left flanking regions). This method takes advantage of the general pattern in which UCE core regions are highly conserved whereas the variability of the flanking regions increases with their distance from the core (FAIRCLOTH *et al.*, 2012). The resulting data subsets were then analyzed using ModelFinder (KALYAANAMOORTHY *et al.*, 2017) as implemented in IQ-TREE multicore v.1.6.12 (NGUYEN *et al.*, 2015), setting the selection criterion as AICc, and the search algorithm as

rclusterf (LANFEAR *et al.*, 2017). We also partitioned the alignments by each locus. Each dataset was analyzed as non-partitioned, SWSC-EN partitioned, and partitioned by locus.

We performed Maximum Likelihood (ML) analyses on the three generated dataset alignments with their respective partitioning schemes using IQ-TREE multicore v.1.6.12 (NGUYEN *et al.*, 2015), estimating branch support with ultrafast bootstrapping set at 1000 replicates (HOANG *et al.*, 2018), and other settings kept at the default conditions.

2.2.3 Divergence time inference

To estimate species divergence times, we analyzed a reduced dataset (Atta73t_div) in which, for each species, we included specimens with the largest number of UCE loci and with consideration of their locations on the tree. We input the reduced alignment and topology to the program MCMCTree in the PAML v4.9j package (YANG, 2007) using the approximate-likelihood approach. To calibrate our analysis, we used a Dominican amber fossil [*Mycetomoellerius primaevus* (Baroni Urbani); see BARONI URBANI, 1980]. This fossil species, which was previously used to calibrate analyses (BRANSTETTER *et al.*, 2017a; LI *et al.*, 2018; SCHULTZ; BRADY, 2008), was recently placed in the newly created genus *Mycetomoellerius* in a recent study in which the formerly paraphyletic higher-attine genus *Trachymyrmex* s.l. was divided into three monophyletic genera (SOLOMON *et al.*, 2019). However, this placement is associated with a high degree of uncertainty (T. R. SCHULTZ and J. SOSA-CALVO, personal observation). Due to this uncertainty, we conservatively chose to use the fossil, as was done in the previous studies cited above, to calibrate the ancestral crown node of all the higher-attine ants corresponding, in the present study, to the most recent common ancestor (MRCA) of *Mycetomoellerius* and *Atta*, rather than to calibrate the stem node of the genus *Mycetomoellerius*. The fossil calibration was specified as a truncated Cauchy probability distribution indicated by $L(tL, p, c)$, where tL = minimum-age bound (set as 15 Ma), p = offset value (default value of 0.1), and c = the scale parameter value (default value of 1.0) representing a heavy-tailed density (INOUE; DONOGHUE; YANG, 2010). Since the dating of Dominican amber is ambiguous, ranging from 15 to 20 Ma (GRIMALDI; AGOSTI, 2000; ITURRALDE-VINENT; MACPHEE, 1996), we chose a conservative minimum age of 15 Ma and employed a relatively flat ($c = 1.0$) prior probability distribution to accommodate a wide range of prior dates. Because of the lack of a fossil with which to directly calibrate the root node, we employed a secondary calibration based on the inferred age of the corresponding internal node from Branstetter *et al.* (2017a), Ješovnik *et al.* (2017), and Li *et al.* (2018). The root node was

calibrate with the both soft minimum (25.9 Ma) and maximum (37.2 Ma) bounds, to incorporate the 95% highest posterior density (HPD) value range estimated in the studies listed above.

We performed the MCMCTree dating analyses using an unpartitioned concatenated alignment, the independent-rates clock model, and the HKY85+G model of sequence evolution. For each analysis, we ran two independent chains for 50 million generations at a sampling frequency of 500 and a burn-in of 20%. We assessed run convergence and performance by examining the mcmc.txt files in Tracer v1.7.1 (RAMBAUT *et al.*, 2018) and convergence plots in Excel.

2.2.4 Biogeographical analysis

To estimate ancestral areas and reconstruct radiation patterns of *Atta*, we used the BioGeoBEARS R package (MATZKE, 2013, 2015) and a modified version of the BioGeoBEARS original R scripts (A.F. SÁNCHEZ-RESTREPO, personal communication; MAGALHAES, 2021). As input, we used the Bayesian inference tree from the divergence dating analysis (Fig. 3) adapted to one specimen per species, and the data matrix of occurrence geographic of *Atta* species and outgroup taxa (see Supplementary Table S3). We assigned extant species distributions based on ten bioregions that we selected and adapted from MORRONE's, (2006) classification of Neotropical entomofauna. We used the following bioregion tags: A = North America; B = Caribbean; C = Central / NW South America; D = Guiana Shield; E = Amazonia; F = Cerrado; G = Caatinga; H = Atlantic Forest; I = Chaco; J = Pampas (from the map regions in Fig. 2). We classified the ant species as present or absent in each region based on their known distributions from our sampling, the literature, and records gathered from specific databases (DAGUERRE, 1945; FARJI-BRENER; RUGGIERO, 1994; FERNÁNDEZ; SENDOYA, 2004; FERNÁNDEZ; SERNA, 2019; FOWLER, 1985, 1988; GONCALVES, 1961; GUÉNARD *et al.*, 2017; KEMPF, 1972; RANDO; FORTI, 2005; WEBER, 1966, 1969; WILSON, 1986; JANICKI *et al.*, 2016) (see Supplementary Table S4).

We tested and compared six commonly implemented models: the likelihood-based Dispersal-Extinction Cladogenesis model (DEC; REE *et al.*, 2005; REE & SMITH, 2008), the likelihood-based version of Dispersal-Vicariance Analysis model (DIVA-like; MATZKE, 2013; RONQUIST, 1997), the Bayesian Binary model (BayArea-like; LANDIS *et al.*, 2013; MATZKE, 2013), and all three models with the additional parameter of founder-event speciation (+J) (MATZKE, 2014) as recommended in BioGeoBEARS. We used the Akaike Information Criterion (AICc) score to compare the fit of the models to our data.

2.3 Results

2.3.1 UCE sequencing

The mean DNA post-extraction concentration of the 246 taxa extracted for this study was 3.01 ng/μL (range: 0.06–31.3 ng/μL) and 24.21 ng/μL (range: 4.36–53 ng/μL) for the post-PCR libraries. The mean number of raw reads sequenced was 2,083,262.2 (range: 78,145–7,307,553) and the mean number of UCE loci captured was 2307.45 (range: 1088–2447) (Table 3). Full UCE data and sequencing statistics for each taxon are presented in Supplementary Table S5.

Table 3. Summary of ultraconserved element (UCE) processing and sequencing statistics for all taxa extracted in this study. For more detailed statistics per taxon, see Supplementary Table S5.

	DNA conc. extract (ng/μL)	DNA conc. post-PCR (ng/μL)	Raw reads	Contigs	UCE loci
Mean	3.01	24.21	2083262.2	38133.73	2307.45
Min	0.06	4.36	78145	1276	1088
Max	31.3	53	7307553	236430	2447
SD	4.4	9	984256.78	32721.06	164.38

SD, standard deviation

2.3.2 Phylogenetic reconstruction and divergence dating

Here, we provide the most comprehensive phylogenetic estimate to date for the leaf-cutting ant genus *Atta* and its associated outgroups based on the sequence capture of ultraconserved elements (Fig. 2a). The results of the SWSC-EN partitioned phylogeny recovered the leaf-cutting ants as a monophyletic group that consists of three reciprocally monophyletic genera: *Atta*, *Acromyrmex*, and *Amoimyrmex*. Our phylogeny also indicates that the monophyly of our target group, the genus *Atta*, is maximally well supported and recovered the 14 studied species and separated them into four clades, each supported by maximum bootstrap frequency (Fig. 2a). These clades correspond to previously recovered species groups (BACCI *et al.*, 2009) and to previously recognized subgenera of *Atta*, including *Archeatta*, *Atta* s.s., *Epiatta*, and *Neoatta* (Fig. 2a, 2b). Hereafter we use these subgenus names, currently considered synonyms of the genus *Atta* (BOLTON *et al.*, 2006), to refer to specific clades within *Atta* as informal species names.

All *Atta* species studied are monophyletic with maximal support (Fig. 2a). The Archeatta clade includes the North and Central American as well as the Caribbean species, is composed of *Atta mexicana* (Smith) (Fig. 2c), *Atta insularis* Guérin (Fig. 2d), and *Atta texana* (Buckley) (Fig. 2e), and is the sister clade to all the remaining *Atta* species, which occupy North, Central, and South America. The species of the *Atta* s.s. clade, *Atta colombica* Guérin (Fig. 2f), and *Atta cephalotes* (Linnaeus) (Fig. 2g), are from North, Central and South America. Our results indicate that Epiatta is the most species-rich clade and includes species with biogeographic distributions restricted to South America: *Atta saltensis* Forel (Fig. 2h), *Atta vollenweideri* Forel (Fig. 2i), *Atta goiana* Gonçalves (Fig. 2j), *Atta bisphaerica* Forel (Fig. 2k), *Atta capiguara* Gonçalves (Fig. 2l), *Atta opaciceps* Borgmeier (Fig. 2m), and *Atta laevigata* (Smith) (Fig. 2n). Within the Epiatta clade, *A. saltensis* and *A. vollenweideri* form the sister to the remaining species. Our phylogeny provides the first evidence that *A. goiana* belongs to Epiatta. In the case of the Neoatta clade, we recovered two species, *Atta robusta* Borgmeier (Fig. 2o), one of the most biogeographically restricted species in the genus *Atta*, and *Atta sexdens* (Linnaeus) (Fig. 2p), from Central and South America, and another of the most widely distributed species in the genus (for more details on the distribution of each species see Supplementary Table S4).

Our results indicate that the higher-attine ants originated around 23.2 Ma (crown age; 95% HPD: 16.4–30.6 Ma). The leaf-cutting ants subsequently arose around 18.9 Ma (stem age; 95% HPD: 12.9–24.9 Ma) and radiated relatively rapidly (crown age; 18.2, 95% HPD: 12.4–24.1 Ma). The stem and crown estimated divergence times of the genus *Atta* are 16.7 Ma (95% HPD: 11.3–22.3 Ma) and 8.5 Ma (95% HPD: 4.9–12.5 Ma), respectively, indicating that a period of approximately 8.2 million years separates the stem age of *Atta* from the most-recent common ancestor of all extant species (i.e., the crown-group age), suggesting either a relatively long delay until the first speciation event or subsequent extinction of early-diverging lineages (Fig. 3 and Table 4; for more details on the divergence dates see Supplementary Table S6).

Table 4. Estimated divergence dates from the MCMCTree analysis for major clades and subclades of genus *Atta*. For more detailed estimates by clade, see Supplementary Table S6.

Clade	Mean	95% HPD
Higher-attine ants crown	23.2	16.4–30.6
MRCA <i>Trachymyrmex</i> + <i>Atta</i>	18.9	12.9–24.9
MRCA <i>Amoimyrmex</i> + <i>Atta</i>	18.2	12.4–24.1
<i>Acromyrmex</i> + <i>Atta</i>	16.7	11.3–22.3
<i>Atta</i> crown	8.5	4.9–12.5
Archeatta crown	4.8	2.3–7.8
<i>Atta</i> s.s. + <i>Epiatta</i> + <i>Neoatta</i> crown	7.5	4.2–11.2
<i>Atta</i> s.s. crown	3.3	1.5–5.5
<i>Epiatta</i> + <i>Neoatta</i> crown	3.7	2.0–5.7
<i>Epiatta</i> crown	2.2	1.3–3.3
<i>Neoatta</i> crown	2.2	1.1–3.5

HPD, highest posterior density. Ages in millions of years ago (Ma)

The Archeatta clade exhibits the oldest crown-group age (4.8, 95% HPD: 2.3–7.8 Ma) but at the same time consists of notably fewer species suggesting either a lower rate of speciation or higher rate of extinction among this North American and Caribbean clade. Another three clades, *Atta* s.s., *Epiatta*, and *Neoatta*, share a common ancestor around 7.5 Ma (95% HPD: 4.2–11.2 Ma). Interestingly, the species *A. cephalotes* is divided into two distinct clades that diverged around 1.1 Ma (95% HPD: 0.6–1.7 Ma). This divergence is correlated with the species biogeography, with one clade inhabiting North, Central, and the northern part of South America northwest of the Andes and contiguous with Central America, and with a second clade inhabiting northern South America, including the Guiana Shield and Amazonia, and the Atlantic Forest from northeastern Brazil (Fig. 2a). The common ancestor of the *Epiatta* and *Neoatta* clades arose approximately 3.7 Ma (95% HPD: 2.0–5.7 Ma), and both groups subsequently diversified roughly simultaneously during the Pleistocene, 2.2 Ma (95% HPD: 1.3–3.3 Ma) and 2.2 Ma (95% HPD: 1.1–3.5 Ma), respectively.

2.3.3 Historical biogeography

The BioGeoBEARS analysis identified the biogeographical model BayArea-like as the model that best fits the data to explain the ancestral-area reconstructions (see Table 5). The BayArea-like model, however, is of limited usefulness for understanding the historical biogeography of *Atta* because it was clearly affected by the presence of widespread species (see Supplementary tree Fig. S1). As a result, ancestral-area reconstructions at deeper nodes were all maximally widespread, even for the ancestors of groups that are currently narrowly distributed (e.g., *Trachymyrmex*). We addressed this problem in two main ways: (i) by focusing on the results of the DIVA-like model and (ii) by analyzing a data set from which the widespread taxa were eliminated.

Table 5. Values from BioGeoBEARS results for the six compared biogeographical models.

Model	LnL	k	AICc	AICw	d	e	j
Test A - complete distribution							
BayArea-like	-254.1984015	2	512.6758728	0.844482377	0.01186702	0.086564095	0
BayArea-like+J	-254.7441935	3	516.0598156	0.155516602	0.009041475	0.012694358	0.036029265
DEC	-268.1059421	2	540.490954	0.00000077	0.015331749	1E-12	0
DEC+J	-268.0808702	3	542.733169	0.000000251	0.015285824	1E-12	0.001946843
DIVA-like	-277.923955	2	560.1269798	4.19E-11	0.018144552	0.009506919	0
DIVA-like+J	-277.9269757	3	562.42538	1.33E-11	0.018117484	0.00851877	0.00001
Test B - without widespread species distribution							
BayArea-like+J	-217.5517462	3	441.674921	0.915912698	0.005755516	0.035622088	0.018058444
BayArea-like	-221.0859911	2	446.4510519	0.084087302	0.007482382	0.064570302	0
DEC+J	-249.1880738	3	504.9475761	1.67E-14	0.012940127	1E-12	0.018504611
DEC	-250.4176607	2	505.1143912	1.54E-14	0.01421674	0.008328203	0
DIVA-like	-250.82884	2	505.9367498	1.02E-14	0.015199999	0.004676356	0
DIVA-like+J	-250.6550025	3	507.8814337	3.85E-15	0.014506165	1E-12	0.005266356

LnL, log-likelihood; k, No. parameters; AIC, akaike information criteria; d, dispersal; e, extinction; j, founder

Compared to the results of other models, the DIVA-like and DIVA-like + J analyses, which do not allow widespread sympatry (MATZKE, 2013), resolved ancestral areas for our data with less ambiguity. We give more credence to the results of the DIVA-like and DIVA-like + J analyses for this and the following reasons: (i) the AICc criterion is not necessarily decisive for selecting among models (see Statistical Model Selection in <http://phylo.wikidot.com/advice-on-statistical-model-comparison-in-biogeobears#zen>); (ii) a

recent study has shown that the DEC and DEC + J models are problematic models with important limitations and that they cannot be directly compared, e.g., using the AICc (REE; SANMARTÍN, 2018); and (iii) the inclusion of founder-event speciation is not crucial for explaining evolutionary dispersal events in intra-continently distributed taxa with a large degree of sympatry across widespread ranges such as *Atta* and *Acromyrmex* (MATZKE, 2013). Also, as previously mentioned, in a separate analysis we treated the widespread condition of some *Atta* and *Acromyrmex* species (*A. cephalotes*, *A. laevigata*, *A. sexdens*, and *Acromyrmex coronatus* Fabricius) as a derived character state and coded the distributions of these widespread taxa with the same areas as their more geographically restricted sister taxa. In this analysis, the AICc identified BayArea-like + J as the best-fitting biogeographical model, for which the results were very similar to the DIVA-like model from the original analysis in which those species were coded as widespread (see Table 5 and Supplementary tree Fig. S2). Here, we therefore present and discuss the results of the DIVA-like (Fig. 4).

Most of the lineages in our analysis arose during the Miocene and Pliocene approximately 20.0–5.0 Ma. The analysis indicates that the leaf-cutting ants arose in the North American region in the early Miocene and subsequently dispersed to Central and South America. Likewise, the genus *Atta* and, subsequently, the ancestor of the *Archeatta* clade, were inferred to have originated in North America during the late Miocene, subsequently rapidly radiating in the Pliocene and Pleistocene (Fig. 3, 4). The ancestral lineage of the remaining three clades (*Atta* s.s., *Epiatta*, and *Neoatta*) expanded southward throughout Central America, which is explicitly supported by the BayArea-like + J model, giving rise to two clades. One daughter clade, *Atta* s.s., remained restricted to Central and northwestern South America (north of the Andes) until much later, but the ancestor of the sister clade consisting of *Epiatta* and *Neoatta*, crossed the Andes into the Amazon forest and rapidly spread into South America, reaching the Atlantic Forest through the ancient connection between the two forests (BATALHA-FILHO *et al.*, 2013). This range expansion led to the largest burst of speciation in the genus diversifying into the newly formed and expanding Cerrado habitats and adjacent forests.

2.4. Discussion

2.4.1 Reconstruction of *Atta* phylogeny and divergence dating

In this study, we inferred a comprehensive molecular phylogeny of the leaf-cutting ant genus *Atta* utilizing phylogenomic markers and sampling a large number of taxa to capture diversity and population variation across the biogeographic range of this widely distributed ant genus. Our well-resolved and well-supported phylogeny clarifies relationships between species and species groups and reveals previously unknown historical divergences that allow us to test hypotheses about the origin of the genus *Atta*, the divergences of its species, and their historical dispersal into North, Central, and South America as well as the Caribbean. Our study adds to a growing body of phylogenetic research that utilizes UCEs to infer comprehensive, well-resolved, and statistically well-supported phylogenies that allow for inferring insect evolution as well as testing evolutionary and biogeographic hypotheses (BLAIMER *et al.*, 2016a; BRANSTETTER *et al.*, 2017c, 2021; FAIRCLOTH *et al.*, 2012, 2015). Lending support to the conclusions of multiple prior studies, our results indicate that UCEs are extremely effective for reconstructing divergences in higher-attine ants, and other groups of ants, at a wide range of levels, from ancient (> 30 Ma) to very recent, including the delimitation of species and populations, even in very recent, short-branched evolutionary radiations, (BLAIMER *et al.*, 2016b; BOROWIEC; COVER; RABELING, 2020; FERNANDES *et al.*, 2021; JESOVNIK *et al.*, 2017; PREBUS, 2020; VAN ELST *et al.*, 2021; WILLIAMS *et al.*, 2020; RABELING *et al.*, in prep.). These qualities recommend phylogenomic markers over traditional molecular genetic markers (COI, TRNA leucine, COII, EF1-alpha F1, etc.) (BLAIMER *et al.*, 2015; DO AMARAL *et al.*, 2015) used in earlier studies of higher-attine ants, some of which included the genus *Atta* (BACCI *et al.*, 2009; CRISTIANO *et al.*, 2020; CRISTIANO; CARDOSO; FERNANDES-SALOMÃO, 2013; SOLOMON *et al.*, 2008, 2019; SOSA-CALVO *et al.*, 2017, 2018).

Our phylogeny supports the monophyly of the leaf-cutting ants and of the genus *Atta*, in agreement with previous phylogenetic studies (BACCI *et al.*, 2009; CRISTIANO *et al.*, 2020; CRISTIANO; CARDOSO; FERNANDES-SALOMÃO, 2013; SCHULTZ; BRADY, 2008), and our estimated dates for both the stem and crown ages of leaf-cutting ants and for the stem age of *Atta* are similar to those found in previous studies (BRANSTETTER *et al.*, 2017a; JEŠOVNIK *et al.*, 2016; NYGAARD *et al.*, 2016; SCHULTZ; BRADY, 2008). Some of the divergence dates inferred here, however, are slightly older, such as the root of our phylogeny

and the *Atta* crown-group age (Table 4 and Supplementary Table S6). Our phylogeny additionally provides new and unprecedented information about the relationships of the species within the genus *Atta*, and our divergence-dating analyses provide a comprehensive view and new perspectives on the timing of the origin and subsequent diversification of leaf-cutting ant species in the genus *Atta*.

The leaf-cutting ant genus *Atta* is remarkably young, originating between 16.7 (stem) and 8.5 (crown) million years ago at the boundary of the Miocene and Pliocene. Leaf-cutting agriculture, originating ~19 million years ago, is young as well, although some previous studies have suggested that the origins of leaf-cutting ants and their fungal cultivars may not have occurred simultaneously, whether judged by stem or crown-group ages (MIKHEYEV; MUELLER; ABBOT, 2010; MUELLER *et al.*, 2017; NYGAARD *et al.*, 2016). Unlike the diversification pattern in *Acromyrmex*, our data indicate a long delay separating the stem from the crown-group of *Atta*, followed by a burst of diversification, producing extant *Atta* species, that occurred during the past 4–5 million years, i.e., following the origins of the clades within the genus. A similar pattern was observed in the fungus-growing ant genus *Sericomyrmex*, which also diversified during the past 4 million years (JEŠOVNIK *et al.*, 2017). In fact, Ješovnik *et al.* (2017) compared *Sericomyrmex* with *Atta* when they explained the possible evolutionary processes underlying the recent and rapid radiations of both genera; our results support this prior conjecture. *Atta* species have conquered a wide diversity of habitats spanning a vast geographical range, differing in climatic conditions and in phytophysiognomies (e.g., Amazon forest, Cerrado, restinga, and Caatinga, among others). This radiation has been accompanied by few phenotypic changes, particularly in the morphology of smaller workers. Like *Sericomyrmex*, *Atta* is the product of a large amount of initial phenotypic evolution, making it immediately distinguishable from other leaf-cutting genera as well as from any other fungus-growing ant species. Our data and those of Ješovnik *et al.* (2017) suggest that the radiations of both *Atta* and *Sericomyrmex* are correlated with the rise and great expansion of Cerrado habitats in South America during the past 4 million years (MEYER *et al.*, 2014; PRADO; GIBBS, 2012; SILVA, 2011).

Our results indicate that *Atta* comprises four well-defined clades, which correspond to the clades recovered in a previous phylogeny of the genus (BACCI *et al.*, 2009) and to the subgenera that were previously defined on the basis of morphological characters (BORGMEIER, 1950; GONÇALVES, 1942). The topology of our phylogeny differs from the mitochondrial phylogeny inferred by Bacci *et al.* (2009), which recovered *Archeatta* and *Atta* s.s. as sister clades, and it agrees with the topologies inferred from nuclear genes and from

alignments that combined both mitochondrial and nuclear DNA, which, like ours, placed *Archeatta* as the sister group to the remaining species of the genus (BACCI *et al.*, 2009). *Atta* species were originally grouped into subgenera based primarily on the morphology of males (BORGMEIER, 1950, 1959; GONÇALVES, 1942, 1986), but Bolton *et al.* (2006) synonymized the subgenera under the genus *Atta*. Although our results support the reciprocal monophyly of the *Atta* clades (former subgenera) and conform to clear biological and biogeographical patterns, revisionary taxonomy is beyond the scope of the present study, including any changes to the current status of the synonymized subgenera (Table 6).

Table 6. History of the subgenera and their species composition of genus *Atta*.

Species	Proposal subgenres						
	Emery (1922)	Gonçalves (1942)	Borgmeier (1950)	Borgmeier (1959)	Gonçalves (1986)	Bacci <i>et al.</i> (2009)	This study
<i>A. mexicana</i>	-	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i> clade
<i>A. texana</i>	-	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i> clade
<i>A. insularis</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i>	<i>Archeatta</i> clade
<i>A. cubana</i>	-	-	-	-	-	-	Not available
<i>A. cephalotes</i>	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s. clade
<i>A. colombica</i>	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s.	<i>Atta</i> s.s. clade
<i>A. saltensis</i>	-	-	-	<i>Palaeatta</i>	<i>Palaeatta</i>	<i>Epiatta</i>	<i>Epiatta</i> clade
<i>A. vollenweideri</i>	-	<i>Neoatta</i>	<i>Epiatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Epiatta</i>	<i>Epiatta</i> clade
<i>A. gioana</i>	-	<i>Neoatta</i>	<i>Palaeatta</i>	<i>Palaeatta</i>	<i>Palaeatta</i>	-	<i>Epiatta</i> clade
<i>A. bisphaerica</i>	-	<i>Neoatta</i>	<i>Palaeatta</i>	<i>Palaeatta</i>	<i>Palaeatta</i>	<i>Epiatta</i>	<i>Epiatta</i> clade
<i>A. capiguara</i>	-	-	<i>Epiatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Epiatta</i>	<i>Epiatta</i> clade
<i>A. opaciceps</i>	-	<i>Neoatta</i>	<i>Epiatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Epiatta</i>	<i>Epiatta</i> clade
<i>A. laevigata</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Epiatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Epiatta</i>	<i>Epiatta</i> clade
<i>A. robusta</i>	-	<i>Neoatta</i>	<i>Epiatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Neoatta</i> clade
<i>A. sexdens</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Neoatta</i>	<i>Neoatta</i> clade

Adapted from Bacci *et al.* (2009).

2.4.2 Phylogenetic relationships within the genus *Atta*

Our study indicates, like phylogenetic studies using nuclear genes (BACCI *et al.*, 2009; CRISTIANO; CARDOSO; FERNANDES-SALOMÃO, 2013), that *Archeatta* is the sister clade to all other species of *Atta*. This result contradicts Gonçalves' (1986) theory that *A. colombica* (belonging to *Atta* s.s. clade) occupies an early-diverging position in the genus. The only *Atta* species that is not included in our study, *A. cubana*, likely also belongs to the *Archeatta* group. Known only from its original description (FONTENLA RIZO, 1995), this species has never been included in a phylogenetic analysis. Based on the species description, and assuming that it is a valid species (rather than conspecific with *A. insularis*), *A. cubana* is

likely the sister species of *A. insularis* the two species occur in sympatry. If so, the two species very likely diverged on the island of Cuba, as is suggested by their differing habitat preferences. Whereas *A. cubana* generally occupies coastal regions and sandy soils, *A. insularis* prefers forest and grassland habitats (FONTENLA RIZO, 1995; J.L. FONTENLA RIZO, personal communication).

Our UCE analysis reconstructed the *Atta* s.s. clade as the sister clade to the remaining Central and South American species in the *Epiatta* and *Neoatta* clades and the transitional group between those two clades and *Archeatta*, consistent with the results inferred by a previous phylogeny (BACCI *et al.*, 2009), as well as with inferences in early morphological studies (BORGMEIER, 1950, 1959; GONÇALVES, 1986). The phylogenetic position of the *Atta* s.s. clade suggests that the ancestral species of this clade diverged in during *Atta* evolution and that its daughter species occupied the northernmost regions of South America. *Atta colombica* is a forest-dwelling species that lives mainly in lower-elevation regions of Central America from Guatemala to Colombia in northwestern South America. In contrast, *A. cephalotes*, which is sympatric with *A. colombica* in Central America, can inhabit higher-elevation regions and is distributed from Mexico in the north to South America as far south as the coast of eastern Brazil, making it one of the most widely distributed species in the genus (FERNÁNDEZ; CASTRO-HUERTAS; SERNA, 2015; FERNÁNDEZ & SENDOYA, 2004; FORTI *et al.*, 2020; WEBER, 1969;). However, the northernmost extension of the Andes seems to be a biogeographic barrier potentially restricting gene flow between *A. cephalotes* populations, as suggested by the clear separation of the northern and southern clades of *A. cephalotes* (Fig. 2a; see also Supplementary Fig. S3). In fact, these two well-supported, reciprocally monophyletic sister groups of *A. cephalotes* may be separate species (LOVATO, 2006), a hypothesis that needs to be tested by future taxonomic and phylogenetic analyses. With regard to a similar phylogenetic split in the southern clade, the absence of *A. cephalotes* in the Cerrado regions separating the Amazonian and Atlantic Forests is consistent with the hypothesis that the Amazonian and Atlantic Forest populations of *A. cephalotes* arose in allopatry after they were separated by a climatic barrier, because *A. cephalotes* is restricted to the wet forest (SOLOMON *et al.*, 2008) and absent from the semi-arid Cerrado (GONÇALVES, 1960).

Containing seven species, the *Epiatta* clade represents the largest rapid radiation in the genus (see historical biogeography section). Although closely related, the species of *Epiatta* have different biological and ecological characteristics. *Atta saltensis*, *A. vollenweideri*, *A. goiana*, *A. bisphaerica*, *A. capiguara*, and *A. opaciceps* occur in semi-arid and dry regions of South America and have restricted geographic distributions. In contrast, *A. laevigata* is widely

distributed (Fig. 2a) (BORGMEIER, 1959; DAGUERRE, 1945; FORTI *et al.*, 2020; GONÇALVES, 1942, 1960; HÖLLDOBLER; WILSON, 1990; SABATTINI *et al.*, 2017; SOLOMON *et al.*, 2008). The geographic distributions are correlated with the degree of specialized foraging: *A. vollenweideri*, *A. goiana*, *A. bisphaerica*, and *A. capiguara* forage mainly for monocotyledonous plants whereas *A. saltensis* and *A. opaciceps* forage exclusively for dicotyledonous plants, and, in contrast to both other groups, *A. laevigata* is a generalist that forages for both types of plants (FOWLER *et al.*, 1989; GONÇALVES, 1971; MUELLER *et al.*, 2017). This generalist foraging behavior likely allowed *A. laevigata* to occupy novel ecological niches and expand its geographic range, and it is consistent with its ability to live in both arid and humid environments (SOLOMON *et al.*, 2008). This foraging behavior also made *A. laevigata* an important pest of human agriculture in some regions (DELLA LUCIA, 2003).

Our analyses inferred the reciprocal monophyly and sister-group relationship of *A. capiguara* and *A. opaciceps*, differing from the topology reconstructed by Bacci *et al.* (2009). Previous studies placed these two species in the subgenus *Neoatta* because of morphological similarities to the other species that belonged to this group (*A. sexdens*, *A. bisphaerica*, and *A. laevigata*), mainly relying on characters of the male genitalia (BORGMEIER, 1950; GONÇALVES 1942, 1944, 1986). In contrast, our results indicate that *A. capiguara* and *A. opaciceps* are members of the *Epiatta* clade, which is consistent with the molecular phylogenetic results of Bacci *et al.* (2009). *Atta capiguara* inhabits secondary, open forests and grassland habitats, mainly in the Brazilian Cerrado, and it was originally known only from São Paulo State. It was subsequently found to occur in Mato Grosso, Mato Grosso do Sul, Goiás, Minas Gerais, and Paraná (DELLA LUCIA; FOWLER; MOREIRA, 1993; FORTI; BOARETTO, 1997; FORTI *et al.*, 2020). *Atta opaciceps*, the only leaf-cutting ant species endemic to the Caatinga, a dry, desert-like forest biome, is restricted to the northeastern region of Brazil (BRANDÃO, 1995; SIQUEIRA *et al.*, 2018; ULYSSÉA; BRANDÃO, 2013). Adaptations to high temperatures and low humidity in the dry forest are traits shared by these two species.

We originally included two specimens of *A. goiana* (10023 BR-MT and 9900 BR-MG) in our analyses, which formed a strongly supported clade. However, the taxon 10023 BR-MT arose on an extremely long branch and we excluded the sample from subsequent analyses, as were other anomalously long-branched taxa (see Materials and Methods section). The sister-group relationship of *A. goiana* and *A. bisphaerica* is consistent with the prior results of Gonçalves (1986) based on morphological characters that indicate species-level rather than population-level differences. Major-worker specimens of 10023 BR-MT and 9900 BR-MG

were positively identified as *A. goiana* based on the morphological characters described by the author of the species (GONÇALVES, 1971), including, when compared to *A. bisphaerica*: larger size, shinier head and gaster, reduced sculpture on the head and gaster, shallower occipital groove, coarser sculpture on the mesosoma, and more developed anterior mesonotal spines (see Fig. 2j, k). This is the first time that *A. goiana* was included in a molecular phylogenetic analysis. Although our study indicates that *A. goiana* is distinct from the five included specimens of *A. bisphaerica*, future analyses will need to evaluate this result by including specimens from different populations and locations as well as more comprehensive taxonomic study. *Atta goiana* was originally placed in the no longer recognized subgenus *Palaeatta*, consisting of *A. bisphaerica*, *A. saltensis*, and *A. goiana* (BORGMEIER, 1950, 1959; GONÇALVES, 1986). As in the previous analyses of Bacci *et al.* (2009), our analyses contradict the monophyly of a clade equivalent to *Palaeatta* because, although *A. bisphaerica* and *A. goiana* are sister species, they are not closely related to *A. saltensis*.

The clear monophyly of *A. sexdens* in our study resolves the (weakly supported) polytomy of *A. sexdens* species with respect to *A. robusta* recovered in the previous study of Bacci *et al.* (2009). The well-supported subclades of *A. sexdens* in our study could be interpreted as different species or as geographically correlated, divergent populations (Fig. 2a and Supplementary Fig. S5). Our results are consistent with those of Martins (2011), who demonstrated that mitochondrial alleles of *A. sexdens* are divided into three distinct clades. The lineages in our phylogeny and the taxonomic identification of these taxa, however, are not strictly correlated with previously recognized subspecies of *A. sexdens* including *A. sexdens sexdens* (Linnaeus), *A. sexdens rubropilosa* Forel, and *A. sexdens piriventris* Santschi (GONÇALVES, 1963). The subspecies of *A. sexdens* were synonymized by Borgmeier (1959) and this synonymization was subsequently upheld by Bolton (1995, 2021). Because Bolton (2021) does not accept the proposals of Gonçalves (1963) and Mayhé-Nunes (2002) to revive the subspecies of *A. sexdens*, these infraspecific names are currently considered junior synonyms of the nominal species.

The species of the Neoatta clade exhibit an evolutionary pattern that is similar to that discussed previously for the Epiatta clade, in which closely related species have distinctly different ecologies. *Atta robusta* is endemic to the restingas in the States of Rio de Janeiro and Espírito Santo in Brazil (DÁTTILO; FALCÃO; TEIXEIRA, 2012; TEIXEIRA; SCHOEREDER; MAYHÉ-NUNES, 2003). *Atta robusta* is very well adapted to the semi-arid climate of this region, building its nests in sandy soil, producing medium-sized adult colonies, and specializing on dicotyledonous plants (GONÇALVES, 1945; TEIXEIRA;

SCHOEREDER, 2003; TEIXEIRA; SCHOEREDER; ANDRADE, 2008). Because it is restricted to such a narrow ecological environment, *A. robusta* has been registered in the National List of Endangered Species of Brazilian Fauna since 2003 (IBAMA 2003; ICMBio, 2018; MACHADO; DRUMMOND; PAGLIA, 2008). In contrast, its sister species *A. sexdens* is distributed from Central America to northeastern Argentina and western Uruguay (i.e., the southernmost limit of the distribution of the genus) and is adapted to a wide variety of environments across a larger climate range (GONÇALVES, 1963; HÖLLDOBLER; WILSON, 1990; SOLOMON *et al.*, 2008; WEBER, 1966). For these reasons, it is a widely distributed pest of human agriculture (DELLA LUCIA, 2003). *Atta sexdens* builds extremely large and populous nests and forages on a wide range of plants (FOWLER, 1985; GONÇALVES, 1945; MUELLER *et al.*, 2017). For example, in the south, central, and northwestern parts of its distribution, *A. sexdens* forages mainly on dicotyledonous plants, but less frequently on monocotyledonous plants, whereas in southeastern Brazil it exclusively forages on dicotyledonous plants (FARJI-BRENER; RUGGIERO, 1994; FOWLER, 1985; GONÇALVES, 1967, 1971).

2.4.3 Historical biogeography and evolution

Our phylogeny strongly supports the monophyly of all fourteen species of *Atta*. However, for the three most widely distributed species, *A. cephalotes*, *A. laevigata*, and *A. sexdens*, it also strongly supports intraspecific subgroups (Fig. 2a). *Atta cephalotes* is divided into well-supported northern and southern subclades (Supplementary Fig. S3), as described above, and our data support a scenario that this species secondarily dispersed into the south (i.e., into Ecuador and Brazil) from the north. *Atta laevigata* is divided into three subclades, including a clade located in northeastern Brazil and two clades with overlapping distributions in central and southeastern Brazil (Supplementary Fig. S4). Finally, *A. sexdens* is divided into three subclades that are also correlated with geography. The first subclade occupies Uruguay and southern Brazil, the second subclade is restricted to northeastern Brazil, and the third subclade occupies a large area encompassing southeastern, central western, and northern South America (Supplementary Fig. S5). The northern and southern subclades appear to be divided by the Tropic of Capricorn (or the South Tropic) at Latitude 23°26', so sampling in this transition zone would allow testing for the presence or absence of gene flow and thus for reproductive isolation and thereby determine the species-level status of these subclades. In addition, both *A. laevigata* and *A. sexdens* include subclades composed of taxa from

northeastern Brazil, suggesting the presence of some environmental and/or geographic barrier that restricts gene flow from other populations into this region (CARNAVAL; MORITZ, 2008).

Our results indicate estimated crown-group ages for extant *Atta* species between 0.3–1.8 Ma (95% HPD: 0.1–3.3 Ma) (see Supplementary Table S6). Interestingly, within each clade, the species with the broadest distribution conforms to a common pattern with regard to its age of divergence. The crown node age of each widespread species is somewhat older (between 1.0–2.0 Ma) than the crown-node age of less widespread species, which may be correlated with the longer time required to colonize multiple regions. Most of the geographically restricted species were younger (less than 1.0 Ma), with the exception of two *Epiatta* species: (i) *Atta saltensis*, which could be restricted in distribution due to environmental barriers, such as climatic differences between the dry Chaco and the wet Chaco of Paraguay to the north (WILD, 2007; WILLIG *et al.*, 2000) and the decrease in temperature in the extreme south (central-southern region of Argentina) (FARJI-BRENER; RUGGIERO, 1994; SÁNCHEZ-RESTREPO *et al.*, 2019); and (ii) *A. capiguara*, which presents an unusual case because its currently recognized distribution may be due to poor sampling. Recently, it was found that the increase of human-disturbed areas, in which native vegetation was replaced with grassland, facilitated the geographic expansion of this species (FORTI *et al.*, 2020). Even if *A. capiguara* speciated simultaneously with *A. laevigata*, perhaps it has not achieved a similar geographic range due to its specialization on cutting monocotyledonous plants.

Our biogeographic results (Fig. 4) are consistent with an origin of higher-attine ants in dry habitats in South America as proposed by Branstetter *et al.* (2017a), and they further suggest that leaf-cutting ants may have originated in North America contradicting previous theories (BRANSTETTER *et al.*, 2017a; CRISTIANO *et al.* 2020; FOWLER, 1983; GONÇALVES, 1986; KUSNEZOV, 1963; MUELLER *et al.*, 2017). This interpretation should be regarded as preliminary because, in this study, we did not include all species of *Acromyrmex* leaf-cutting ants. Furthermore, this North American origin, however, still presents problems for the biogeographic history of the leaf-cutting ants. Significant uncertainty remains about the biogeographic sequence connecting the most-recent common ancestor of the non-leaf-cutting and leaf-cutting higher-attine ants, shared with the genus *Trachymyrmex*, in which extant species are almost entirely restricted to North America, and the most-recent common ancestor of the leaf-cutting genera, shared by (*Atta* + *Acromyrmex*) with *Amoimyrmex*, in which extant species are restricted to southern South America. These extant distributions suggest at least two broad hypotheses: (i) the ancestral species of *Amoimyrmex* and (*Acromyrmex* + *Atta*) arose in North or Central America and its daughter lineages were once more widespread or (ii) the

ancestor of *Trachymyrmex* + the leaf-cutting ants arose in South America and/or the ancestor of the leaf-cutting ants arose in South America and there have been multiple dispersals by ancestors from South America into Central and North America.

Our biogeographic reconstruction suggests that the common ancestor of the genus *Atta* arose in North America, and that the species of the Archeatta clade subsequently spread to Central America and the Caribbean islands. The current distribution of the species of this clade (see Supplementary Table S4) and paleogeographic evidence, which indicate that the island of Cuba separated from the continent more than 34 million years ago (ITURRALDE-VINENT, 2006), support the hypothesis that the dispersal of the ancestor of (*A. insularis* + *A. cubana*) was not impeded by the oceanic barrier (BACCI *et al.*, 2009; MUELLER *et al.*, 2017). *Atta texana*, restricted to the southern United States and northern Mexico, is the sister species of *A. insularis*, suggesting that the colonization and distribution of *Atta* to Cuba likely occurred from North America and not from Central America, unless the ancestral *A. texana* inhabited Central America..

The common ancestor of the Atta s.s., Epiatta, and Neoatta clades was inferred to have originated in the Central/NW South America region approximately 7.5 Ma, subsequently spreading into South America. The open water separating Central America from northwestern South America prior to the connection of the Isthmus of Panama approximately 6–3 Ma (BACON *et al.*, 2015) may not have necessarily represented a hard barrier to over-water dispersal because (i) flying queens may have been able to disperse prior to the establishment of the land bridge and (ii) biological evidence suggests three earlier connections, including one that occurred 8.7 Ma (BACON *et al.*, 2015). The same biological evidence suggests, however, that the lack of a land connection presented a significant barrier to dispersal for other, comparable animal groups. Following their origins, one lineage could have dispersed over the Andes and rapidly spread into South America giving rise to the ancestor of the Epiatta and Neoatta clades. The species *A. cephalotes* likely dispersed into South America approximately 3.0 Ma, coincident with the date of the last closure of the Isthmus. Later, the ancestor of one subclade within the species *A. cephalotes* likely expanded into South America, dispersing into the Atlantic Forest via an ancient connection with the Amazon forest through gallery forests within the dry diagonal of South America in northeastern Brazil (Cerrado and Caatinga) during the Pliocene and the Pleistocene, an event associated with wetter quaternary climatic periods in this region (AULER *et al.*, 2004; BATALHA-FILHO *et al.*, 2013; DE OLIVEIRA; BARRETO; SUGUIO, 1999; WANG *et al.*, 2004).

We hypothesize that the common ancestor of the Epiatta and Neoatta clades arrived in southern South America through an even older connection between Amazonian and Atlantic forests during the Miocene, through the transition between southern Cerrado (Mato Grosso) and northern Chaco from Paraguay and southeastern Bolivia, possibly associated with geotectonic events (BATALHA-FILHO *et al.*, 2013; COSTA, 2003). The evolution of South American *Atta* species in the Epiatta and Neoatta clades was likely associated with adaptations to dry habitats and the expansion of the Cerrado around 4-8 Ma. This rapid radiation is correlated with environmental and climatic changes, as well as with the increase of forest clearings and edges during the Pleistocene due to the increasing interpolation of grasslands, Cerrado, and forest, which likely created conditions that favored the diversification of species distributed in a South-to-North direction (MEYER *et al.*, 2014; PRADO; GIBBS, 1993; SILVA, 2011). If correct, this would explain why the current distributions of species such as *A. laevigata* and *A. sexdens* can include both Cerrado and rainforest habitats. Our results suggest that a mosaic of dry and moist habitats were critical to the diversification of most South American *Atta* species, driving a burst of phenotypic diversification, speciation, and range expansion into other regions.

ACKNOWLEDGMENTS

We wish to thank the following colleagues that sent specimens and assisted us in museums visits, fieldtrips and/or laboratory work, for their generous help: André Rodrigues, Antônio Mayhé-Nunes, Carlos R. Brandão, Clarisa Decuyper, Clarissa Knoechelmann, Corrie S. Moreau, Daniela M. Rodríguez, Eder B. França, Emília Z. Albuquerque, Fabrício B. Baccaro, Felipe Vivallo, Geancarlo Alarcon, Grazielle Santiago, Heraldo L. Vasconcelos, Inara R. Leal, Itanna O. Fernandes, Jack T. Longino, Jacques H.C. Delabie, Jani Pereira, Janete Andrade, John E. Lattke, Júlio Chaul, Kelli Ramos, Kyle Gray, Livia P. do Prado, Marcio L. de Oliveira, Mariane Nickele, Martín Bolazzi, Matheus T. Fontanelle, Matthew Prebus, Mayara L. Pessoa, Milene Ferro, Mônica A. Ulysea, Paulo R. de Souza, Pedro Elias, Pedro Senna, Philip S. Ward, Rodolfo Probst, Renata Z. Aquino, Ricardo Vicente, Rodrigo M. Feitosa, Rogério R. da Silva, Sabrina Simon, and Steven Messer. We are also grateful to Andrés F. Sánchez-Restrepo (FuEDEI, Argentina) and Ivan L. F. Magalhaes (MACN, Argentina) for assistance with BioGeoBEARS scripts; and Milene Ferro (UNESP, Brazil) for help with the biogeographical analyses; Andrés F. Sánchez-Restrepo, Fernando Fernández, Gabriela Camacho, Heraldo L. Vasconcelos, and Scott Solomon for their constructive comments and advice on earlier versions of this manuscript. Permission to collect samples in Brazil (SISBio 33487-5) was granted by the Chico Mendes Institute for Biodiversity Conservation (ICMBio). This study was financed in part by the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil* (CAPES) - Financing Code 001; *Universidade Estadual Paulista* (UNESP) (CB, MB); *Fundação de Apoio à Pesquisa do Estado de São Paulo* [2019/03746-0, 2019/24470-2 (MB)]; Arizona State University; the Smithsonian National Museum of Natural History Small Grants Program (JSC & TRS); and the U.S. National Science Foundation [NSF CAREER DEB-1943626 (CR), NSF DEB-1654829 (CR & TRS), and NSF DEB-1927224 (TRS & JSC)].

REFERENCES

- AULER, A. S. *et al.* Quaternary ecological and geomorphic changes associated with rainfall events in presently semi-arid northeastern Brazil. **Journal of Quaternary Science**, v. 19, n. 7, p. 693–701, 2004.
- BACCI, M. *et al.* Biopolymer-degrading bacteria from nests of the leaf-cutting ant *Atta sexdens rubropilosa*. **Brazilian Journal of Medical and Biological Research**, v. 28, n. 1, p. 79–82, 1995.
- BACCI, M. *et al.* Phylogeny of leafcutter ants in the genus *Atta* Fabricius (Formicidae: Attini) based on mitochondrial and nuclear DNA sequences. **Molecular Phylogenetics and Evolution**, v. 51, n. 3, p. 427–437, 2009.
- BACON, C. D. *et al.* Biological evidence supports an early and complex emergence of the Isthmus of Panama. **Proceedings of the National Academy of Sciences of the United States of America**, v. 112, n. 24, p. 6110–6115, 2015. DOI: 10.1073/pnas.1423853112
- BARBOSA, J. T. V *et al.* Mitochondrial genomes of genus *Atta* (Formicidae: Myrmicinae) reveal high gene organization and giant intergenic spacers. **Genetics and Molecular Biology**, v. 42, 2019. DOI: 10.1590/1678-4685-gmb-2018-0055
- BARONI URBANI, C. First description of fossil gardening ants (Amber collection Stuttgart and Natural History Museum Basel; Hymenoptera: Formicidae. I: Attini.). **Stuttgarter Beiträge zur Naturkunde. Serie B**, v. 54, 1–13, 1980.
- BATALHA-FILHO, H.; FJELDSÅ, J.; FABRE, P. H.; MIYAKI, C. Y. Connections between the Atlantic and the Amazonian forest avifaunas represent distinct historical events. **Journal of Ornithology**, v. 154, n. 1, p. 41–50, 2013.
- BEJERANO, G. *et al.* Ultraconserved elements in the human genome. **Science**, v. 304, n. 5675, p. 1321–1325, 2004.
- BELT, T. **The naturalist in Nicaragua**. London: University Press of the Pacific, 1974.
- BLAIMER, B. B. *et al.* Phylogenomic methods outperform traditional multi-locus approaches in resolving deep evolutionary history: a case study of formicine ants. **BMC Evolutionary Biology**, v. 15, n. 1, p. 271, 2015. DOI: 10.1186/s12862-015-0552-5
- BLAIMER, B. B. *et al.* Sequence capture and phylogenetic utility of genomic ultraconserved elements obtained from pinned insect specimens. **PLoS One**, v. 11, 161531, 2016. a.
- BLAIMER, B. B.; LAPOLLA, J. S.; BRANSTETTER, M. G.; LLOYD, M. W.; BRADY, S. G. Phylogenomics, biogeography and diversification of obligate mealybug-tending ants in the genus *Acropyga*. **Molecular Phylogenetics and Evolution**, v. 102, p. 20–29, 2016. b.
- BOLGER, A. M.; LOHSE, M.; USADEL, B. Trimmomatic: a flexible trimmer for Illumina sequence data. **Bioinformatics**, v. 30, n. 15, 2114–2120, 2014.

BOLTON, B. **A new general catalogue of the ants of the world**. Harvard University Press, Cambridge, MA, 1995.

BOLTON, B. **An online catalog of the ants of the world**. 2021. Disponível em: <https://antcat.org>. Acesso em: 10 oct. 2020.

BOLTON, B. *et al.* **Bolton's catalogue of ants of the world: 1758–2005**. Harvard University Press, Cambridge, MA, 2006.

BORGMEIER, T. Estudos sobre *Atta* (Hym. Formicidae). **Memórias do Instituto Oswaldo Cruz**, v. 48, p. 239–263, 1950.

BORGMEIER, T. Revision der Gattung *Atta* Fabricius (Hym., Formicidae). **Studia Entomologica**, v. 2, n. 1–4, p. 321–390, 1959.

BOROWIEC, M. L. Convergent evolution of the army ant syndrome and congruence in big-data phylogenetics. **Systematic Biology**, v. 68, n. 4, p. 1–15, 2019. a.

BOROWIEC, M. L. Spruceup: fast and flexible identification, visualization, and removal of outliers from large multiple sequence alignments. **Journal of Open Source Software**, v. 4, n. 42, p. 1635, 2019. b. DOI: 10.21105/joss.01635

BOROWIEC, M. L.; COVER, S. P.; RABELING, C. The evolution of social parasitism in *Formica* ants revealed by a global phylogeny. **bioRxiv**, 2020. DOI: 10.1101/2020.12.17.423324

BRANDÃO, C. R. F. **Formigas dos Cerrados e Caatingas**. 1995. Tese de Doutorado - Instituto de Biociências da Universidade de São Paulo, Departamento de Zoologia, São Paulo, 1995.

BRANSTETTER, M. G. *et al.* Dry habitats were crucibles of domestication in the evolution of agriculture in ants. **Proceedings of the Royal Society B: Biological Sciences**, v. 284, n. 1852, p. 20170095, 2017. a. DOI: 10.1098/rspb.2017.0095

BRANSTETTER, M. G. *et al.* Enriching the ant tree of life: enhanced UCE bait set for genome-scale phylogenetics of ants and other Hymenoptera. **Methods in Ecology and Evolution**, v. 8, n. 6, p. 768–776, 2017. b.

BRANSTETTER, M. G. *et al.* Phylogenomic Insights into the Evolution of Stinging Wasps and the Origins of Ants and Bees. **Current Biology**, v. 27, n. 7, p. 1019–1025, 2017. c.

BRANSTETTER, M. G. *et al.* Ultraconserved element phylogenomics and biogeography of the agriculturally important mason bee subgenus *Osmia* (*Osmia*). **Systematic Entomology**, v. 46, n. 2, p. 453–472, 2021. DOI: 10.1111/syen.12470

CARNAVAL, A. C.; MORITZ, C. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. **Journal of Biogeography**, v. 35, n. 7, p. 1187–1201, 2008.

CHERNOMOR, O.; VON HAESELER, A.; MINH, B. Q. Terrace aware data structure for phylogenomic inference from supermatrices. **Systematic Biology**, v. 65, n. 6, 997–1008, 2016.

CHERRETT, J. M. Biology, pest status and control of leaf-cutting ants. In: RUSSELL G. E. (ed.). **Biology and population dynamics of invertebrate crop pests**. Intercept, Andover, MN, 1989. p. 1–38.

COSTA, L. P. The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. **Journal of biogeography**, v. 30, n. 1, p. 71–86, 2003.

CRAWFORD, N. G. *et al.* More than 1000 ultraconserved elements provide evidence that turtles are the sister group of archosaurs. **Biology Letters**, v. 8, n. 5, p. 783–786, 2012.

CRISTIANO, M. P.; CARDOSO, D. C.; FERNANDES-SALOMÃO, T. M. Cytogenetic and Molecular Analyses Reveal a Divergence between *Acromyrmex striatus* (Roger, 1863) and Other Congeneric Species: Taxonomic Implications. **PLoS One**, v. 8, n. 3, 2013.

CRISTIANO, M. P.; CARDOSO, D. C.; GÓMEZ, V. E. S.; SIMÕES-GOMES, F. C. *Amoimyrmex* Cristiano, Cardoso & Sandoval, gen. nov. (Hymenoptera: Formicidae): a new genus of leaf - cutting ants revealed by multilocus molecular phylogenetic and morphological analyses. **Austral Entomology**, v. 59, n. 4, p. 643–676, 2020.

CURRIE, C. R. *et al.* Ancient tripartite coevolution in the attine ant-microbe symbiosis. **Science**, v. 299, n. 5605, p. 386–388, 2003.

DAGUERRE, J. B. Hormigas del genero *Atta* Fabricius de la Argentina (Hymenop. Formicidae). **Revista de la Sociedad Entomológica Argentina**, v. 12, p. 438–460, 1945.

DÁTILLO, W.; FALCÃO, J. C. F.; TEIXEIRA, M. C. Predictive model of distribution of *Atta robusta* Borgmeier 1939 (Hymenoptera: Formicidae): subsidies for conservation of a Brazilian leaf-cutting ant endangered species. **Studies on Neotropical Fauna and Environment**, v. 47, n. 3, p. 193–201, 2012.

DE FINE LICHT H. H. *et al.* Laccase detoxification mediates the nutritional alliance between leaf-cutting ants and fungus-garden symbionts. **Proceedings of the National Academy of Sciences**, v. 110, n. 2, p. 583–587, 2013.

DELABIE, J. H. C. *Atta silvai* Gonçalves, sinônimo júnior de *Atta laevigata* (Fred Smith) (Hymenoptera, Formicidae, Attini). **Revista Brasileira de Entomologia**, v. 2, p. 339–341, 1998.

DELLA LUCIA, T. M. C. Hormigas de importância econômica en la región Neotropical. In: FERNÁNDEZ, F. (ed.). **Introducción a las hormigas de la región Neotropical**. Bogotá: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, 2003. p. 337–349.

DELLA LUCIA, T. M. C., FOWLER, H. G. & MOREIRA, D. D. O. Espécies de formigas cortadeiras no Brasil. *In*: DELLA LUCIA T. M. C. (ed.). **As formigas cortadeiras**. Viçosa: Folha de Viçosa, 1993. p. 26–32.

DELLA LUCIA, T. M. C.; SOUZA, D. J. **Formigas-cortadeiras: da bioecologia ao manejo**. Viçosa: Editora UFV, 2011.

DE OLIVEIRA, P. E.; BARRETO, A. M. F.; SUGUIO, K. Late Pleistocene/Holocene climatic and vegetational history of the Brazilian Caatinga: the fossil dunes of the middle São Francisco River. **Palaeogeography, Palaeoclimatology, Palaeoecology**, v. 152, n. 3–4, p. 319–337, 1999.

DO AMARAL, F. R. *et al.* Ultraconserved elements sequencing as a low-cost source of complete mitochondrial genomes and microsatellite markers in non-model amniotes. **PLoS One**, v. 10, n. 9, p. 1–9, 2015. DOI: 10.1371/journal.pone.0138446

DUFOUR, D. L. Insects as food: a case study from the Northwest Amazon. **American Anthropologist**, v. 89, n. 2, p. 383–397, 1987.

EMERY, C. Études sur les Myrmicinae. [V–VII.]. **Annales de la Société Entomologique de Belgique**, v. 57, p. 250–262, 1913.

EMERY, C. Hymenoptera. Fam. Formicidae, subfam. Myrmicinae. *In*: WYTSMAN, P. (ed.). **Genera insectorum**. Brussels: Verteneuil and Desmet, 1922. p. 207–327. (174B, v.).

FAIRCLOTH, B. C. **Illumiprocessor: a trimmomatic wrapper for parallel adapter and quality trimming**. 2013. Disponível em: <http://dx.doi.org/10.6079/J9ILL>. Acesso em: 18 jul. 2019.

FAIRCLOTH, B. C. PHYLUCE is a software package for the analysis of conserved genomic loci. **Bioinformatics**, v. 32, n. 5, p. 786–788, 2016.

FAIRCLOTH, B. C. *et al.* Target enrichment of ultraconserved elements from arthropods provides a genomic perspective on relationships among hymenoptera. **Molecular Ecology Resources**, v. 15, n. 3, p. 489–501, 2015.

FAIRCLOTH, B. C. *et al.* Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. **Systematic Biology**, v. 61, n. 5, p. 717–726, 2012.

FAIRCLOTH, B. C.; GLENN, T. C. Not all sequence tags are created equal: designing and validating sequence identification tags robust to indels. **PLoS One**, v. 7, n. 8, p. e42543, 2012.

FARJI-BRENER, A. G.; RUGGIERO, A. Leaf-cutting ants (*Atta* and *Acromyrmex*) inhabiting Argentina: patterns in species richness and geographical range sizes. **Journal of Biogeography**, v. 21, n. 4, p. 391–399, 1994.

FERNANDES, I. O. *et al.* A global phylogenetic analysis of trap-jaw ants, *Anochetus* Mayr and *Odontomachus* Latreille (Hymenoptera: Formicidae: Ponerinae). **Systematic Entomology**, 2021. DOI: 10.1111/syen.12483

FERNÁNDEZ, F.; CASTRO-HUERTAS, V.; SERNA, F. **Hormigas cortadoras de hojas de Colombia: *Acromyrmex* & *Atta* (Hymenoptera: Formicidae)**. Fauna de Colombia, Monografía No. 5, Bogotá: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, 2015.

FERNÁNDEZ, F.; SENDOYA, S. Synonymic list of Neotropical ants (Hymenoptera: Formicidae). **Biota Colombiana**, v. 5, n. 1, p. 3–105, 2004.

FERNÁNDEZ, F.; SERNA, F. J. Subfamilia Myrmicinae. In: FERNÁNDEZ, F.; GUERRERO, R. J; DELSINNE, T. (eds.). **Hormigas de Colombia**. Bogotá: Universidad Nacional de Colombia. Facultad de Ciencias. Instituto de Ciencias Naturales, 2019. p. 791–888.

FISCHER, M. **Forest health: leaf-cutting ant**. Texas A&M Forest Service. Lufkin, Texas, 2015. Disponível em: <http://texasforests.tamu.edu/LeafCuttingAnt/>. Acesso em: 17 fev. 2020.

FISHER, S. *et al.* A scalable, fully automated process for construction of sequence-ready human exome targeted capture libraries. **Genome Biology**, v. 12, n. 1, p. 1–15, 2011.

FONTENLA RIZO, J. L. Nueva especie de *Atta* (Hymenoptera: Formicidae) del archipiélago cubano. **Avicennia**, v. 3, p. 77–86, 1995.

FORTI, L. C. *et al.* Bionomics and identification of *Acromyrmex* (Hymenoptera: Formicidae) through an illustrated key. **Sociobiology**, v. 48, n. 2, p. 1–18, 2006.

FORTI, L. C. *et al.* Occurrence of leaf-cutting and grass-cutting ants of the genus *Atta* (Hymenoptera: Formicidae) in geographic regions of Brazil. **Sociobiology**, v. 67, n. 4, p. 514–525, 2020. DOI: 10.13102/sociobiology.v67i4.5741

FORTI, L. C.; BOARETTO, M. Ap C. **Formigas cortadeiras: biologia, ecologia, danos e controle**. Botucatu: Editora UNESP, 1997.

FOWLER, H. G. Latitudinal gradients and diversity of the leaf-cutting ants (*Atta* and *Acromyrmex*) (Hymenoptera: Formicidae). **Revista de Biología Tropical**, v. 31, n. 2, p. 213–216, 1983.

FOWLER, H. G. Leaf-cuttings ants of the genera *Atta* and *Acromyrmex* of Paraguay (Hymenoptera Formicidae). **Deutsche Entomologische Zeitschrift**, v. 32, p. 19–34, 1985.

FOWLER, H. G. Taxa of the neotropical grass-cutting ants, *Acromyrmex* (*Moellerius*) (Hymenoptera: Formicidae: Attini). **Científica, São Paulo**, v. 16, n. 2, p. 281–296, 1988.

FOWLER, H. G. *et al.* A pest is a pest is a pest? The dilemma of neotropical leaf-cutting ants: Keystone taxa of natural ecosystems. **Environmental Management**, v. 13, n. 6, p. 671–675, 1989.

FOWLER, H. G. *et al.* Economics of grass-cutting ants. In: LOFGREN, C. S.; VANDERMEER, R. K. (eds.). **Fire ants and leaf-cutting ants**. Boulder: Westview Press, 1986. p.18–35.

- GLENN, T. C. *et al.* Adapterama I: universal stubs and primers for 384 unique dual-indexed or 147,456 combinatorially-indexed Illumina libraries (iTru & iNext). **PeerJ**, v. 7, p. e7755, 2019.
- GONÇALVES, C. R. As formigas cortadeiras da Amazônia, dos generos "*Atta*" Fabr. e "*Acromyrmex*" Mayr (Hym., Formicidae). **Atas do Simpósio sobre a Biota Amazônica**, v. 5, p. 181–202, 1967.
- GONÇALVES, C. R. As saúvas do Mato Grosso, Brasil (Hymenoptera, Formicidae). **Arquivos do Museu Nacional (Rio de Janeiro)**, v. 54, p. 249–253, 1971.
- GONÇALVES, C. R. Contribuição para o conhecimento do gênero *Atta* Fabr., das formigas saúvas. **Boletim da Sociedade Brasileira de Agronomia**, v. 5, p. 333–358, 1942.
- GONÇALVES, C. R. Descrição de uma nova saúva brasileira (Hym., Form.). **Revista Brasileira de Biologia**, v. 4, p. 233–238, 1944.
- GONÇALVES, C. R. Distribuição, biologia e ecologia das saúvas. **Divulgação Agrônômica**, v. 1, p. 2–10, 1960.
- GONÇALVES, C. R. Filogenia do gênero *Atta* Fabricius (Hymenoptera, Formicidae). Anais do VI Congresso Brasileiro de Zoologia. **Publicações Avulsas do Museu Nacional, Rio de Janeiro**, v. 65, p. 13–17, 1986.
- GONÇALVES, C. R. O gênero *Acromyrmex* no Brasil (Hym. Formicidae). **Studia Entomologica**, v. 4, n. 1-4, p. 113–180, 1961.
- GONÇALVES, C. R. Nota sobre a sistemática de *Atta sexdens* (L, 1758) e de suas sub-espécies (Hym., Formicidae). **Bol. Fitossanitário**, v. 9, p. 1–3, 1963.
- GRABHERR, M. G. *et al.* Full-length transcriptome assembly from RNA-Seq data without a reference genome. **Nature Biotechnology**, v. 29, n. 7, p. 644–652, 2011.
- GRIMALDI, D.; AGOSTI, D. A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. **Proceedings of the National Academy of Sciences**, v. 97, n. 25, p. 13678–13683, 2000.
- GUENARD, B. *et al.* The Global Ant Biodiversity Informatics (GABI) database: synthesizing data on the geographic distribution of ant species (Hymenoptera: Formicidae). **Myrmecological News**, v. 24, p. 83–89, 2017.
- HARRIS, R. S. **Improved pairwise Alignment of genomic DNA**. 2008. Tese (Doutorado em Filosofia) - The Graduate School College of Engineering, Pennsylvania State University, University Park, Pennsylvania, 2007.
- HOANG, D. T. *et al.* UFBoot2: improving the ultrafast bootstrap approximation. **Molecular biology and evolution**, v. 35, n. 2, p. 518–522, 2018.
- HÖLDOBLER, B.; WILSON, E. O. **The ants**. Cambridge: Harvard University Press, 1990.

HÖLLDOBLER, B.; WILSON, E. O. **The leafcutter ants: civilization by instinct**. London and New York: W. W. Norton & Company, Inc., 2011.

INOUE, J.; DONOGHUE, P. C. J.; YANG, Z. The impact of the representation of fossil calibrations on Bayesian estimation of species divergence times. **Systematic Biology**, v. 59, n. 1, p. 74–89, 2010.

ITURRALDE-VINENT, M. A. Meso-Cenozoic Caribbean paleogeography: Implications for the historical biogeography of the region. **International Geology Review**, v. 48, n. 9, p. 791–827, 2006.

ITURRALDE-VINENT, M. A.; MACPHEE, R. D. E. Age and paleogeographical origin of Dominican amber. **Science**, v. 273, n. 5283, p. 1850–1852, 1996.

JANICKI, J. *et al.* Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. **Ecological Informatics**, v. 32, p. 185–193, 2016.

JEŠOVNIK, A.; GONZÁLEZ, V. L.; SCHULTZ, T. R. Phylogenomics and divergence dating of fungus-farming ants (Hymenoptera: Formicidae) of the genera *Sericomyrmex* and *Apterostigma*. **PLoS One**, v. 11, n. 7, p. 1–18, 2016.

JESOVNIK, A.; SOSA-CALVO, J.; LLOYD, M. W.; BRANSTETTER, M. G.; FERNÁNDEZ, F.; SCHULTZ, T. R. Phylogenomic species delimitation and host-symbiont coevolution in the fungus-farming ant genus *Sericomyrmex* Mayr (Hymenoptera: Formicidae): ultraconserved elements (UCEs) resolve a recent radiation. **Systematic Entomology**, v. 42, n. 3, p. 523–542, 2017.

JONES, C. G.; LAWTON, J. H.; SHACHAK, M. Organisms as ecosystem engineers. In: SAMSON, F. B.; KNOPF, F. L. (eds.). **Ecosystem management**. New York: Springer, 1994. p. 130–147.

KALYAANAMOORTHY, S. *et al.* ModelFinder: fast model selection for accurate phylogenetic estimates. **Nature Methods**, v. 14, n. 6, p. 587–589, 2017.

KATOH, K.; STANDLEY, D. M. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. **Molecular Biology and Evolution**, v. 30, n. 4, p. 772–780, 2013.

KEMPF, W. W. Catálogo abreviado das formigas da região Neotropical (Hymenoptera: Formicidae). **Studia Entomologica**, v. 15, n. 1–4, p. 1–344, 1972.

KUSNEZOV, N. Hormigas argentinas: clave para su identificación, **Miscelánea Fundación Miguel Lillo, Tucumán, Argentina**, v. 61, 1978.

KUSNEZOV, N. Zoogeografía de las hormigas en Sudamérica. **Acta Zoologica Lilloana**, v. 19, p. 25–186, 1963.

LANDIS, M. J. *et al.* Bayesian analysis of biogeography when the number of areas is large. **Systematic Biology**, v. 62, n. 6, p. 789–804, 2013. DOI: 10.1093/sysbio/syt040

LANFPEAR, R. *et al.* PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. **Molecular Biology and Evolution**, v. 34, n. 3, p. 772–773, 2017.

LEAL, I.; WIRTH, R.; TABARELLI, M. The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified Neotropical forests. **Biotropica**, v. 46, n. 5, p. 516–528, 2014. DOI: 10.1111/btp.12126/full

LEMMON, E. M.; LEMMON, A. R. High-throughput genomic data in systematics and phylogenetics. **Annual Review of Ecology, Evolution, and Systematics**, v. 44, n. 1, p. 99–121, 2013.

LI, H. *et al.* Convergent evolution of complex structures for ant-bacterial defensive symbiosis in fungus-farming ants. **Proceedings of the National Academy of Sciences**, v. 115, n. 42, p. 10720–10725, 2018.

LOVATO, L. **Estudos morfológicos e análises de sequências do gene mitocondrial citocromo oxidase I (COI) em populações de *Atta cephalotes* (L., 1758)**. 2006. Tese (Mestrado em Ciências Biológicas) - Universidade Federal do Paraná, Curitiba, 2006. Disponível em: <https://www.acervodigital.ufpr.br/handle/1884/4640>. Acesso em: 7 fev. 2021.

MACHADO, A. B. M.; DRUMMOND, G. M.; PAGLIA, A. P.. Livro vermelho da fauna brasileira ameaçada de extinção. *In: Livro vermelho da fauna brasileira ameaçada de extinção*. 2008. p. 1420–1420.

MAGALHAES, I. L. F. **BGB_model_selection**: Script to perform model selection using BioGeoBEARS. 2021. Disponível em: https://github.com/ivanlfm/BGB_model_selection. Acesso em: 10 mar. 2021.

MARTINS, J. J. **Filogenia Molecular de *Atta sexdens* (Myrmicinae: Attini) e investigação de pseudogenes em formigas da tribo Attini**. 2011. Tese (Doutorado em Ciências Biológicas) - Universidade Estadual Paulista, Rio Claro, 2011. Disponível em: <https://repositorio.unesp.br/handle/11449/100527>. Acesso em: 9 jul. 2020.

MASIULIONIS, V. E. *et al.* A Brazilian population of the asexual fungus-growing ant *Mycocepurus smithii* (Formicidae, Myrmicinae, Attini) cultivates fungal symbionts with gongylidia-like structures. **PLoS One**, v. 9, n. 8, p. e103800, 2014.

MATZKE, N. J. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. **Systematic Biology**, v. 63, n. 6, p. 951–970, 2014.

MATZKE, N. J. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. **Frontiers of Biogeography**, v. 5, n. 4, 2013.

MATZKE, N. J. **Script: example that should run out of the box: Hawaiian *Psychotria***. 2015. Disponível em: <http://phylo.wikidot.com/biogeobears#script>. Acesso em: 10 nov. 2020.

MAYHÉ-NUNES, A. J. A controvérsia sobre as subespécies de *Atta sexdens* (L., 1758) das formigas saúvas (Hymenoptera: Formicidae: Myrmicinae: Attini). **Folha Florestal**, v. 101, 2002.

MEHDIABADI, N. J. *et al.* Symbiont fidelity and the origin of species in fungus-growing ants. **Nature Communications**, v. 3, n. 840, p. 1–7, 2012.

MEHDIABADI, N. J.; SCHULTZ, T. R. Natural history and phylogeny of the fungus-farming ants (Hymenoptera: Formicidae: Myrmicinae: Attini). **Myrmecological News**, v. 13, p. 37–55, 2009.

MEIRELLES, L. A. *et al.* Shared *Escovopsis* parasites between leaf-cutting and non-leaf-cutting ants in the higher attine fungus ant symbiosis. **Royal Society Open Science**, v. 2, n. 9, p. 150257, 2015. DOI: 10.1098/rsos.150257

MEYER, K. E. B.; CASSINO, R. F.; LORENTE, F. L.; RACZKA, M.; PARIZZI, M. G. Paleoclima e paleoambiente do Cerrado durante o Quaternário com base em análises palinológicas. **Paleontologia: Cenários da Vida - Paleoclimas**, n. 5, p. 403–420, 2014.

MIKHEYEV, A. S.; MUELLER, U. G.; ABBOT, P. Comparative dating of attine ant and lepiotaceous cultivar phylogenies reveals coevolutionary synchrony and discord. **American Naturalist**, v. 175, n. 6, p. E126–E133, 2010.

MIKHEYEV, A. S.; MUELLER, U. G.; ABBOT, P. Cryptic sex and many-to-one coevolution in the fungus-growing ant symbiosis. **Proceedings of the National Academy of Sciences**, v. 103, n. 28, p. 10702–10706, 2006.

MÖLLER, A. Die Pilzgärten einiger Südamerikanischer Ameisen. **Botanische Mitteilungen aus den Tropen**, v. 6, p. 1–127, 1893.

MOSER, J. C. Estimating timber losses from a town ant colony with aerial photographs. **Southern Journal of Applied Forestry**, v. 10, n. 1, p. 45–47, 1986.

MORRONE, J. J. Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. **Annual Review of Entomology**, v. 51, n. 125, p. 467–494, 2006.

MUELLER, U. G. *et al.* Biogeography of mutualistic fungi cultivated by leafcutter ants. **Molecular Ecology**, v. 26, n. 24, p. 6921–6937, 2017.

MUELLER, U. G. *et al.* Phylogenetic patterns of ant–fungus associations indicate that farming strategies, not only a superior fungal cultivar, explain the ecological success of leafcutter ants. **Molecular Ecology**, v. 27, n. 10, p. 2414–2434, 2018.

MUELLER, U. G.; RABELING, C. A breakthrough innovation in animal evolution. **Proceedings of the National Academy of Sciences**, v. 105, n. 14, p. 5287–5288, 2008.

MUELLER, U. G.; REHNER, S. A.; SCHULTZ, T. R. The evolution of agriculture in ants. **Science**, v. 281, n. 5385, p. 2034–2038, 1998.

NGUYEN, L. T. *et al.* IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. **Molecular Biology and Evolution**, v. 32, n. 1, p. 268–274, 2015.

NYGAARD, S. *et al.* Reciprocal genomic evolution in the ant-fungus agricultural symbiosis. **Nature Communications**, v. 7, p. 1–9, 2016.

PEREIRA, T. T. P. *et al.* Molecular phylogenetic reconstruction and localization of the (TTAGG) n telomeric repeats in the chromosomes of *Acromyrmex striatus* (Roger, 1863) suggests a lower ancestral karyotype for leafcutter ants (Hymenoptera). **Comparative Cytogenetics**, v. 12, n. 1, p. 13–26, 2018.

PRADO, D. E.; GIBBS, P. E. Patterns of species distributions in the dry seasonal forests of South America. **Annals of the Missouri Botanical Garden**, v. 80, n. 4, p. 902–927, 2012.

PREBUS, M. Phylogenomic species delimitation in the ants of the *Temnothorax salvini* group (Hymenoptera: Formicidae): an integrative approach. **Systematic Entomology**, 2020. DOI: 10.1111/syen.12463

RABELING, C. *et al.* *Acromyrmex charruanus*: a new inquiline social parasite species of leaf-cutting ants. **Insectes Sociaux**, v. 62, n. 3, p. 335–349, 2015.

RABELING, C. *et al.* *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. **Insectes Sociaux**, v. 66, n. 3, p. 435–451, 2019. DOI: 10.1007/s00040-019-00705-z

RABELING, C. *et al.* A social parasite evolved reproductive isolation from its fungus-growing ant host in sympatry. **Current Biology**, v. 24, n. 17, p. 2047–2052, 2014.

RABELING, C. *et al.* Cryptic sexual populations account for genetic diversity and ecological success in a widely distributed, asexual fungus-growing ant. **Proceedings of the National Academy of Sciences**, v. 108, n. 30, p. 12366–12371, 2011.

RABELING, C. *et al.* Reconstructing the evolutionary history of leaf-cutting ants reveal multiple origins of inquiline social parasitism via sympatric speciation. In: INTERNATIONAL CONFERENCE OF THE UNION FOR THE STUDY OF SOCIAL INSECTS, 18., 2018, Guarujá. **Anais [...]**. Guarujá, São Paulo, Brasil: IUSSI, 2018.

RAMBAUT, A. *et al.* Posterior summarization in Bayesian phylogenetics using Tracer 1.7. **Systematic Biology**, v. 67, n. 5, p. 901–904, 2018.

RANDO, J. S. S.; FORTI, L. C. Ocorrência de formigas *Acromyrmex* Mayr, 1865, em alguns municípios do Brasil. **Biological Sciences**, v. 27, n. 2, p. 129–133, 2005.

REE, R. H. *et al.* A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. **Evolution**, v. 59, n. 11, p. 2299–2311, 2005. DOI: 10.1111/j.0014-3820.2005.tb00940.x

- REE, R. H.; SANMARTÍN, I. Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. **Journal of Biogeography**, v. 45, n. 4, p. 741–749, 2018.
- REE, R. H.; SMITH, S. A. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. **Systematic Biology**, v. 57, n. 1, p. 4–14, 2008. DOI: 10.1080/10635150701883881
- RODRIGUES, A. *et al.* Variability of non-mutualistic filamentous fungi associated with *Atta sexdens rubropilosa* nests. **Folia Microbiologica**, v. 50, n. 5, p. 421–425, 2005.
- ROHLAND, N.; REICH, D. Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. **Genome Research**, v. 22, n. 5, p. 939–946, 2012.
- RONQUIST, F. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. **Systematic Biology**, v. 46, n. 1, p. 195–203, 1997. DOI: 10.1093/sysbio/46.1.195
- SABATTINI, J. A. *et al.* Distribución geográfica potencial de *Atta vollenweideri* Forel en la provincia de Entre Ríos (Argentina). **Ambiência**, v. 13, n. 1, p. 31–46, 2017.
- SÁNCHEZ-RESTREPO, A. F. *et al.* Distribution and diversity of leaf-cutting ants in Northeastern Argentina: species most associated with forest plantations. **International Journal of Pest Management**, v. 65, n. 3, p. 244–257, 2019.
- SCHOWALTER, T. D.; RING, D. R. Biology and management of the Texas leafcutting ant (Hymenoptera: Formicidae). **Journal of Integrated Pest Management**, v. 8, n. 1, p. 16, 2017.
- SCHRADER, L. *et al.* Relaxed selection underlies genome erosion in socially parasitic ant species. **Nature communications**, v. 12, n. 1, p. 1–13, 2021.
- SCHULTZ, T. R. *et al.* The most relictual fungus-farming ant species cultivates the most recently evolved and highly domesticated fungal symbiont species. **The American Naturalist**, v. 185, n. 5, p. 693–703, 2015.
- SCHULTZ, T. R.; BRADY, S. G. Major evolutionary transitions in ant agriculture. **PNAS**, v. 105, n. 14, p. 5435–5440, 2008.
- SHORTHOUSE, D. P. **SimpleMappr, an online tool to produce publication-quality point maps**. 2010. Disponível em: <http://www.simplemappr.net>. Acesso em: 29 set. 2020.
- SILVA, M. L. DA. A dinâmica de expansão e retração de Cerrados e Caatingas no período Quaternário: uma análise segundo a perspectiva da teoria dos refúgios e redutos florestais. **Revista Brasileira de Geografia Física**, v. 06, p. 1275–1291, 2011.
- SILVA-PINHATI, A. C. O. *et al.* Low variation in ribosomal DNA and internal transcribed spacers of the symbiotic fungi of leaf-cutting ants (Attini: Formicidae). v. 37, p. 1463–1472, 2004.

SIQUEIRA, C. G. De. *et al.* Metabolism of plant polysaccharides by *Leucoagaricus gongylophorus*, the symbiotic fungus of the leaf-cutting ant *Atta sexdens* L. **Applied and Environmental Microbiology**, v. 64, n. 12, p. 4820–4822, 1998.

SIQUEIRA, F. F. S. *et al.* Human disturbance promotes herbivory by leaf-cutting ants in the Caatinga dry forest. **Biotropica**, v. 50, n. 5, p. 779–788, 2018.

SMITH, B. T. *et al.* Target capture and massively parallel sequencing of ultraconserved elements for comparative studies at shallow evolutionary time scales. **Systematic Biology**, v. 63, n. 1, p. 83–95, 2014.

SOLOMON, S. E. *et al.* Paleodistributions and comparative molecular phylogeography of leafcutter ants (*Atta* spp.) provide new insight into the origins of Amazonian diversity. **PLoS One**, v. 3, n. 7, 2008.

SOLOMON, S. E. *et al.* The molecular phylogenetics of *Trachymyrmex* Forel ants and their fungal cultivars provide insights into the origin and coevolutionary history of ‘higher-attine’ ant agriculture. **Systematic Entomology**, v. 44, n. 4, p. 939–956, 2019.

SOSA-CALVO, J. *et al.* *Cyatta abscondita*: taxonomy, evolution, and natural history of a new fungus-farming ant genus from Brazil. **PLoS One**, v. 8, n. 11, p. e80498, 2013.

SOSA-CALVO, J. *et al.* Evolution, systematics, and natural history of a new genus of cryptobiotic fungus-growing ants. **Systematic Entomology**, v. 43, n. 3, p. 549–567, 2018.

SOSA-CALVO, J. *et al.* Rediscovery of the enigmatic fungus-farming ant “*Mycetosoritis*” asper Mayr (Hymenoptera: Formicidae): Implications for taxonomy, phylogeny, and the evolution of agriculture in ants. **PLoS One**, v. 12, n. 5, p. e0176498, 2017. DOI: 10.1371/journal.pone.0176498

SUMNER, S. *et al.* The evolution of social parasitism in *Acromyrmex* leaf-cutting ants: a test of Emery’s rule. **Insectes Sociaux**, v. 51, n. 1, p. 37–42, 2004.

TAGLIACOLLO, V. A.; LANFEAR, R. Estimating improved partitioning schemes for ultraconserved elements. **Molecular Biology and Evolution**, v. 35, n. 7, p. 1798–1811, 2018.

TALAVERA, G.; CASTRESANA, J. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. **Systematic Biology**, v. 56, n. 4, p. 564–577, 2007.

TEIXEIRA, M. C.; SCHOEREDER, J. H. The effect of plant cover on *Atta robusta* (Hymenoptera: Formicidae) distribution in restinga vegetation. **Sociobiology**, v. 41, n. 3, p. 615–623, 2003.

TEIXEIRA, M. C.; SCHOEREDER, J. H.; ANDRADE, I. *Atta robusta* (Hymenoptera: Formicidae): endemismo, extinção ou ausência de estudos. In: VILLELA, E.; SCHOEREDER, J.H.; ANDRADE, I. (eds.) **Insetos Sociais: da biologia à aplicação**. Viçosa: Universidade Federal de Viçosa, 2008. v. 1, p. 359–367.

- TEIXEIRA, M. C.; SCHOEREDER, J. H.; MAYHÉ-NUNES, A. J. Geographic distribution of *Atta robusta* Borgmeier (Hymenoptera: Formicidae). **Neotropical Entomology**, v. 32, n. 4, p. 719–721, 2003.
- ULYSSEÁ, M. A.; BRANDÃO, C. R. F. Ant species (Hymenoptera, Formicidae) from the seasonally dry tropical forest of northeastern Brazil: a compilation from field surveys in Bahia and literature records. **Revista Brasileira de Entomologia**, v. 57, n. 2, p. 217–224, 2013.
- URBAS, P. *et al.* Cutting more from cut forests: edge effects on foraging and herbivory of leaf-cutting ants in Brazil. **Biotropica**, v. 39, n. 4, p. 489–495, 2007.
- VAN ELST, T. *et al.* Comprehensive phylogeny of *Myrmecocystus* honey ants highlights cryptic diversity and infers evolution during aridification of the American Southwest. **Molecular Phylogenetics and Evolution**, v. 155, p. 107036, 2021. DOI: 10.1016/j.ympev.2020.107036.
- WANG, X. *et al.* Wet periods in northeastern Brazil over the past 210 kyr linked to distant climate anomalies. **Nature**, v. 432, n. 7018, p. 740–743, 2004.
- WARD, P. S. *et al.* The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). **Systematic Entomology**, v. 40, n. 1, p. 61–81, 2015.
- WARD, P. S.; BLAIMER, B. B.; FISHER, B. L. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*. **Zootaxa**, v. 4072, n. 3, p. 343–357, 2016.
- WEBER, N. A. Ecological relations of three *Atta* species in Panama. **Ecology**, v. 50, n. 1, p. 141–147, 1969.
- WEBER, N. A. Fungus Ants. In: HERMANN, H. R. (ed.). **Social insects**. New York: Academic Press, 1982. p. 255–363.
- WEBER, N. A. Fungus-Growing Ants. **Science**, v. 153, p. 587–604, 1966.
- WEBER, N. A. **Gardening ants, the Attines**. Philadelphia: The American Philosophical Society, 1972.
- WEBER, N. A. Tobago Island fungus-growing ants (Hymenoptera: Formicidae). **Entomological News**, v. 74, p. 141–145, 1968.
- WIENS, J. J.; MORRILL, M. C. Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. **Systematic Biology**, v. 60, n. 5, p. 719–731, 2011. DOI: 10.1093/sysbio/syr025
- WILD, A. L. A catalogue of the ants of Paraguay (Hymenoptera: Formicidae). **Zootaxa**, v. 55, n. 1622, p. 1–55, 2007.

WILLIAMS, J. L. *et al.* A. Global domination by crazy ants: phylogenomics reveals biogeographical history and invasive species relationships in the genus *Nylanderia* (Hymenoptera : Formicidae). **Systematic Entomology**, v. 45, n. 4, p. 1–15, 2020.

WILLIG, M. R. *et al.* Composition and structure of bat assemblages in Paraguay: a subtropical–temperate interface. **Journal of Mammalogy**, v. 81, n. 2, p. 386–401, 2000.

WILSON, E. O. The defining traits of fire ants and leaf-cutting ants. *In*: LOFGREN, C. S., VANDER MEER, R. K. (eds.). **Fire ants and leaf-cutting ants**. Boulder: Westview Press, 1986. cap; 1, p. 1–9.

WILSON, E. O.; BROWN, W. L. The subspecies concept and its taxonomic application. **Systematic Zoology**, v. 2, n. 3, p. 97–111, 1953.

WIRTH, R. *et al.* **Herbivory of leaf-cutting ants: a case study on *Atta colombica* in the tropical rainforest of Panama**. New York: Springer-Verlag Berlin Heidelberg, 2003.

WIRTH, R. *et al.* Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest. **Journal of Tropical Ecology**, v. 23, n. 4, p. 501–505, 2007.

YANG, Z. PAML 4: phylogenetic analysis by maximum likelihood. **Molecular Biology and Evolution**, v. 24, n. 8, p. 1586–1591, 2007.

FIGURES

Figure captions

Fig. 1. Map of collection sites sampled for specimens of *Atta* used in the phylogenetic analyses.

Fig. 2. Ultraconserved element (UCE) phylogeny of *Atta* and outgroups. (a) The maximum likelihood phylogeny produced in IQ-TREE from the 70% complete SWSC-EN partitioned UCE matrix. Coloured circles at nodes represent less than 100% support and colour indicates maximum-likelihood bootstraps supports (see figure key). Roman numerals I, II, and III represent within species subclades. Samples are listed by species name and DNA extraction number. Locality tags (small coloured boxes) to the right of taxon names indicate the collection country (including state for Brazil) and bioregion (by colour, see figure key) as follows. AR, Argentina; BR, Brazil (AC, Acre, AL, Alagoas, AP, Amapá, AM, Amazonas, BA, Bahia, CE, Ceará, ES, Espírito Santo, DF, Distrito Federal, GO, Goiás, MA, Maranhão, MG, Minas Gerais, MS, Mato Grosso do Sul, MT, Mato Grosso, PA, Para, PB, Paraíba, PR, Paraná, PE, Pernambuco, PI, Piauí, RJ, Rio de Janeiro, RO, Rondônia, RR, Roraima, RS, Rio Grande do Sul, SC, Santa Catarina, SP, São Paulo, SE, Sergipe, TO, Tocantins); BO, Bolivia; CO, Colombia; CR, Costa Rica; CU, Cuba; EC, Ecuador, FG, French Guiana; GU, Guatemala; GY, Guyana; HO, Honduras; MX, Mexico; NI, Nicaragua; PN, Panama; PR, Paraguay; PE, Peru; UR, Uruguay; US, United States of America; VN, Venezuela. (b) Phylogram of collapsed clades Archeatta (purple branches), *Atta* s.s. (orange branches), Epiatta (yellow branches), and Neoatta (red branches) and species of *Atta*. (c-p) Images of *Atta* worker voucher specimens (individuals from the same nest as those sampled for DNA). Unique specimen identifiers of the extracted voucher and collection repository follow the taxon name. (c) *Atta mexicana*, ASU-SIBR00000689, Museu de Zoologia da Universidade de São Paulo (MZUSP). (d) *Atta insularis*, ASU-SIBR00000676, Instituto de Ciências Biológicas e da Saúde (ICBS) (e) *Atta texana*, ASU-SIBR00000690, MZUSP. (f) *Atta colombica*, ASU-SIBR00000691, MZUSP. (g) *Atta cephalotes*, ASU-SIBR00000692, MZUSP. (h) *Atta saltensis*, ASU-SIBR00000693, MZUSP. (i) *Atta vollenweideri*, ASU-SIBR00000694, MZUSP. (j) *Atta goiana*, ASU-SIBR00000695, MZUSP. (k) *Atta bisphaerica*, ASU-SIBR00000696, MZUSP. (l) *Atta capiguara*, ASU-SIBR00000697, MZUSP. (m) *Atta opaciceps*, ASU-SIBR00000699, MZUSP. (n) *Atta laevigata*, ASU-SIBR00000701, MZUSP. (o) *Atta robusta*, ASU-SIBR00000702, MZUSP. (p) *Atta sexdens*, ASU-SIBR00000703, MZUSP. Scale bars represent 0.6 mm. Ant photos were taken and edited by Corina Barrera.

Fig. 3. Divergence date estimates based on Bayesian analyses conducted in MCMCTree. For each node, the number indicates the mean age and blue bars represent 95% highest posterior density (HPD) values. Ages are in millions of years ago (Ma).

Fig. 4. Chronogram of historical biogeography corresponding to the DIVA-like model constructed using the programme BioGeoBEARS. The letters at nodes represent the most probable ancestral geographic ranges (by letter for the single bioregions, see figure key). Ages are in millions of years ago (Ma).

Supporting information

Figure captions

Fig. S1. BayArea-like model from BioGeoBEARS analyses. Letters on nodes represent the most probable ancestral geographic range (by letter for each bioregions, see key in the Figure 4).

Fig. S2. BayArea-like + J model from BioGeoBEARS analyses. Letters on nodes represent the most probable ancestral geographic range (by letter for each bioregions, see key in the Figure 4).

Fig. S3. Map of collection sites sampled for *Atta cephalotes*.

Fig. S4. Map of collection sites sampled for *Atta laevigata*.

Fig. S5. Map of collection sites sampled for *Atta sexdens*.

Fig. 1

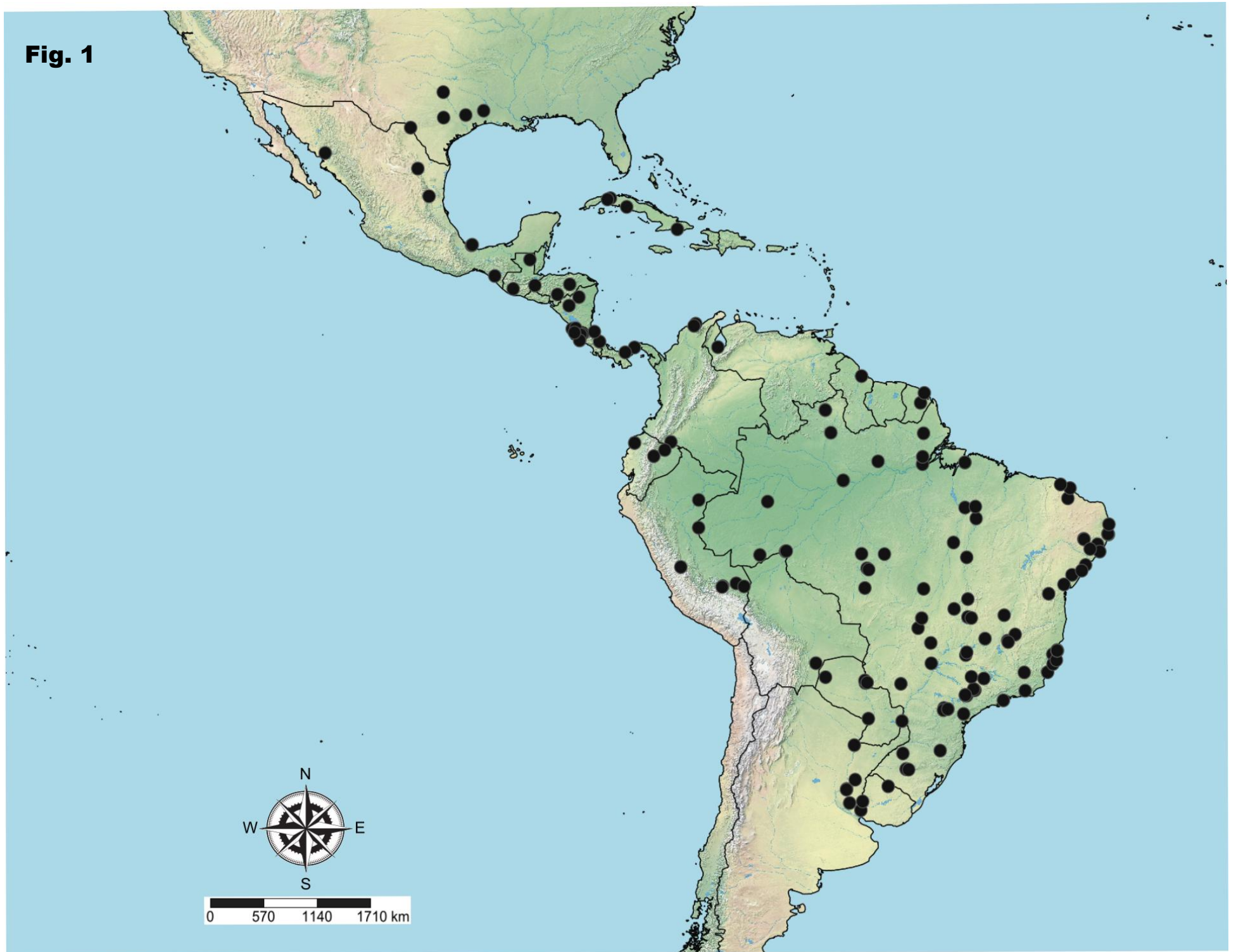
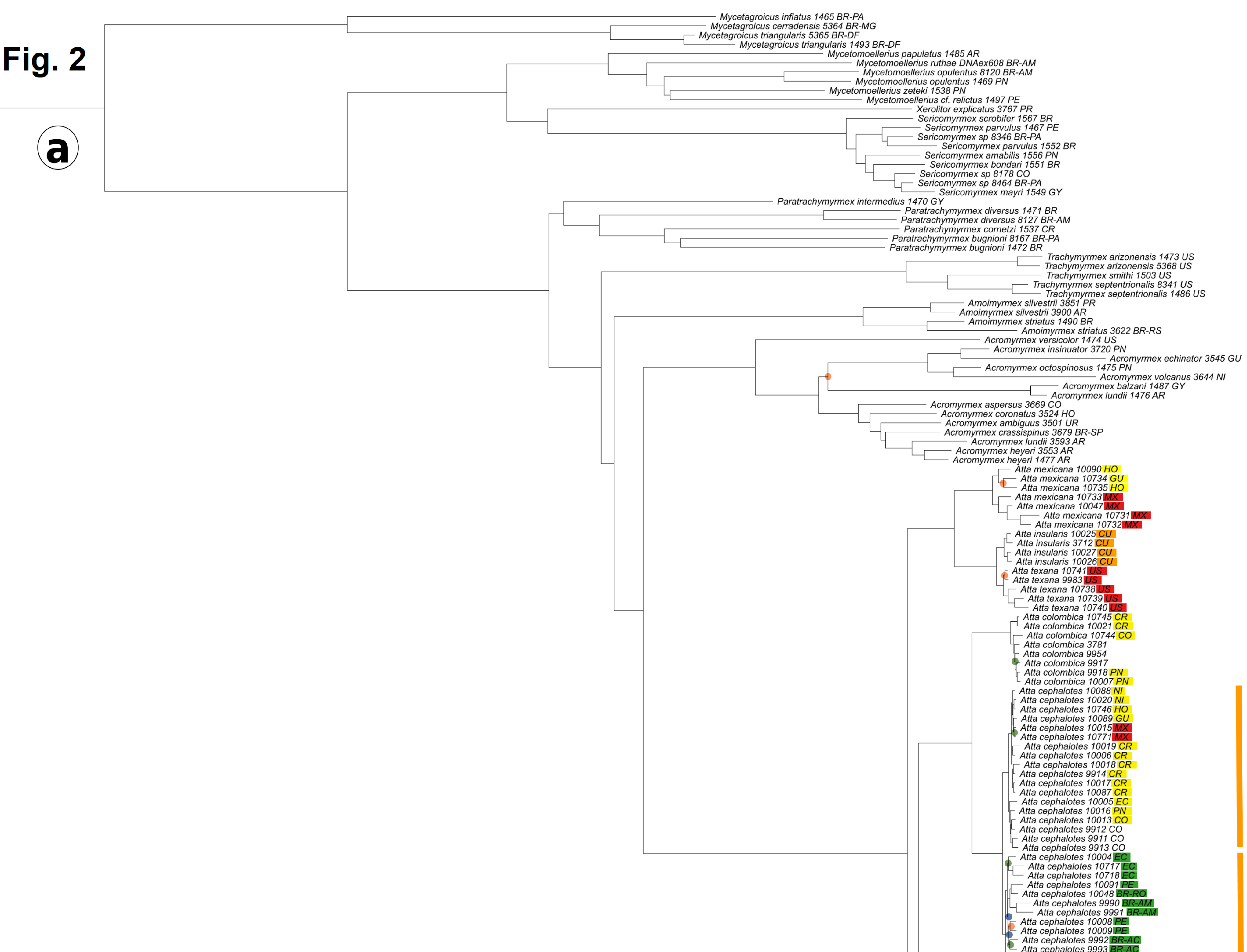


Fig. 2

a



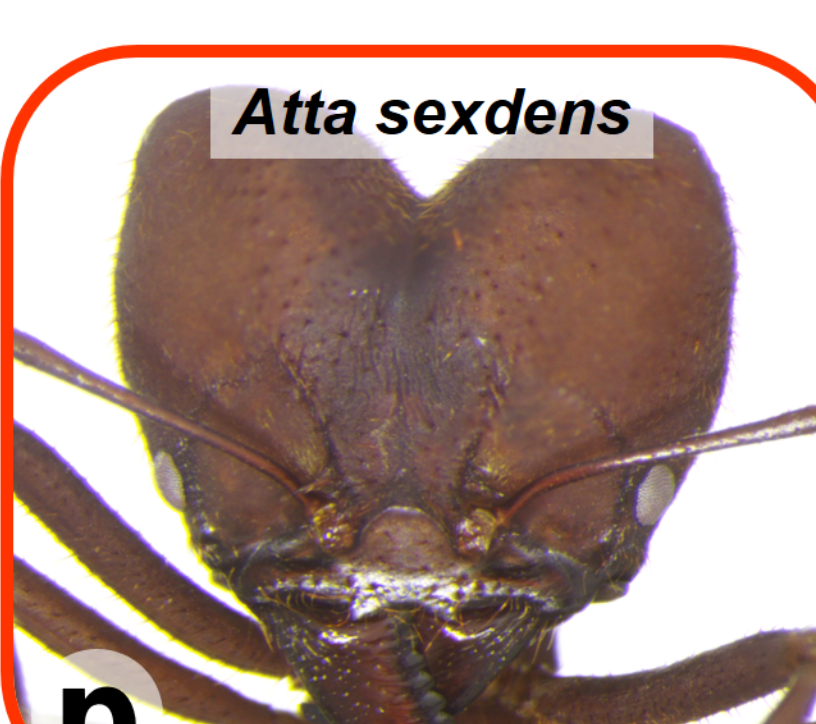
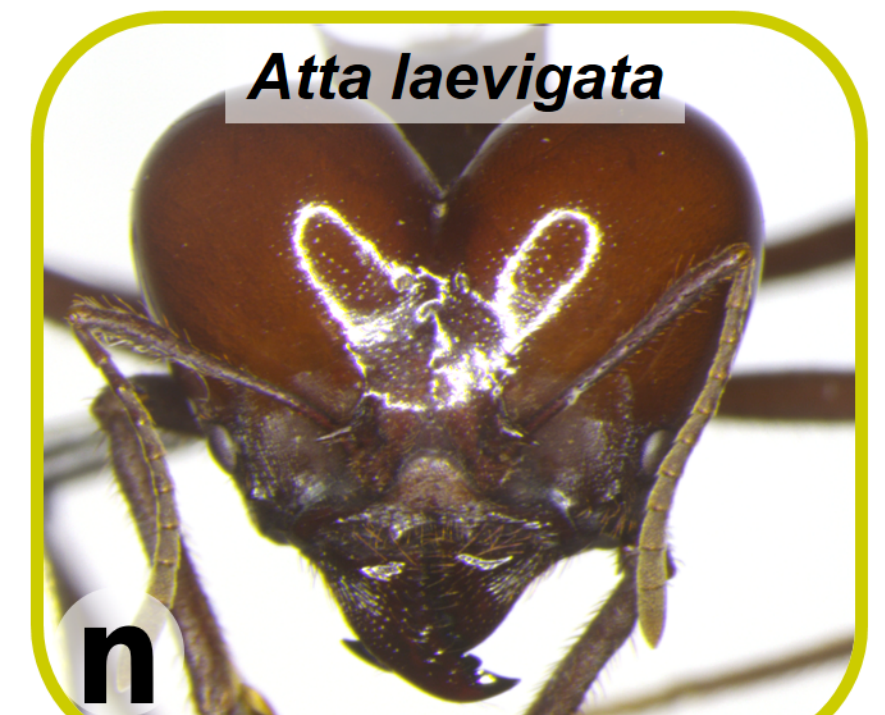
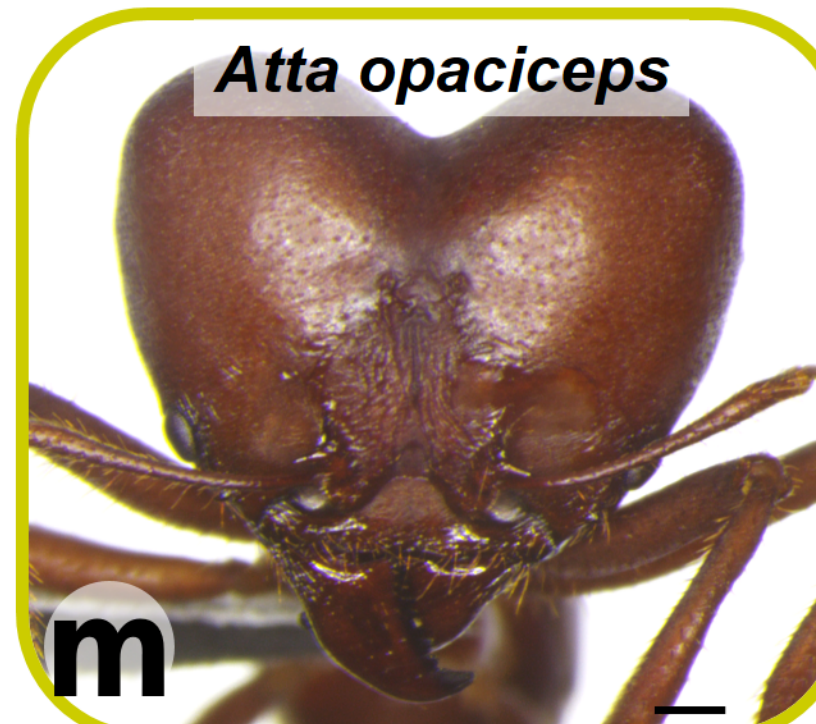
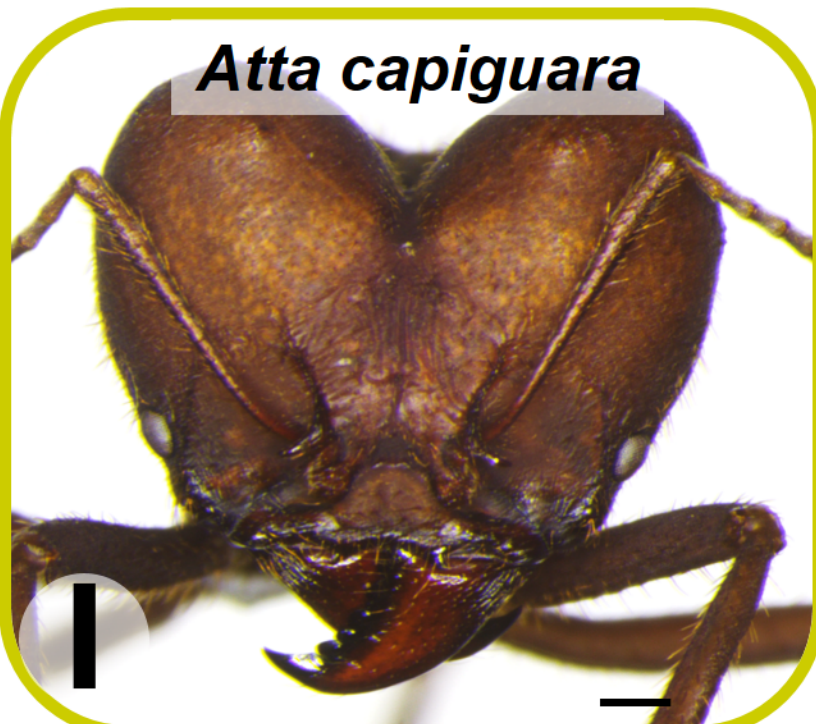
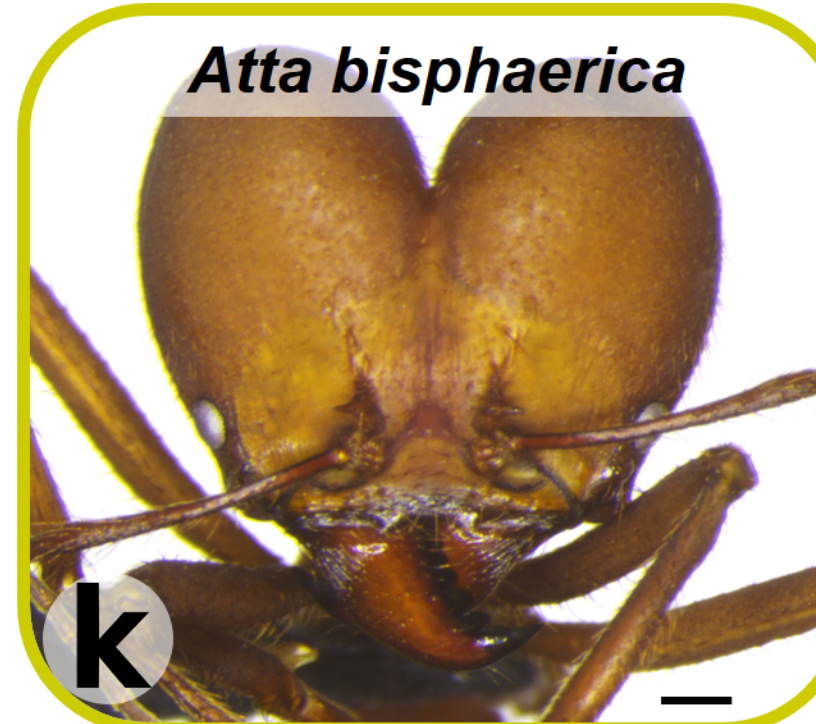
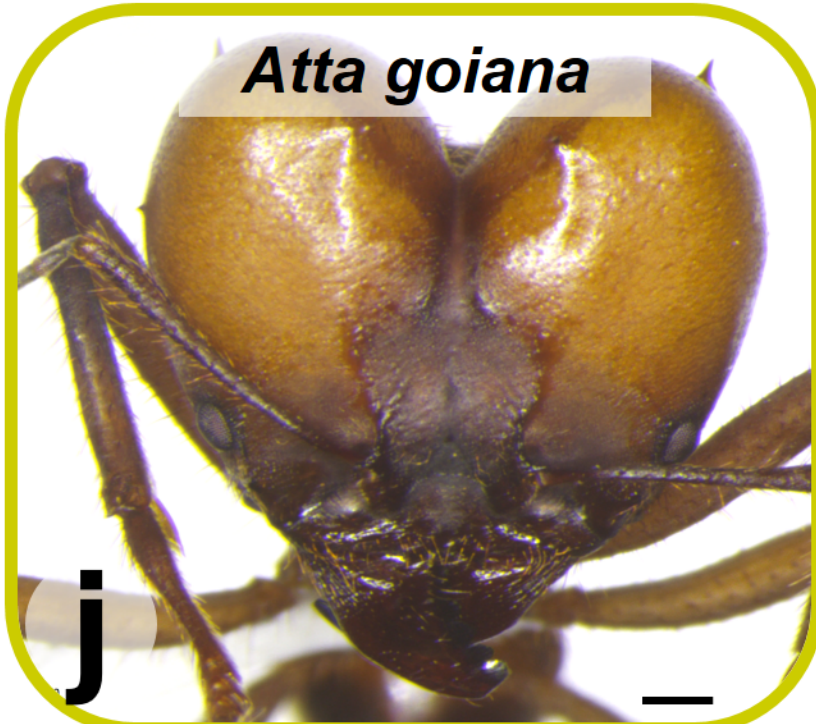
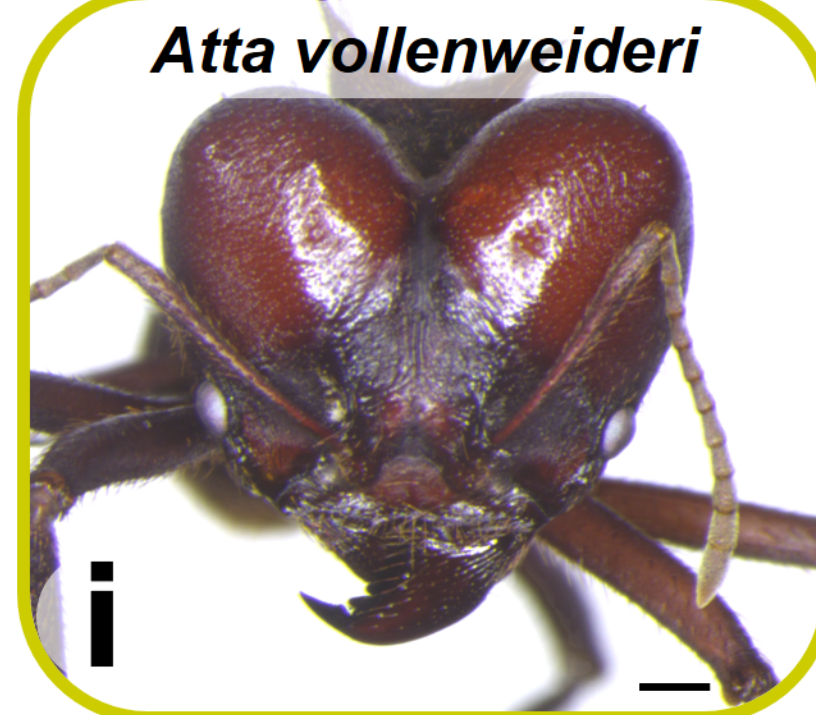
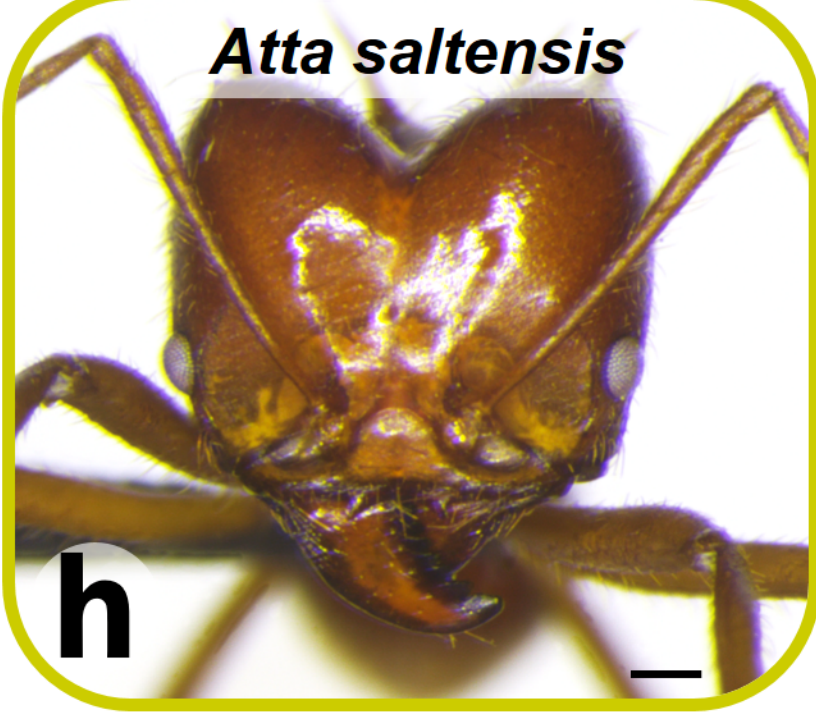
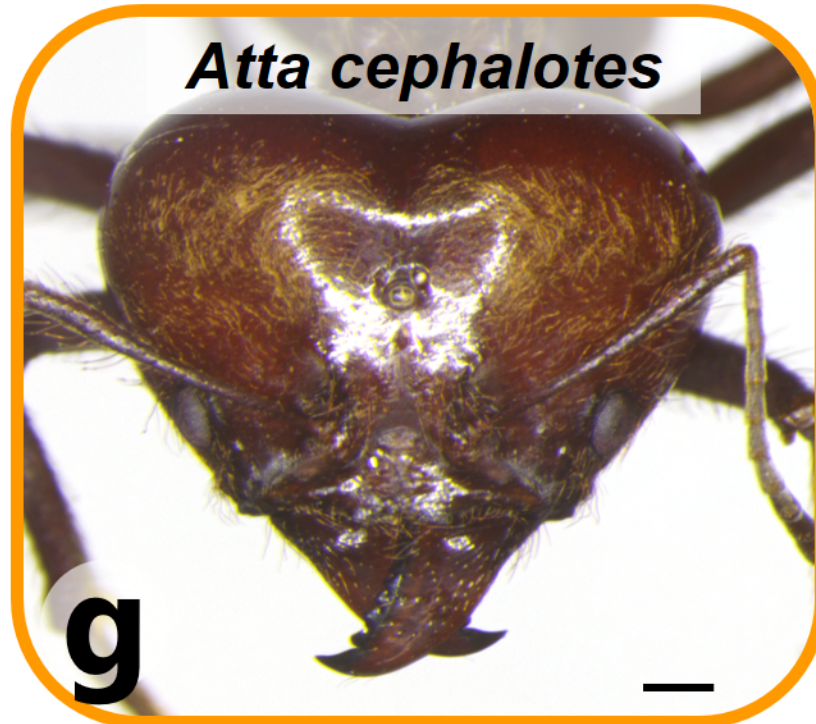
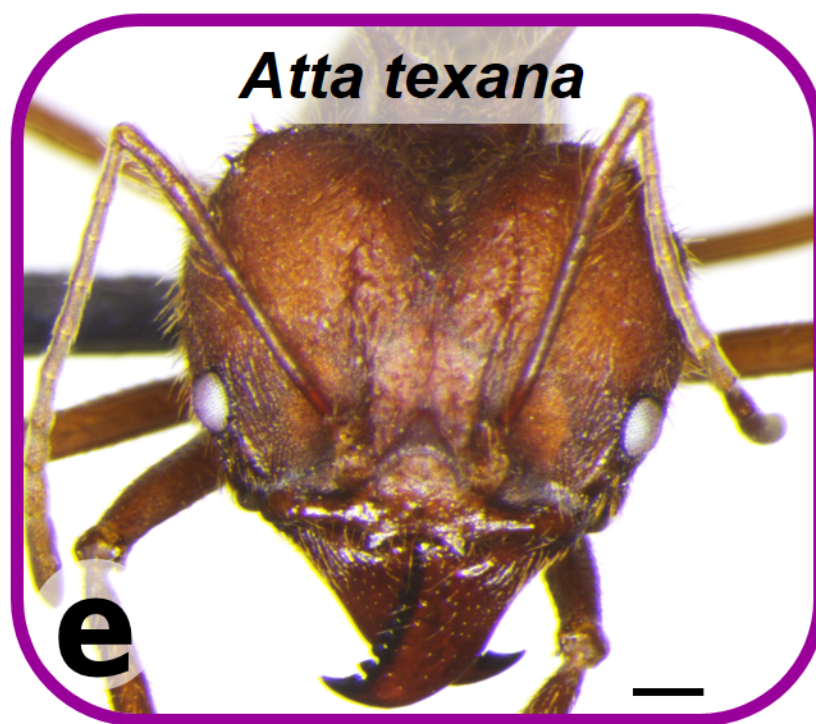
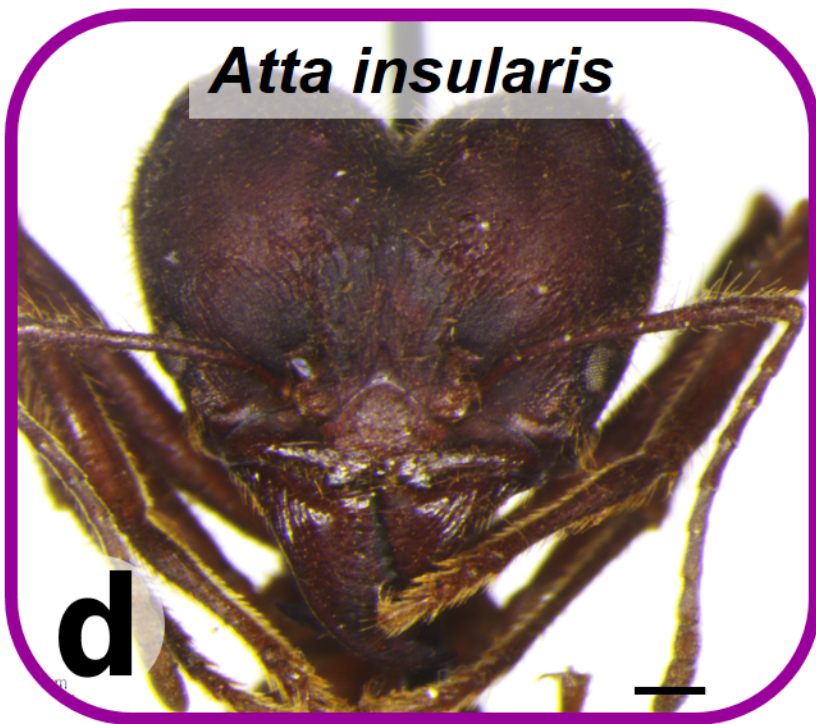
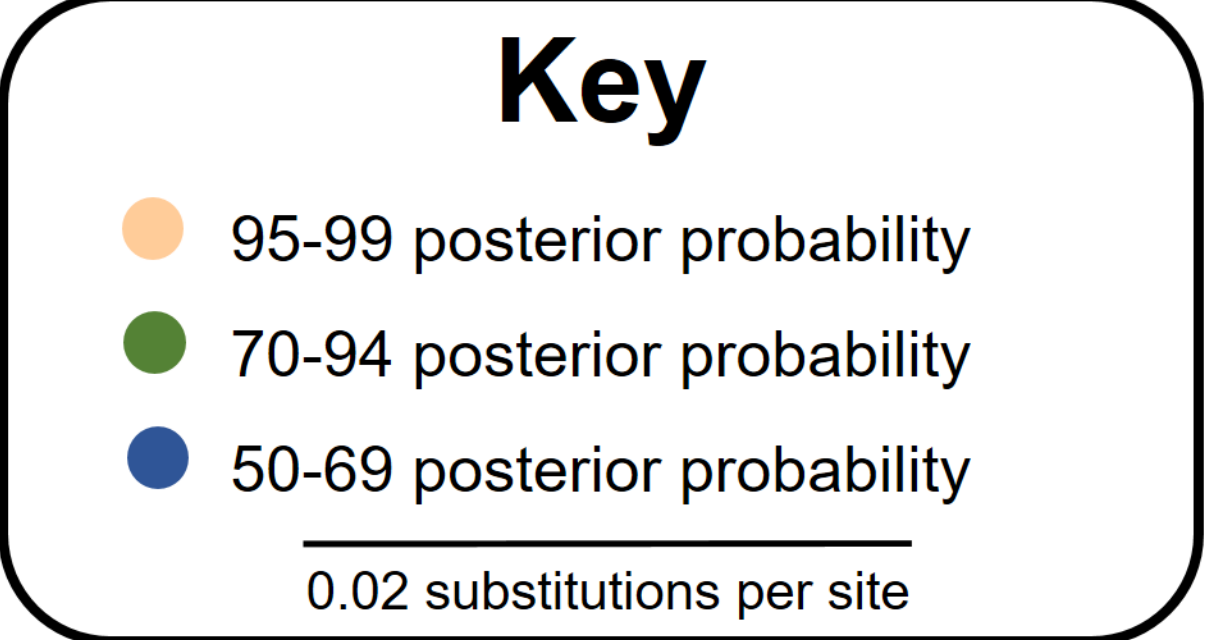
Outgroups

Archaeata
clade

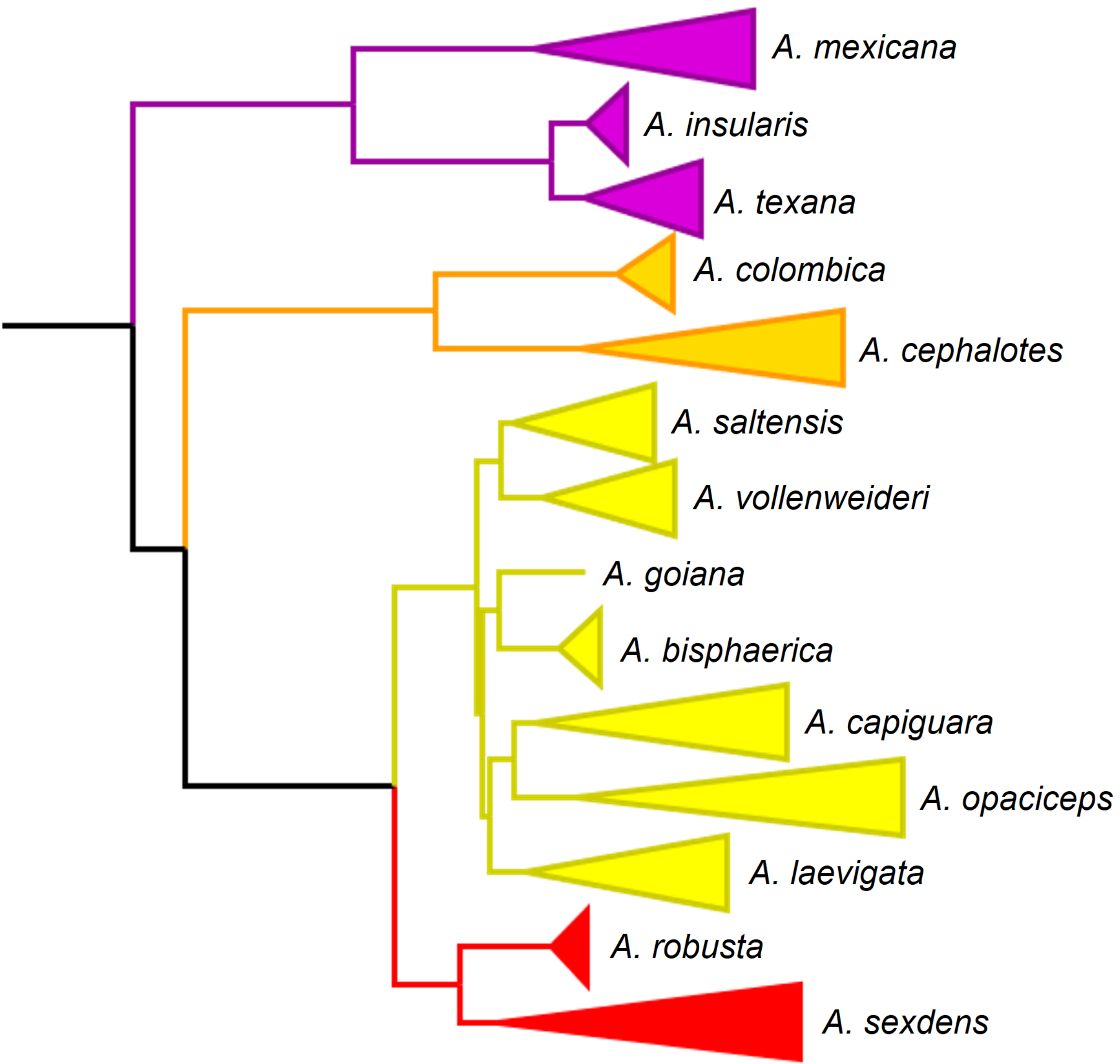
Atta s.s.
clade

Epiahta
clade

Neoahta
clade



b



Region tags



Fig. 3

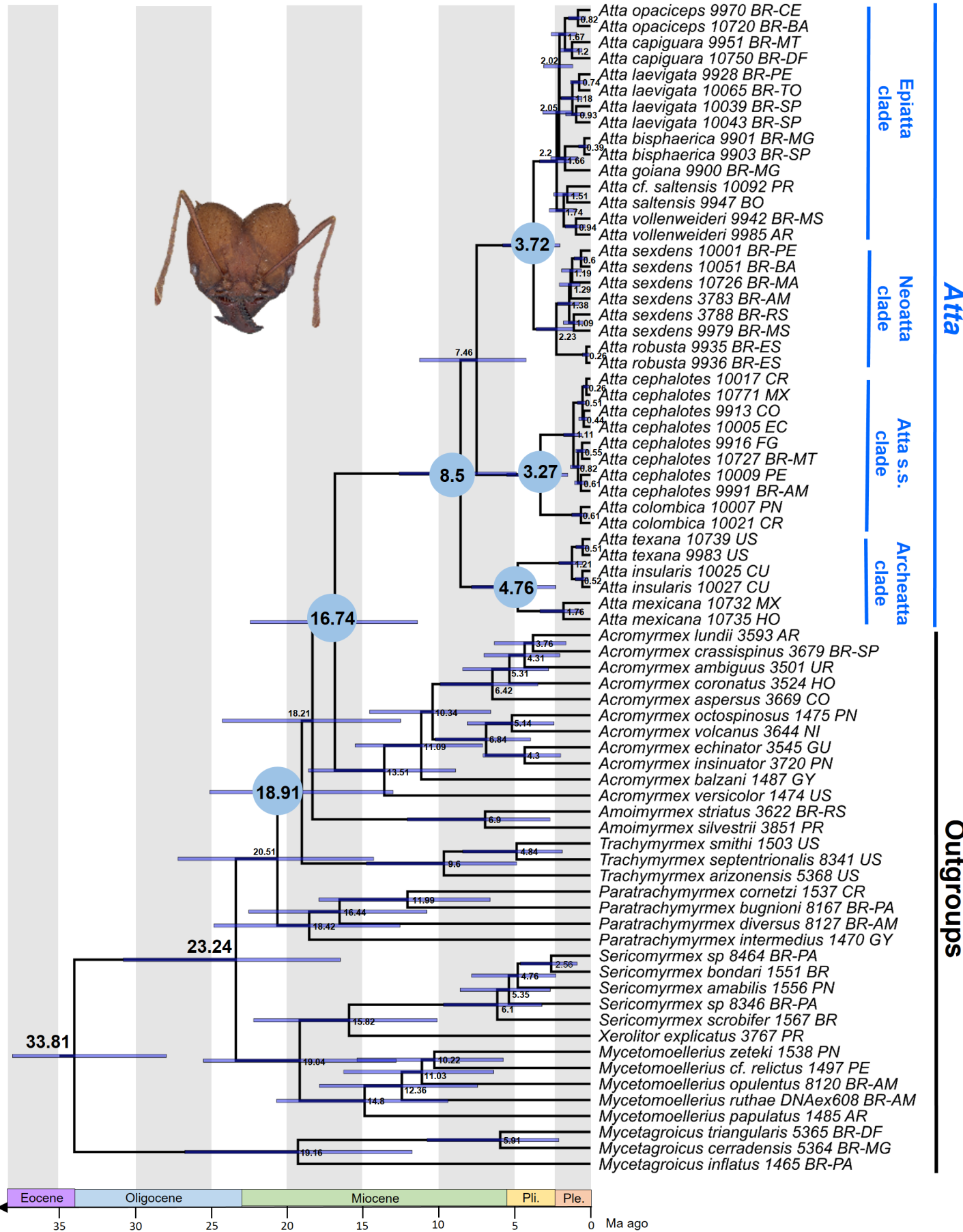


Fig. 4

Region Tags

- A= North America
- B= Caribbean
- C= Central/NW South America
- D= Guiana Shield
- E= Amazonia
- F= Cerrado
- G= Caatinga
- H= Atlantic Forest
- I= Chaco
- J= Pampas

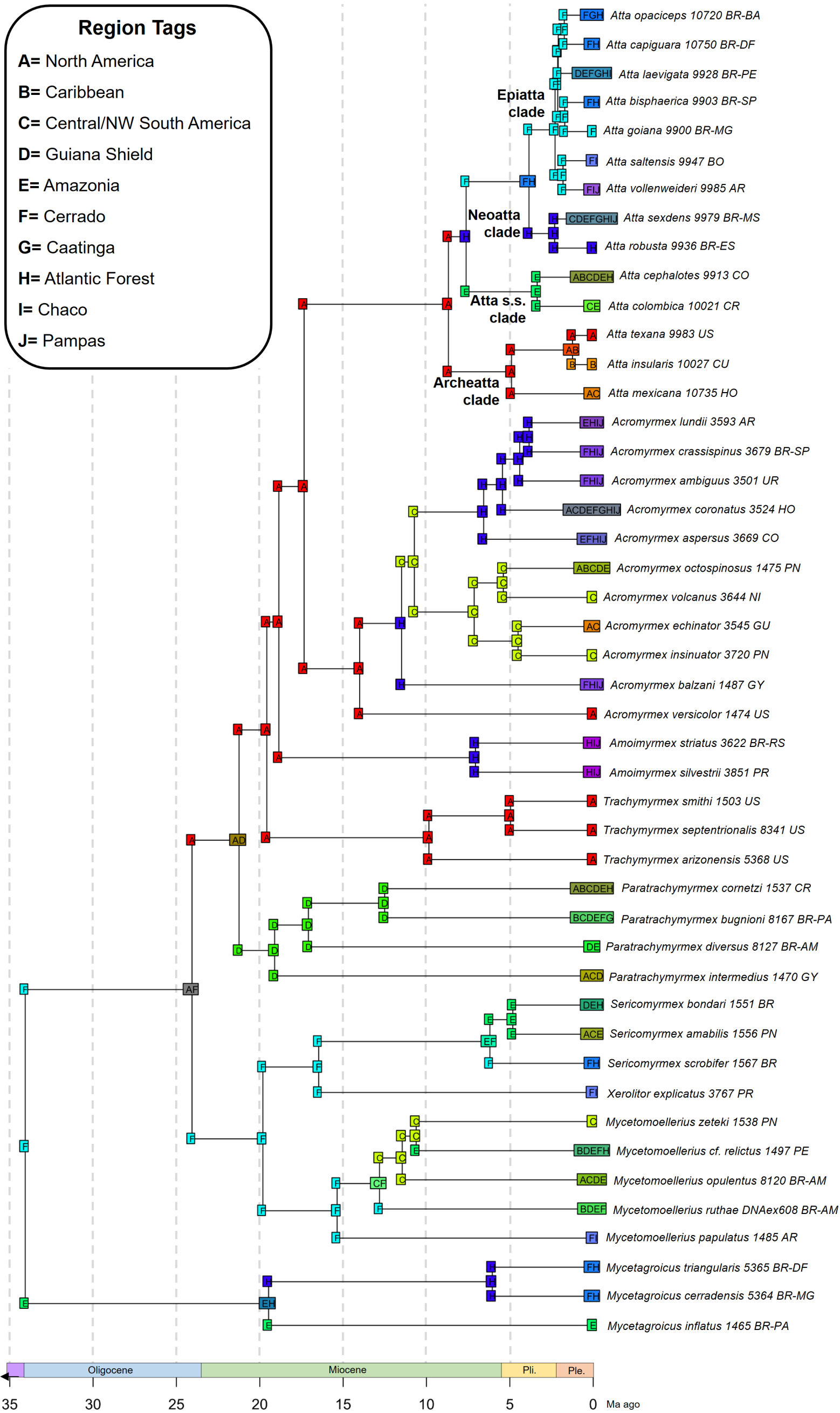


Fig. S1

results_Atta_geo_10reg_new/BioGeoBears_BAL_unconstrained
 ancstates: global optim, 9 areas max. d=0.0119; e=0.0866; j=0; LnL=-254.20

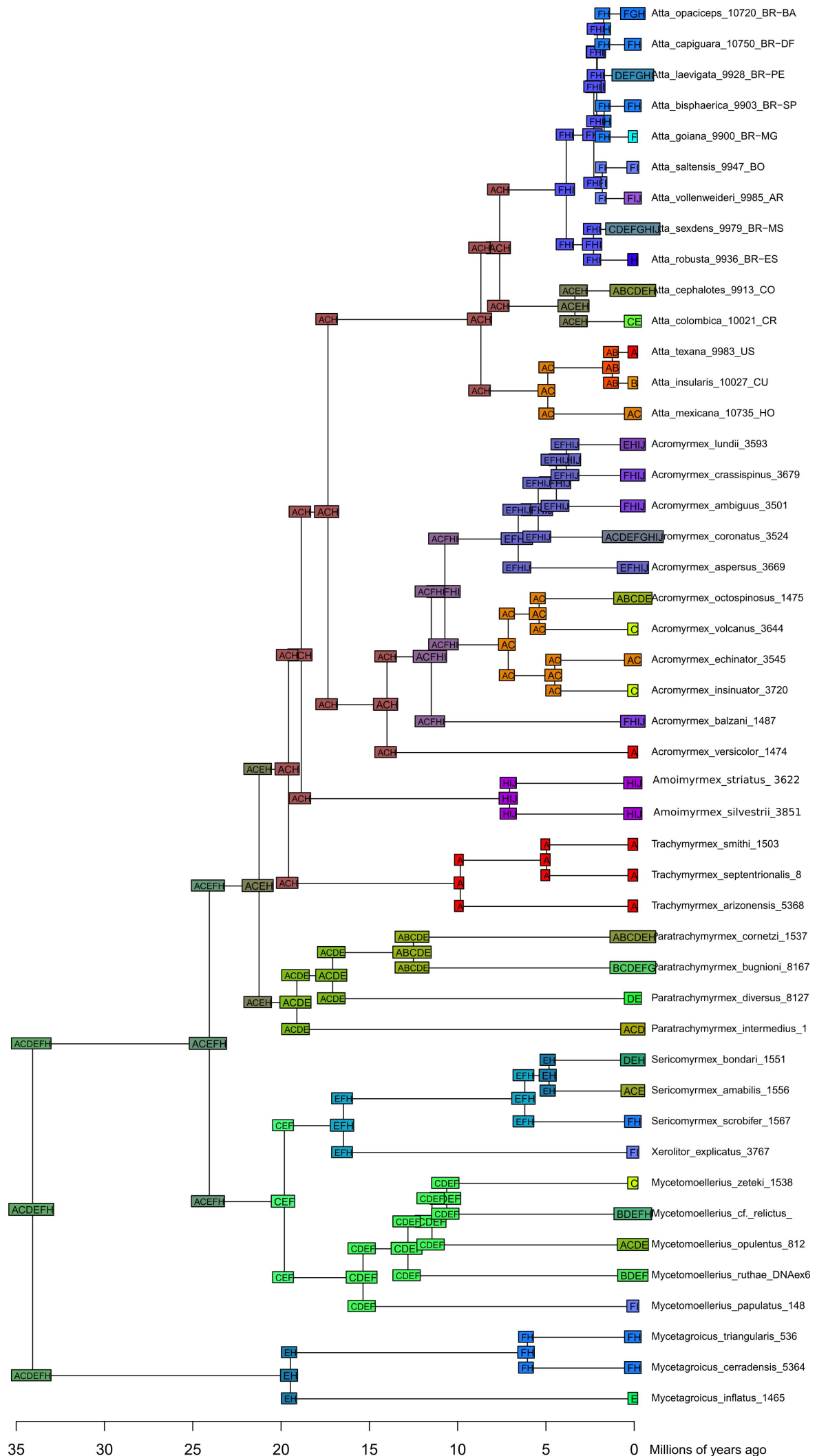


Fig. S2

results_Atta_geo_10reg_new_widelydist_reduc/BioGeoBears_BALJ_unconstrained
ancstates: global optim, 6 areas max. d=0.0058; e=0.0356; j=0.0181; LnL=-217.55

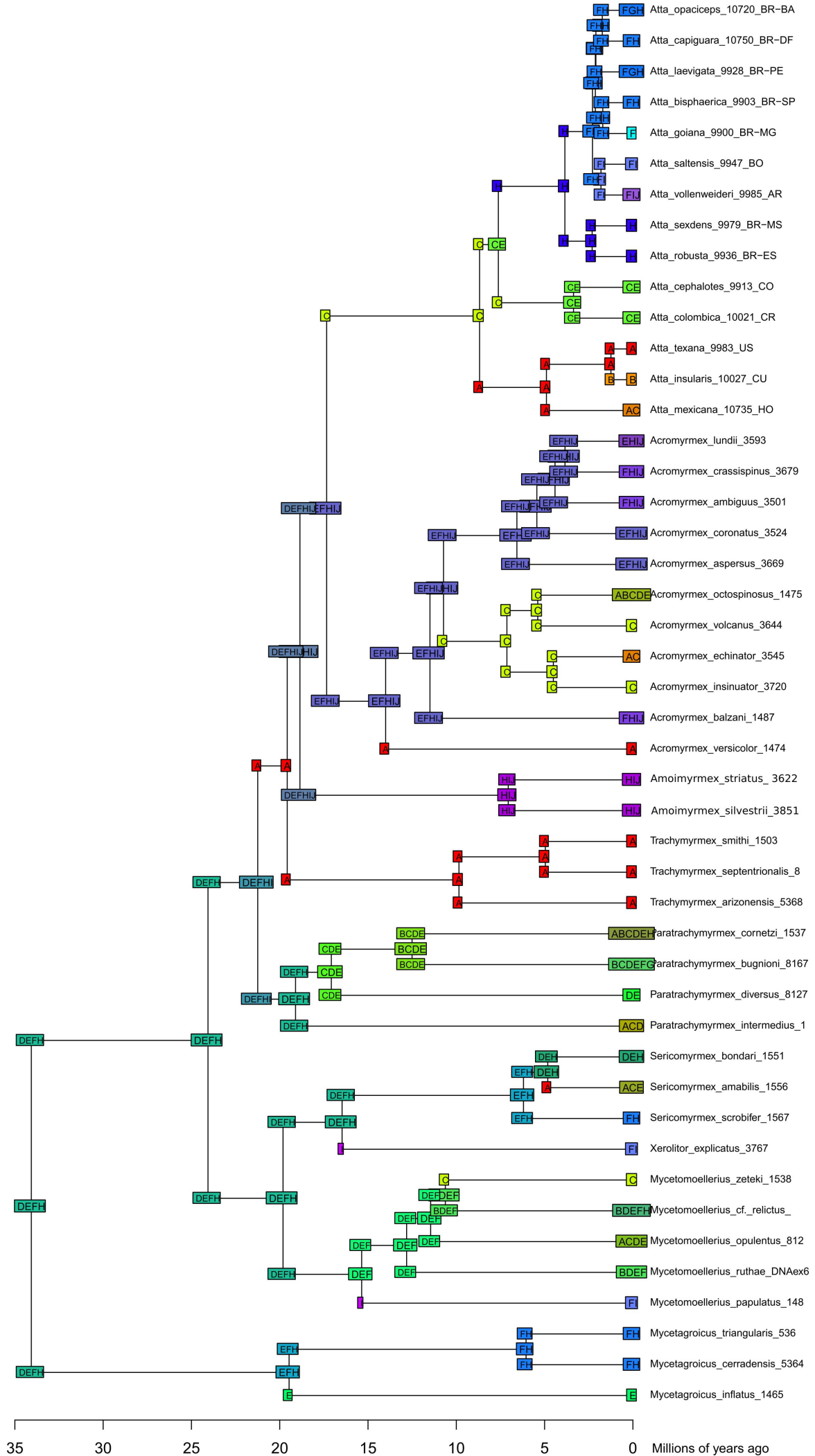


Fig. S3. Map of collection sites sampled for *Atta cephalotes*.

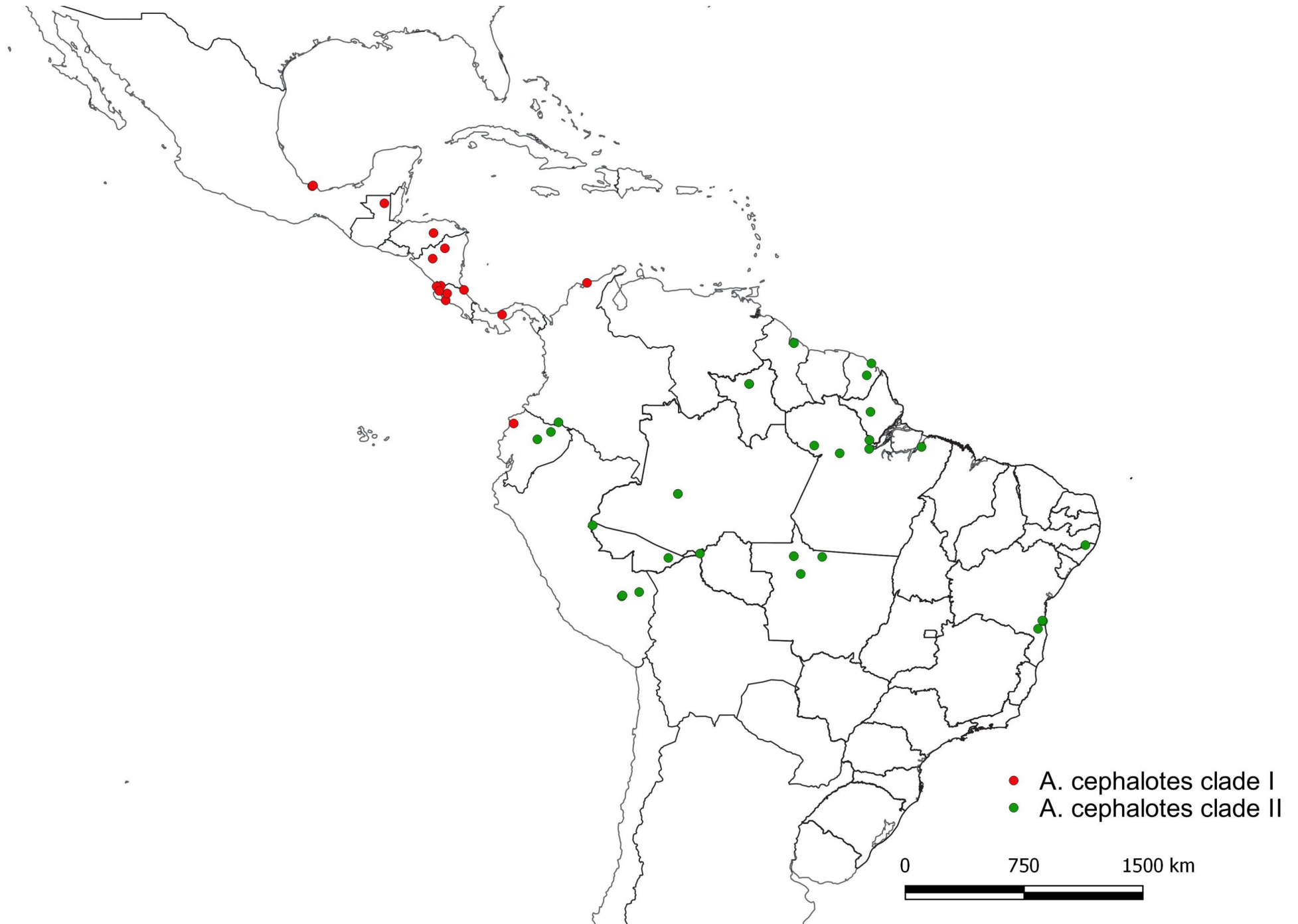


Fig. S4. Map of collection sites sampled for *Atta laevigata*.

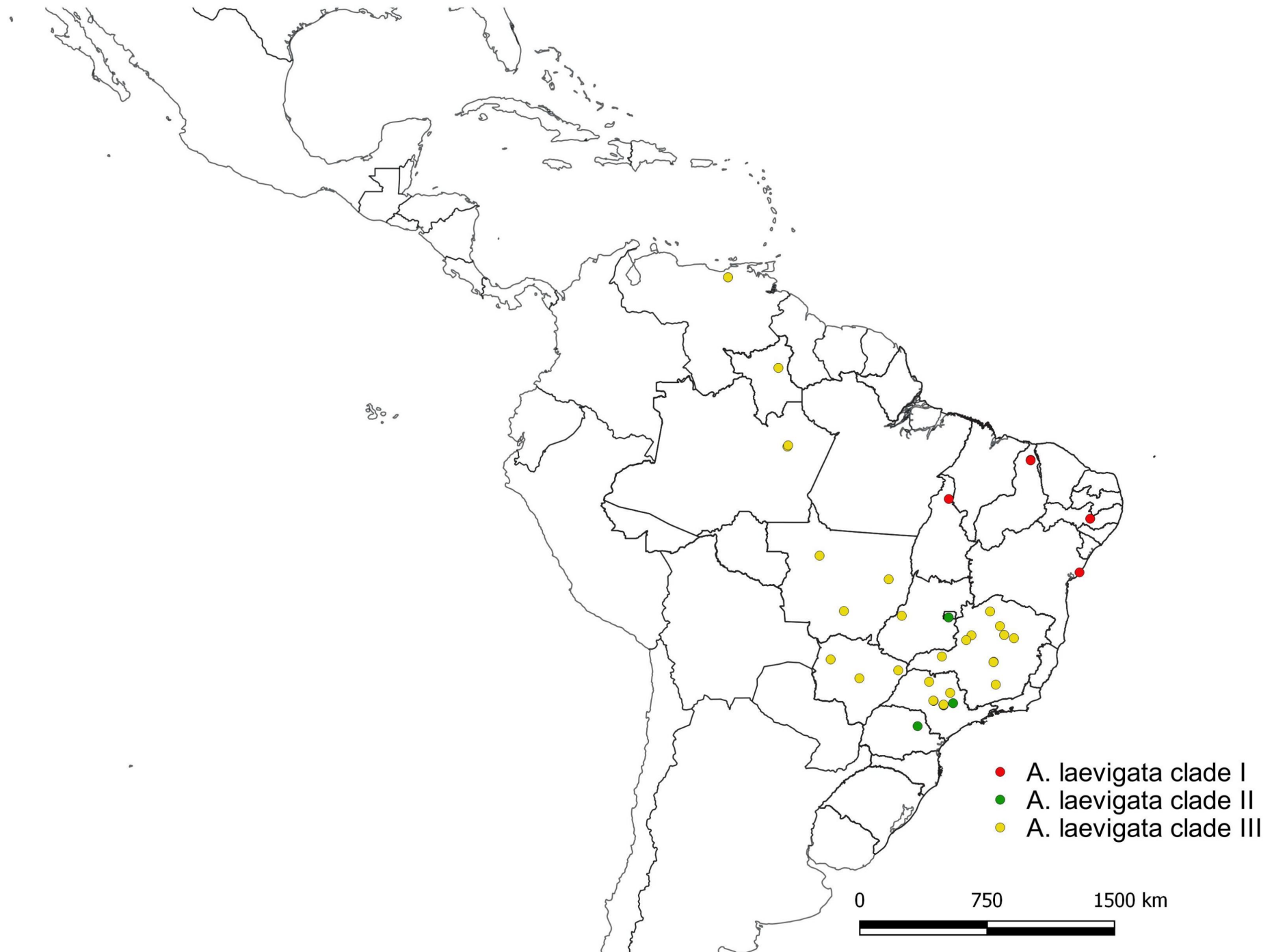
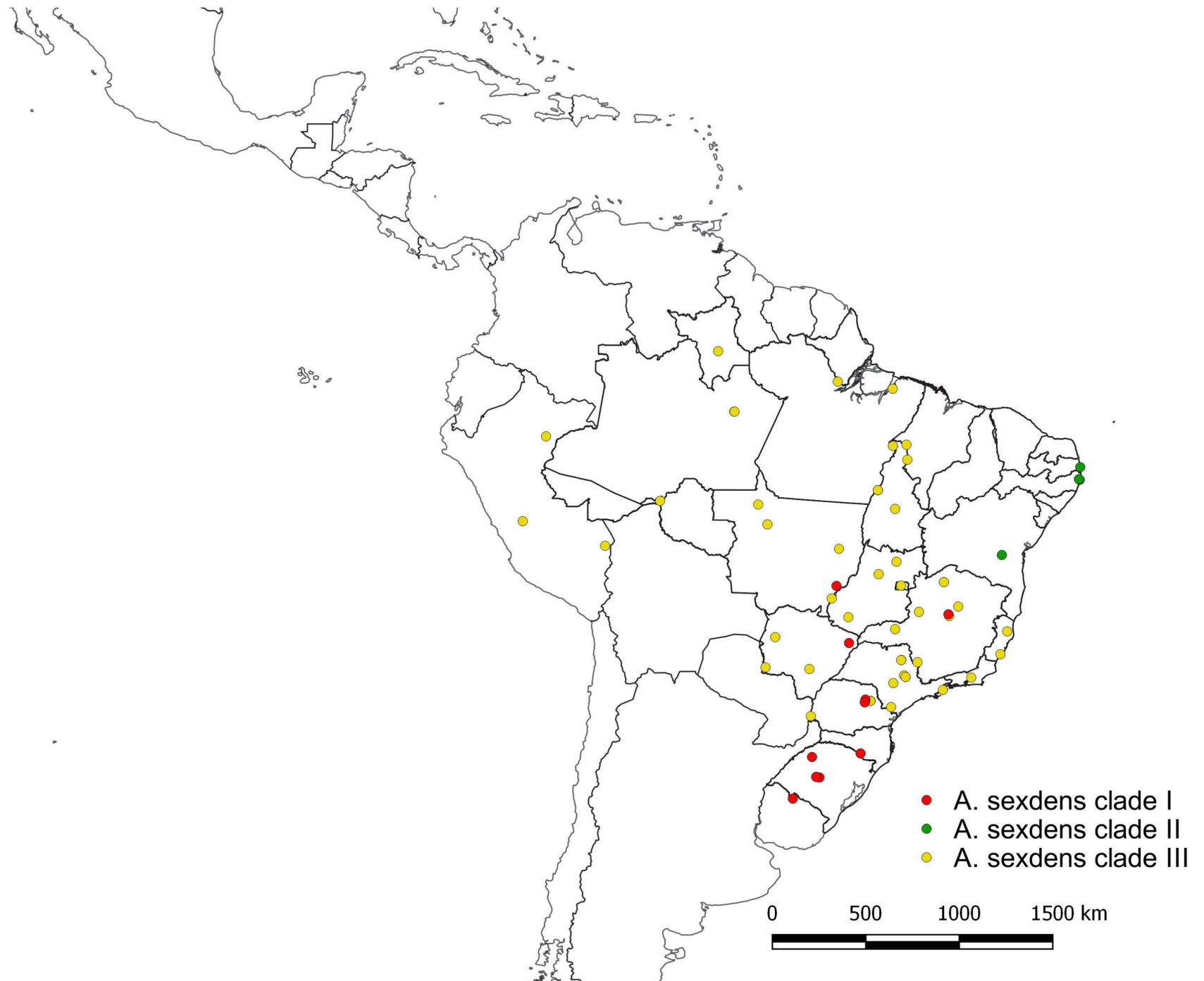


Fig. S5. Map of collection sites sampled for *Atta sexdens*.



SUPPLEMENTARY TABLES

Phylogenomic reconstruction reveals new insights into the evolution and biogeography of *Atta* leaf-cutting ants (Hymenoptera: Formicidae).

Appendix 1. Supplementary tables.

Author List:

*Corina A. Barrera^{1,2}, Jeffrey Sosa-Calvo^{2,3}, Ted R. Schultz³, Christian Rabeling², *Maurício Bacci Jr.¹

¹Universidade Estadual Paulista (UNESP), Instituto de Biociências, Centro de Estudos de Insetos Sociais (CEIS), Rio Claro, SP, Brazil.

²School of Life Sciences, Arizona State University, Tempe, AZ, U.S.A.

³Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

***Corresponding Authors:**

Corina Anahí Barrera

Universidade Estadual Paulista (UNESP), Instituto de Biociências, Centro de Estudos de Insetos Sociais (CEIS). Av. 24-A, 1515, Bela Vista, Rio Claro, 13506-900, SP, Brazil. E-mail: corinabarrera@gmail.com

Mauricio Bacci Jr.

Universidade Estadual Paulista (UNESP), Instituto de Biociências, Centro de Estudos de Insetos Sociais (CEIS). Av. 24-A, 1515, Bela Vista, Rio Claro, 13506-900, SP, Brazil. E-mail: mauricio.bacci@unesp.br

Supplemental Table Captions

Table S1. List of specimens analyzed in this study.

Table S2. Summary statistics for the final alignment matrices analyzed.

Table S3. Ecoregions data matrix used as input for biogeographical analysis.

Table S4. List of *Atta* species and their detailed distribution in the Americas.

Table S5. List of UCE data collection and sequencing statistics for all taxa sequenced in this study.

Table S5b. List of UCE data collection and sequencing statistics for the taxa included in this study from another reference.

Table S6. Divergence date estimates for clades of ingroup and outgroup taxa.

Supporting Information
Supplementary Table S1 List of specimens analyzed in this study.

Genus	Species	Extraction code	Identified by	Collecting code	Preservation extracted material	Extracted material	Voucher ID	Deposited *	Collected by	Country	First Admin. District	Locality	Collecting date	Latitude**	Longitude**	Elevation (m)	Reference
<i>Acromyrmex</i>	<i>ambiguus</i>	3501	C. Rabeling	1MB	point-mounted	worker	ASU-SIBR00000677	SIBR	M. Bollazzi	Uruguay	Treinta y Tres	La Teja Farm	Nov 2008	-33.22904722	-54.35764722	51	This study
<i>Acromyrmex</i>	<i>asperus</i>	3669	A. Ortiz	667 (A. Ortiz)	point-mounted	worker	ASU-SIBR00000678	SIBR	A. Ortiz, M. Bacci	Colombia	Antioquia	Andes	no data	5.656422222	-75.87965278	1295	This study
<i>Acromyrmex</i>	<i>balzani</i>	1487					USNM000538359	USNM		Guyana	Olancho						Branstetter et al. (2017)
<i>Acromyrmex</i>	<i>coronatus</i>	3524	C. Rabeling	Ba-C-01-1-02-17	point-mounted	worker	ASU-SIBR00000679	SIBR	J.T. Longino	Honduras		National Park La Muralla	4 May 2010	15.07949167	-86.76175	1264	This study
<i>Acromyrmex</i>	<i>crassispinus</i>	3679	C. Rabeling	E306	point-mounted	worker	ASU-SIBR00000680	SIBR	M. Bacci	Brazil	São Paulo	Rio Claro	no data	-22.41490278	-47.56513889	617	This study
<i>Acromyrmex</i>	<i>echinator</i>	3545	C. Rabeling	CR080108-02	point-mounted	worker	ASU-SIBR00000681	SIBR	C. Rabeling	Guatemala	Petén	Biopoto Cerro Cahui, El Remate	8 Jan 2008	17.00077	-89.70538	124	This study
<i>Acromyrmex</i>	<i>heyeri</i>	1477					USNM000412693	USNM		Argentina							Branstetter et al. (2017)
<i>Acromyrmex</i>	<i>heyeri</i>	3553	C. Rabeling	S. Pielström ZSP	point-mounted	worker	ASU-SIBR00000682	SIBR	S. Pielström	Argentina	Formosa	El Bagual Farm	Nov 2008	-26.1777	-58.17322778	65	This study
<i>Acromyrmex</i>	<i>insinuator</i>	3720	J.J. Boomsma	J.J. Boomsma Ae529	point-mounted	queen	ASU-SIBR00000683	SIBR	J.J. Boomsma	Panama	Colon	Gamboa	May 2012	9.116463889	-79.69651389	54	This study
<i>Acromyrmex</i>	<i>lundii</i>	1476					USNM000419026	USNM		Argentina							Branstetter et al. (2017)
<i>Acromyrmex</i>	<i>lundii</i>	3593	C. Rabeling	S. Pielström ZSP	point-mounted	worker	ASU-SIBR00000684	SIBR	S. Pielström	Argentina	Formosa	El Bagual Farm	Nov 2008	-26.1777	-58.17322778	65	This study
<i>Acromyrmex</i>	<i>octospinosus</i>	1475					USNM000529250	USNM		Panama							Branstetter et al. (2017)
<i>Acromyrmex</i>	<i>silvestrii</i>	3851	C. Rabeling	CR151102-05	ethanol	worker	ASU-SIBR00000685	SIBR	C. Rabeling	Paraguay	Presidente Haye	Rt. 9, 43km SE Pozo Azul	2 Nov 2015	-24.38727	-58.10748	92	This study
<i>Acromyrmex</i>	<i>Amoimymex</i>	3900	C. Rabeling	S. Pielström BSP	point-mounted	worker	ASU-SIBR00000686	SIBR	S. Pielström	Argentina	Salta	Cachi	Nov 2008	-25.12023611	-66.16249722	2345	This study
<i>Acromyrmex</i>	<i>Amoimymex</i>	1490					USNM000924113	USNM		Brazil							Branstetter et al. (2017)
<i>Acromyrmex</i>	<i>striatus</i>	3622	C. Rabeling	CR050109-02	ethanol	worker	ASU-SIBR00000687	SIBR	C. Rabeling	Brazil	Rio Grande do Sul	Botanical Garden of Fundacao Zoobotanica, Porto Alegre	9 Jan 2005	-30.05161667	-51.17716944	60	This study
<i>Acromyrmex</i>	<i>versicolor</i>	1474					CASENT0106056	UCDC		USA							Branstetter et al. (2017)
<i>Acromyrmex</i>	<i>volcanus</i>	3644	J.T. Longino	JTL7491-s	point-mounted	worker	ASU-SIBR00000688	SIBR	J.T. Longino	Nicaragua	Matagalpa	3 km N Rio Blanco	1 May 2011	12.95458	-85.23037	610	This study
<i>Atta</i>	<i>bisphaerica</i>	3711	C. Rabeling	CR120321-02	point-mounted	worker	ASU-SIBR00000689	SIBR	C. Rabeling	Brazil	São Paulo	Campus UNESP, Rio Claro	21 Mar 2012	-22.3965	-47.5444	633	This study
<i>Atta</i>	<i>bisphaerica</i>	9901	J. Chaul	no data	ethanol	worker	ASU-SIBR00000416	SIBR	J. Chaul	Brazil	Minas Gerais	UFV Zootecnia, Vicosas	7 Oct 2012	-20.76656611	-42.861548	675	This study
<i>Atta</i>	<i>bisphaerica</i>	9903	C.A. Barrera	AR090429-01	ethanol	worker	ASU-SIBR00000423	SIBR	A. Rodrigues	Brazil	São Paulo	Botucatu	29 Apr 2009	-22.84298333	-48.43551667	803	This study
<i>Atta</i>	<i>bisphaerica</i>	10097	C. Rabeling	CR110712-01	point-mounted	worker	ASU-SIBR00000418	SIBR	C. Rabeling	Brazil	São Paulo	Campus UNESP, Rio Claro	12 Jul 2011	-22.3955	-47.5424	633	This study
<i>Atta</i>	<i>bisphaerica</i>	10711	C.A. Barrera	E297	ethanol	worker	ASU-SIBR00000417	SIBR	no data	Brazil	São Paulo	Botucatu	7 Mar 2013	-22.89200556	-48.41122222	751	This study
<i>Atta</i>	<i>capiguara</i>	9904	J. S. Pereira	JSP130307-01	ethanol	worker	ASU-SIBR00000424	SIBR	J. Silva Pereira	Brazil	São Paulo	Botucatu	2001	-22.9085	-48.30786667	532	This study
<i>Atta</i>	<i>capiguara</i>	9951	M. Bacci Jr	E409	ethanol	worker	ASU-SIBR00000501	SIBR	M. Bacci	Brazil	Mato Grosso	Sapezal	18 Sep 2001	-12.99938611	-57.93451389	401	This study
<i>Atta</i>	<i>capiguara</i>	10750	C.A. Barrera	5911	point-mounted	worker	ASU-SIBR00000640	ICBS	E. Amante	Brazil	DF	Brasília	29 May 1968	-15.67392222	-48.19767222	1101	This study
<i>Atta</i>	<i>cephalotes</i>	3779	C. Rabeling	CR151023-01	point-mounted	worker	ASU-SIBR00000663	SIBR	C. Rabeling	Brazil	Bahia	Itabuna	23 Oct 2015	-14.75616	-39.23118	57	Li et al. (2018)
<i>Atta</i>	<i>cephalotes</i>	9905	S.E. Solomon	SES040214-11	ethanol	male	ASU-SIBR00000425	SIBR	S.E. Solomon	Brazil	Pará	Alenquer	14 Feb 2004	-1.938372222	-54.74459167	13	This study
<i>Atta</i>	<i>cephalotes</i>	9906	B.M. Santos Reis	BMSR120703-01	ethanol	worker	ASU-SIBR00000426	SIBR	B.M. Santos Reis	Brazil	Bahia	Camaçari	3 Jul 2012	-15.38745	-39.55848333	522	This study
<i>Atta</i>	<i>cephalotes</i>	9907	C.A. Barrera	CAB180402-04	ethanol	worker	ASU-SIBR00000427	SIBR	C.A. Barrera	Brazil	Bahia	Tower trail in UESG, Ilhéus	2 Apr 2018	-14.79549722	-39.17213889	35	This study
<i>Atta</i>	<i>cephalotes</i>	9909	C.A. Barrera	CAB171004-02	ethanol	worker	ASU-SIBR00000429	SIBR	C.A. Barrera	Brazil	Mato Grosso	São Nicolau Farm, Cotriguaçu	4 Oct 2017	-9.823533333	-58.25926667	227	This study
<i>Atta</i>	<i>cephalotes</i>	9910	C.A. Barrera	CAB171006-01	ethanol	worker	ASU-SIBR00000430	SIBR	C.A. Barrera	Brazil	Mato Grosso	São Nicolau Farm, Cotriguaçu	6 Oct 2017	-9.822216667	-58.25906667	234	This study
<i>Atta</i>	<i>cephalotes</i>	9911	C.A. Barrera	440	ethanol	worker	ASU-SIBR00000431	SIBR	no data	Colombia	no data	no data	no data	no data	no data	no data	This study
<i>Atta</i>	<i>cephalotes</i>	9912	C.A. Barrera	E659	ethanol	worker	ASU-SIBR00000432	SIBR	no data	Colombia	no data	no data	no data	no data	no data	no data	This study
<i>Atta</i>	<i>cephalotes</i>	9913	C.A. Barrera	688	ethanol	worker	ASU-SIBR00000433	SIBR	no data	Colombia	no data	no data	no data	no data	no data	no data	This study
<i>Atta</i>	<i>cephalotes</i>	9914	C.S. Moreau	CSM2595	ethanol	worker	ASU-SIBR00000435	SIBR	C.S. Moreau	Costa Rica	Guanacaste	ACG, Santa Rosa sector, Estación Biológica Santa Rosa N.P., Borrochos lat	18 Jun 2012	10.84288889	-85.61588889	293	This study
<i>Atta</i>	<i>cephalotes</i>	9915	C.S. Moreau	CSM3738	ethanol	worker	ASU-SIBR00000436	SIBR	C.S. Moreau	French Guiana	no data	Reserve des Nouragues, Arataye River, Camp Parare Station	17 Mar 2018	4.03792	-52.67284	42	This study
<i>Atta</i>	<i>cephalotes</i>	9916	C.S. Moreau	CSM3740	ethanol	worker	ASU-SIBR00000437	SIBR	C.S. Moreau	French Guiana	no data	La Colline De Montabo park, Cayenne, Centre Littoral	18 Mar 2018	4.94819	-52.31416	18	This study
<i>Atta</i>	<i>cephalotes</i>	9990	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000555	SIBR	T. Ferreira, F. Bacci	Brazil	Amazonas	Carauari	2 Sep 2014	-5.048569444	-67.13435278	102	This study
<i>Atta</i>	<i>cephalotes</i>	9991	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000556	SIBR	T. Ferreira, F. Bacci	Brazil	Amazonas	Carauari	2 Sep 2014	-5.048569444	-67.13435278	102	This study
<i>Atta</i>	<i>cephalotes</i>	9992	C.A. Barrera	no data	ethanol	queen	ASU-SIBR00000557	SIBR	A.C. Ferreira, R.M. Feltosa, T.S. Silva	Brazil	Acre	UFAC Campus, Rio Branco	11 Sep 2016	-9.956652778	-67.86648611	157	This study
<i>Atta</i>	<i>cephalotes</i>	9993	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000558	SIBR	R.M. Feltosa, A.C. Ferreira, T.S. Silva	Brazil	Acre	Máncio Lima	18 Sep 2016	-7.449669444	-73.66050833	234	This study
<i>Atta</i>	<i>cephalotes</i>	9994	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000559	SIBR	R.M. Feltosa, A.M. Oliveira, V. Franco	Brazil	Amapá	Serra do Navio	28 Jul 2017	-1.604444444	-52.48888889	135	This study
<i>Atta</i>	<i>cephalotes</i>	9996	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000579	SIBR	L.P. Prado	Brazil	Pará	MPEG Campus, Belém	Dec 2017	-1.453197222	-48.47574722	22	This study
<i>Atta</i>	<i>cephalotes</i>	9997	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000580	SIBR	R.M. Feltosa, E.Z. Albuquerque, R.R. Silva	Brazil	Pará	Rebio Rio Trombetas, Sta. Rosa, Oriximiná	2 Sep 2016	-1.344102778	-56.69213333	5	This study
<i>Atta</i>	<i>cephalotes</i>	9999	C.A. Barrera	CV mata P6	ethanol	worker	ASU-SIBR00000562	SIBR	no data	Brazil	Pará	Jari	16 Feb	-0.920186111	-52.46953056	20	This study
<i>Atta</i>	<i>cephalotes</i>	10004	C.S. Moreau	CSM0319	ethanol	worker	ASU-SIBR00000569	SIBR	C.S. Moreau	Ecuador	Sucumbios	Amazon Basin on the Rio Napo, Challuacocha Lake, Sani Lodge 70 mi E. Coca	28 Feb 2004	0.43845	-76.27916667	236	This study
<i>Atta</i>	<i>cephalotes</i>	10005	C.S. Moreau	CSM0337	ethanol	worker	ASU-SIBR00000570	SIBR	C.S. Moreau	Ecuador	Esmeraldas	Mache-Chindul Mtns. Bilsa Biological Station, 41 km WSW of Quininde	10 Feb 2004	0.346883333	-79.71133333	554	This study
<i>Atta</i>	<i>cephalotes</i>	10006	C.A. Barrera	CSM2454	ethanol	worker	ASU-SIBR00000571	SIBR	C.S. Moreau	Costa Rica	Guanacaste	ACG, San Cristobal sector, Estación Biologica Caribe at Rio Francia	15 Jun 2012	10.90133333	-85.28880556	369	This study
<i>Atta</i>	<i>cephalotes</i>	10008	C.S. Moreau	CSM0495	ethanol	worker	ASU-SIBR00000573	SIBR	C.S. Moreau	Peru	Madre de Dios	Amazon Basin on the Rio Madre de Dios, Los Amigos Biological Station, 100 km E of Puerto Maldonado	22 Apr 2004	-12.56903333	-70.10095	250	This study
<i>Atta</i>	<i>cephalotes</i>	10009	C.S. Moreau	CSM3030	ethanol	worker	ASU-SIBR00000574	SIBR	C.S. Moreau	Peru	Madre de Dios	Machu Huasi, Manu	11 Agu 2013	-12.82933	-71.37631	525	This study
<i>Atta</i>	<i>cephalotes</i>	10012	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000577	SIBR	R. Probst, O. Guilhe	Brazil	Amapá	Montanhas do Tumucumaque Nat. Park	27 Dec 2018	1.235033333	-52.38813333	148	This study
<i>Atta</i>	<i>cephalotes</i>	10013	C.A. Barrera	RSP566	ethanol	worker	ASU-SIBR00000441	SIBR	R. Probst	Colombia	Magdalena	Minca, Santa Marta	25 Aug 2018	11.1234	-74.09496667	977	This study
<i>Atta</i>	<i>cephalotes</i>	10015	J.T. Longino	JTL9578	ethanol	worker	JTL763297	SIBR	J. Longino	México	Veracruz	Ruiz Cortez, Coatzacoatlán	2 Jun 2016	18.53427	-95.13828	1050	This study
<i>Atta</i>	<i>cephalotes</i>	10016	J.T. Longino	JTL9108	ethanol	worker	CASENT0633700	SIBR	J. Longino	Panama	Codá	Omar Torrijos Nat. Park, El Copé	22 Jan 2015	8.68316	-80.59843	770	This study
<i>Atta</i>	<i>cephalotes</i>	10017	J.T. Longino	JTL8978-s	ethanol	worker	JTL723392	SIBR	J. Longino	Costa Rica	Puntarenas	Monteverde	25 Dec 2014	10.30864	-84.80788	1480	This study
<i>Atta</i>	<i>cephalotes</i>	10018	J.T. Longino	JTL3438	ethanol	worker	INBIOCR001280265	SIBR	J. Longino	Costa Rica	Puntarenas	Puntarenas	29 Mar 1993	9.78333	-84.91667	5	This study
<i>Atta</i>	<i>cephalotes</i>	10019	J.T. Longino	JTL2104-s	ethanol	worker	JTLC-VIAL-000441.22	SIBR	J. Longino	Costa Rica	Limón	Casa Verde, Tortuguero	19 Jun 1988	10.58333	-83.51667	5	This study
<i>Atta</i>	<i>cephalotes</i>	10020	J.T. Longino	JTL7515-s	ethanol	worker	JTL325642	SIBR	J. Longino	Nicaragua	Zelaya	Nat. Park Saslaya	7 May 2011	13.77054	-84.97857	290	This study
<i>Atta</i>	<i>cephalotes</i>	10028	C.A. Barrera	CAB171001-01	ethanol	worker	ASU-SIBR00000428	SIBR	C.A. Barrera	Brazil	Mato Grosso	Downtown, Alta Floresta	1 Oct 2017	-9.878333333	-56.08552222	292	This study
<i>Atta</i>	<i>cephalotes</i>	10048	C.A. Barrera	T9P2	ethanol	worker	ASU-SIBR00000597	SIBR	W. Dáttilo, F. Andric	Brazil	Roraima	Abunã T9P2 area, Porto Velho	20 Sep 2011	-9.626	-65.4319444	122	This study
<i>Atta</i>	<i>cephalotes</i>	10083	C.A. Barrera	23404-4	ethanol	worker	ASU-SIBR00000628	INPA	no data	Brazil	Roraima	Ecological Station Maracá, Amajari	25 Feb 2007	3.381875	-61.68380833	188	This study
<i>Atta</i>	<i>cephalotes</i>	10084	C.A. Barrera	20104-04	ethanol	worker	ASU-SIBR00000629	INPA	no data	Brazil	Roraima	Ecological Station Maracá, Amajari	24 Feb 2007	3.372108333	-61.67445	220	This study
<i>Atta</i>	<i>cephalotes</i>	10087	C. Rabeling	CR071221-11	ethanol	worker	ASU-SIBR00000434	SIBR	C. Rabeling	Costa Rica	Guanacaste	Biological Reserve Lomas Barbudal	21 Dec 2007	10.507	-85.404	41	This study
<i>Atta</i>	<i>cephalotes</i>	10088	C. Rabeling	CR071228-01	ethanol	worker	ASU-SIBR00000438	SIBR	C. Rabeling	Nicaragua	Matagalpa	12km N Matagalpa, Selva Negra	28 Dec 2007	12.981	-85.914	1009	This study
<i>Atta</i>	<i>cephalotes</i>	10089	C. Rabeling	CR080109-07	ethanol	worker	ASU-SIBR00000439	SIBR	C. Rabeling	Guatemala	Tikal	National Park Tikal	9 Jan 2008	17.219	-89.615	249	This study
<i>Atta</i>	<i>cephalotes</i>	10091	C. Rabeling	CR040528	ethanol	worker	ASU-SIBR00000440	SIBR	C. Rabeling	Peru	Koshiyapa	Pillcopata	28 May 2004	-12.90045556	-71.4		

Atta	cephakotes	10723	C.A. Barrera	5427	point-mounted	worker	ASU-SIBR00000634	CPDC	M.M. Correa	Brazil	Alagoas	Ibateguara	15 Aug 2004	-8.973902778	-35.93115278	505	This study
Atta	cephakotes	10727	C.A. Barrera	M3L3	point-mounted	worker	ASU-SIBR00000638	MPEG	no data	Brazil	Mato Grosso	UHE Castanheria, Juara	no data	-11.18821389	-57.73005556	244	This study
Atta	cephakotes	10746	J.T Longino	JTL6487.1-s	point-mounted	worker	CASENT0609939	MPEG	J. Longino	Honduras	Olancho	11km NNE Catacamas	15 May 2009	14.94111	-85.84846	1087	This study
Atta	cephakotes	10748	J.T Longino	JTL24Jan819	point-mounted	worker	JTL0000006116	SIBR	J. Longino	Guyana	Demerara-Maha	Timehri	24 Jan 1981	6.5	-58.25	50	This study
Atta	cephakotes	10771	C.A. Barrera	KWG160531-01	ethanol	worker	ASU-SIBR00000578	SIBR	K. Gray	Mexico	Veracruz	18.4 km NE Catemaco, Los Tuxtlas Biological Station	31 May 2016	18.585	-95.074	148	This study
Atta	colombica	3781	A. Ortiz	E523a	point-mounted	worker	ASU-SIBR00000664	SIBR	A. Ortiz	no data	no data	no data	2 Sep 2000	no data	no data	no data	This study
Atta	colombica	9917	U.G. Mueller	UGM030106-16	ethanol	worker	ASU-SIBR00000443	SIBR	U.G. Mueller	no data	no data	no data	6 Jan 2003	no data	no data	no data	This study
Atta	colombica	9918	C.S. Moreau	CSM3338	ethanol	worker	ASU-SIBR00000443	SIBR	C.S. Moreau	Panama	Panama	STRI, Soberania Nat. Park, Pipeline Rd., Gamboa	16 Jan 2015	9.13449	-79.7224	30	This study
Atta	colombica	9954	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000504	SIBR	no data	no data	no data	no data	2003	no data	no data	no data	This study
Atta	colombica	10007	C.A. Barrera	CSM3366	ethanol	worker	ASU-SIBR00000572	SIBR	C.S. Moreau	Panama	Panama	STRI, Barro Colorado Island, Donato & Wheeler trails	15 Jan 2015	9.1647	-71.83768	34	This study
Atta	colombica	10021	J.T Longino	Ba-E-02-2-01-09	ethanol	worker	JTL929461	SIBR	J. Longino	Costa Rica	Limón	Hito-Cerere Biol. Reserve	12 Jun 2015	9.67067	-83.02634	157	This study
Atta	colombica	10744	J.T Longino	JTL0731-s	point-mounted	worker	JTL0000006118	SIBR	J. Longino	Colombia	Magdalena	Tayrona National Park, Cañaveral	11 Agu 1985	11.31666667	-73.93333333	50	This study
Atta	colombica	10745	J.T Longino	JTL8521	point-mounted	worker	CASENT0635784	SIBR	J. Longino	Costa Rica	Alajuela	Peñas Blancas river, Alajuela	30 Dec 2013	10.36081	-84.64278	460	This study
Atta	goliae	9900	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000415	SIBR	H. Vasconcelos	Brazil	Minas Gerais	Parque Linear do Rio Uberabinha, Uberlândia	Jul 2018	-18.91950556	-48.305	788	This study
Atta	insularis	3712	C. Rabeling	CR050315-03	point-mounted	worker	ASU-SIBR00000665	SIBR	C. Rabeling	Cuba	Artemisa	8km N Surgidero de Batabano, La Serafina	15 Mar 2005	22.7575	-82.279	24	Li et al. (2018)
Atta	insularis	10025	C. Rabeling	CR050317-01	point-mounted	worker	ASU-SIBR00000445	SIBR	C. Rabeling	Cuba	Mayaguez	4km NE Guines Nat. Roadside	18 Mar 2005	22.8699	-82.0021	77	This study
Atta	insularis	10026	C. Rabeling	CR050319-01	point-mounted	worker	ASU-SIBR00000445	SIBR	C. Rabeling	Cuba	Cienfuegos	Castillo de Jagua	19 Mar 2005	22.0706	-80.464	39	This study
Atta	insularis	10027	J.T Longino	RSA2012-007	point-mounted	worker	CASENT0629840	SIBR	R.S. Anderson	Cuba	Santiago de Cuba	Gran Piedra Nat. Park, Santiago de Cuba	26 Jan 2012	20.011	-75.673	545	This study
Atta	laevigata	3842	C. Rabeling	CR131115-28	ethanol	worker	ASU-SIBR00000666	SIBR	C. Rabeling	Brazil	DF	IBGE Ecol. Reserve, Brasília	15 Nov 2013	-15.9483	-47.8788	1127	This study
Atta	laevigata	9902	L.D.M. Rodriguez	ANTC46305	ethanol	worker	ASU-SIBR00000420	SIBR	A. Arnhold	Brazil	Minas Gerais	Linear do Rio Uberabinha Park, Uberlândia	31 Mar 2014	-17.2636	-43.7051	825	This study
Atta	laevigata	9919	M. Bacci Jr	MB161028-02	ethanol	worker	ASU-SIBR00000448	SIBR	M. Bacci	Brazil	Minas Gerais	Paraopeba	28 Oct 2016	-19.283584	-44.490269	711	This study
Atta	laevigata	9920	A. Arnhold	ANTC46307	ethanol	worker	ASU-SIBR00000449	SIBR	A. Arnhold	Brazil	Minas Gerais	João pinheiro	9 Apr 2014	-17.65114	-46.55711	559	This study
Atta	laevigata	9921	A. Arnhold	ANTC46308	ethanol	worker	ASU-SIBR00000450	SIBR	A. Arnhold	Brazil	Minas Gerais	Montes Claros	1 Apr 2014	-16.59761	-44.02272	915	This study
Atta	laevigata	9922	R. Carvalho	no data	ethanol	worker	ASU-SIBR00000451	SIBR	R. Carvalho	Brazil	Minas Gerais	Uberlândia	Jan 2018	-18.88618889	-48.38237778	843	This study
Atta	laevigata	9923	G. Santiago	PIQ1A18-A	ethanol	worker	ASU-SIBR00000452	SIBR	G. Santiago	Brazil	Minas Gerais	Pandeirois	7 Jan 2016	-15.49948611	-44.76109444	509	This study
Atta	laevigata	9924	C.A. Barrera	CAB170704-02	ethanol	worker	ASU-SIBR00000453	SIBR	C.A. Barrera	Brazil	São Paulo	UNESP Campus, Rio Claro	4 Jul 2017	-22.39516944	-47.54229167	612	This study
Atta	laevigata	9925	M. Nickele	ANTC46309	ethanol	worker	ASU-SIBR00000454	SIBR	M. Nickele	Brazil	Paraná	Moquém Farm, Ventania	22 Mar 2013	-24.1227	-50.21054722	822	This study
Atta	laevigata	9926	M. Nickele	T452	ethanol	worker	ASU-SIBR00000455	SIBR	M. Nickele	Brazil	Mato Grosso do	Santa Maria Farm, Paranaíba	8 Jul 2016	-19.92530556	-51.66653333	495	This study
Atta	laevigata	9927	M. Nickele	A3T3P9	ethanol	worker	ASU-SIBR00000456	SIBR	M. Nickele, W. Reis	Brazil	Mato Grosso do	Nhumirim Farm, Corumbá	14 Jan 2016	-19.10450833	-56.74375278	947	This study
Atta	laevigata	9928	P. Elias	PE180213-01	ethanol	worker	ASU-SIBR00000457	SIBR	P. Elias	Brazil	Pernambuco	Catimbu Nat. Park, Buíque	13 Feb 2018	-8.522416667	-37.24005556	99	This study
Atta	laevigata	9929	C.A. Barrera	CAB180409-01	ethanol	worker	ASU-SIBR00000458	SIBR	C.A. Barrera	Brazil	Amazonas	INPA Campus II, Manaus	9 Apr 2018	-3.095230278	-59.98696972	98	This study
Atta	laevigata	9930	C.A. Barrera	CAB180410-02	ethanol	worker	ASU-SIBR00000459	SIBR	C.A. Barrera	Brazil	Amazonas	MUSA Museum, Manaus	10 Apr 2018	-3.007202778	-59.94026111	109	This study
Atta	laevigata	9931	J. Latkke	no data	ethanol	worker	ASU-SIBR00000462	SIBR	J. Latkke	Venezuela	Anzoátegui	La Leona	1980	9.6355	-64.4567	164	This study
Atta	laevigata	9963	C.A. Barrera	MB161025-02	ethanol	worker	ASU-SIBR00000516	SIBR	M. Bacci	Brazil	Minas Gerais	Paraopeba	25 Oct 2016	-19.304113	-44.51086	707	This study
Atta	laevigata	10000	C.A. Barrera	EV5170716-01	ethanol	worker	ASU-SIBR00000565	SIBR	E.V. Santos	Brazil	Minas Gerais	Carbonita	16 Jul 2017	-17.5075	-42.96833333	730	This study
Atta	laevigata	10014	C.A. Barrera	ANTC46304	ethanol	worker	ASU-SIBR00000419	SIBR	A. Arnhold	Brazil	Minas Gerais	João Pinheiro	9 Apr 2014	-17.29485	-46.16288	544	This study
Atta	laevigata	10039	C.M.S. Bezerra	ANTC46312	ethanol	male	ASU-SIBR00000467	SIBR	C.M.S. Bezerra	Brazil	São Paulo	Bauru	no data	-22.20037	-49.02978	611	This study
Atta	laevigata	10040	C.M.S. Bezerra	ANTC46313	ethanol	queen	ASU-SIBR00000468	SIBR	C.M.S. Bezerra	Brazil	São Paulo	Bauru	no data	-22.2173	-49.00977	588	This study
Atta	laevigata	10041	C.M.S. Bezerra	ANTC46314	ethanol	male	ASU-SIBR00000469	SIBR	C.M.S. Bezerra	Brazil	São Paulo	Botucatu	no data	-22.5025	-48.26156	535	This study
Atta	laevigata	10042	C.M.S. Bezerra	ANTC46315	ethanol	worker	ASU-SIBR00000470	SIBR	C.M.S. Bezerra	Brazil	São Paulo	Botucatu	no data	-22.51074	-48.26172	550	This study
Atta	laevigata	10043	C.M.S. Bezerra	ANTC46316	ethanol	male	ASU-SIBR00000471	SIBR	C.M.S. Bezerra	Brazil	São Paulo	Botucatu	no data	-22.55939	-48.25931	534	This study
Atta	laevigata	10044	C.M.S. Bezerra	ANTC46317	ethanol	worker	ASU-SIBR00000472	SIBR	C.M.S. Bezerra	Brazil	São Paulo	Botucatu	no data	-22.50961	-48.26217	550	This study
Atta	laevigata	10045	C.M.S. Bezerra	ANTC46318	ethanol	worker	ASU-SIBR00000473	SIBR	C.M.S. Bezerra	Brazil	São Paulo	Bauru	no data	-22.21727	-49.00978	588	This study
Atta	laevigata	10052	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000601	MZUSP	R.R. Silva, C.R.F. Br	Brazil	Bahia	Mata São João, Sapiranga Reserve	28 Jul 2001	-12.55813889	-38.04311111	61	This study
Atta	laevigata	10058	B.H. Dietz	no data	ethanol	worker	ASU-SIBR00000593	MZUSP	B.H. Dietz	Brazil	São Paulo	São José Rio Preto	17 May 1996	-20.78422222	-49.34634722	482	This study
Atta	laevigata	10065	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000613	MZUSP	R.R. Silva, R.M. Fei	Brazil	Tocantins	Babaculândia	22 Feb 2006	-7.038611111	-47.86761111	447	This study
Atta	laevigata	10075	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000623	MZUSP	R. Silvestre, R.R. Si	Brazil	São Paulo	Jatál Ecological Reserve, Luiz Antônio	23 May 1997	-21.6175	-47.76527778	588	This study
Atta	laevigata	10080	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000624	INPA	A.Y. Harada	Brazil	Mato Grosso	Bindá, Chapada dos Guimarães	23 Nov 1983	-15.46564444	-54.77366667	87	This study
Atta	laevigata	10081	C. Campos	3.13.1	ethanol	queen	ASU-SIBR00000626	INPA	C. Campos	Brazil	Roraima	INPA, Boa Vista	2006	2.820475	-60.67063889	84	This study
Atta	laevigata	10085	C.M.S. Bezerra	ANTC46319	ethanol	queen	ASU-SIBR00000474	SIBR	C.M.S. Bezerra	Brazil	São Paulo	Botucatu	18 Oct 2009	-22.5088	-48.26326	552	This study
Atta	laevigata	10094	C. Rabeling	CR131115-28	ethanol	worker	ASU-SIBR00000447	SIBR	C. Rabeling	Brazil	DF	IBGE RECOR Ecological Reserve, 36km S Brasília	15 Nov 2013	-15.9483	-47.8788	1127	This study
Atta	laevigata	10095	C. Rabeling	CR131208-04	ethanol	worker	ASU-SIBR00000525	SIBR	C. Rabeling	Brazil	Piauí	trail nr. Park HQ, PN Sete Cidades	8 Dec 2013	-4.0906	-41.7138	202	This study
Atta	laevigata	10096	C. Rabeling	CR131209-03	ethanol	worker	ASU-SIBR00000526	SIBR	C. Rabeling	Brazil	Piauí	trail nr. Park HQ, PN Sete Cidades	9 Dec 2013	-4.1357	-41.7157	221	This study
Atta	laevigata	10099	C. Rabeling	CR170928-05	ethanol	worker	ASU-SIBR00000460	SIBR	C. Rabeling	Brazil	Mato Grosso	Forest path 9.35 km SW Juara	28 Sep 2017	-11.30233	-57.5781	266	This study
Atta	laevigata	10100	C. Rabeling	CR171015-02	ethanol	worker	ASU-SIBR00000461	SIBR	C. Rabeling	Brazil	Mato Grosso	54.5 km N Canarana, Tanguro Farm	15 Oct 2017	-13.07648	-52.38057	398	This study
Atta	laevigata	10703	C.A. Barrera	ANTC46305	ethanol	worker	ASU-SIBR00000421	SIBR	A. Arnhold	Brazil	Minas Gerais	Bocaiúva	31 Mar 2014	-17.2636	-43.7051	825	This study
Atta	laevigata	10704	A. Arnhold	ANTC46306	ethanol	worker	ASU-SIBR00000422	SIBR	A. Arnhold	Brazil	Minas Gerais	Bocaiúva	31 Mar 2014	-17.2636	-43.7051	825	This study
Atta	laevigata	10705	J. Latkke	no data	ethanol	worker	ASU-SIBR00000463	SIBR	J. Latkke	Venezuela	Anzoátegui	La Leona	1980	9.6355	-64.4567	164	This study
Atta	laevigata	10716	J. Chaul	UFV000980	point-mounted	worker	UFV-LABECOL-000980	UFV	Padilha et al.	Brazil	Minas Gerais	Ritópolis	Feb 2012	-21	-44.33333333	1158	This study
Atta	laevigata	10730	C. Rabeling	no data	point-mounted	worker	ASU-SIBR00000446	SIBR	C. Rabeling	Brazil	Mato Grosso do	Botanical Garden, Campo Grande	2003	-20.52139167	-54.584875	576	This study
Atta	laevigata	10736	C.A. Barrera	SES080929-03	point-mounted	worker	ASU-SIBR00000508	SIBR	C. Rabeling	Brazil	Goiás	Pau Brasil Farm, Resv. 19	29 Sep 2008	-15.8211	-51.3982	311	This study
Atta	mexicana	10037	K. Gray	KWG190306-05	ethanol	worker	ASU-SIBR00000475	SIBR	K. Gray	Mexico	Sonora	"Uvalama", near Álamos	6 Mar 2019	27.0266	-108.9749	479	This study
Atta	mexicana	10090	C. Rabeling	CR080104-15	ethanol	worker	ASU-SIBR00000478	SIBR	C. Rabeling	Honduras	Copán	Archaeological Site, Copán Ruinas	4 Jan 2008	14.838	-89.14277	629	This study
Atta	mexicana	10731	C. Rabeling	no data	point-mounted	worker	ASU-SIBR00000476	SIBR	S. Sanchez Peña	México	Nuevo León	Guadalupe	29 May 2000	25.59322222	-100.2176694	729	This study
Atta	mexicana	10732	C. Rabeling	CR060626-06	point-mounted	male	ASU-SIBR00000477	SIBR	C. Rabeling	México	Tamaulipas	Gomes Farias	26 Jun 2006	23.04899	-99.15667	1277	This study
Atta	mexicana	10733	J.T Longino	DJC0048	point-mounted	queen	CASENT0609719	SIBR	D.J. Cox	México	Chiapas	3km SE Cuistepec	18 May 2008	15.71443	-92.93794	1740	This study
Atta	mexicana	10734	J.T Longino	JTL6736.1	point-mounted	worker	CASENT0612702	SIBR	J. Longino	Guatemala	Suchitep	5km S Vol. Atitlán	17 Jun 2009	14.53383	-91.19946	1170	This study
Atta	mexicana	10735	J.T Longino	JTL6937	point-mounted	worker	CASENT0615507	SIBR	J. Longino	Honduras	Jr. Morazan	E.A.P. Zamorano	30 Apr 2010	14.01297	-87.00795	800	This study
Atta	opaciceps	3782	C. Rabeling	IS060307-01	point-mounted	worker	ASU-SIBR00000667	SIBR	no data	Brazil	Sergipe	Aracaju	07 Mar 2006	-10.87968333	-37.065025	4	This study
Atta	opaciceps	9932	M. Nickele	ANTC46320	ethanol	worker	ASU-SIBR00000479	SIBR	M. Nickele, W. Reis	Brazil	Ceará	Jul	4 Jul 2012	-4.748111111	-38.74002778	117	This study
Atta	opaciceps	9933	C. Knoechelmann, P. Elias, L.	CMK171108-01	ethanol	worker	ASU-SIBR00000480										

Atta	robusta	9938	A. Silva	AS20070112-1	ethanol	worker	ASU-SIBR00000485	SIBR	A. Silva	Brazil	Espírito Santo	São Mateus	12 Jan 2007	-18.78805556	-39.76583333	4	This study
Atta	robusta	9939	C.A. Barrera	CAB170923-01	ethanol	worker	ASU-SIBR00000486	SIBR	C.A. Barrera	Brazil	Espírito Santo	Regência, Linhares	23 Sep 2017	-19.63558889	-39.82493611	7	This study
Atta	robusta	9940	A. Silva	AS20070112-6	ethanol	worker	ASU-SIBR00000487	SIBR	A. Silva	Brazil	Espírito Santo	São Mateus	12 Jan 2007	-18.7695	-39.75025	29	This study
Atta	saltenis	9947	P. Ward	PSW12342	ethanol	worker	ASU-SIBR00000494	SIBR	P. Ward	Bolivia	Santa Cruz	Charagua, Perforación	12 Dec 1993	-19.91666667	-62.56666667	470	This study
Atta	cf. saltenis	10092	C. Rabeling	CR151029-18	ethanol	worker	ASU-SIBR00000552	SIBR	C. Rabeling	Paraguay	Boquerón	PN Teniente Enciso	29 Oct 2015	-21.20595	-61.65749	257	This study
Atta	saltenis	10707	P. Ward	PSW12342	ethanol	worker	ASU-SIBR00000495	SIBR	P. Ward	Bolivia	Santa Cruz	Charagua, Perforación	13 Dec 1993	-19.91666667	-62.56666667	470	This study
Atta	sexdens	3714	C. Rabeling	CR120321-07	point-mounted	worker	ASU-SIBR00000670	SIBR	C. Rabeling	Brazil	São Paulo	Rio Claro	21 Mar 2012	-22.3965	-47.5444	633	This study
Atta	sexdens	3715	C. Rabeling	CR131029-23	point-mounted	worker	ASU-SIBR00000671	SIBR	M. Bollazzi, C. Rabe	Uruguay	Rivera	Zanja Honda	29 Oct 2013	-31.248	-55.732	184	This study
Atta	sexdens	3783	C. Rabeling	E510	point-mounted	worker	ASU-SIBR00000672	SIBR	A. Ortiz, M. Bacci	Brazil	Amazonas	Manaus	no data	-3.10368889	-59.97047222	77	This study
Atta	sexdens	3784	C. Rabeling	E393	point-mounted	worker	ASU-SIBR00000673	SIBR	A. Ortiz, M. Bacci	Brazil	São Paulo	Campus USP, Ribeirão Preto	no data	-21.16828333	-47.852475	574	This study
Atta	sexdens	3787	C. Rabeling	JM061010-01	point-mounted	worker	ASU-SIBR00000674	SIBR	J. Martins	Brazil	Rio Grande do S	Santa Maria	10 Oct 2006	-29.665787	-54.033274	150	This study
Atta	sexdens	3788	C. Rabeling	JM061010-06	point-mounted	worker	ASU-SIBR00000675	SIBR	J. Martins	Brazil	Rio Grande do S	Santa Maria	10 Oct 2006	-29.663621	-54.033627	144	This study
Atta	sexdens	8168	S.E. Solomon	SES080912-03	point-mounted	worker	USNMNT01125098	USNM	S.E. Solomon	Brazil	Mato Grosso do	São Bento Farm, Capão 3	12 Sep 2008	-19.50146	-57.01016	88	This study
Atta	sexdens	9948	C.A. Barrera	ANTC46324	ethanol	worker	ASU-SIBR00000492	SIBR	P.R. de Souza	Brazil	Mato Grosso do	Patolá Farm, Carandazal. Campo Grande	8 Mar 2012	-21.70008333	-57.11880556	99	This study
Atta	sexdens	9948	C.A. Barrera	CAB170910-01	ethanol	worker	ASU-SIBR00000496	SIBR	C.A. Barrera	Brazil	Rio De Janeiro	REGUA, Cachoeiras de Macacu	10 Sep 2017	-22.44497222	-42.77514722	37	This study
Atta	sexdens	9949	C.A. Barrera	CAB171006-03	ethanol	worker	ASU-SIBR00000497	SIBR	C.A. Barrera	Brazil	Mato Grosso	São Nicolau Farm, Cotriguaçu	6 Oct 2017	-9.855	-58.24856667	224	This study
Atta	sexdens	9950	C.A. Barrera	E676	ethanol	worker	ASU-SIBR00000500	SIBR	no data	Brazil	Mato Grosso	Ponte Branca	19 Jul 2003	-16.69008056	-52.90537778	455	This study
Atta	sexdens	9952	C.A. Barrera	CAB180410-01	ethanol	worker	ASU-SIBR00000502	SIBR	C.A. Barrera	Brazil	Amazonas	INPA Campus II, Manaus	10 Apr 2018	-3.097011111	-59.98861667	93	This study
Atta	sexdens	9955	C.A. Barrera	E672	ethanol	worker	ASU-SIBR00000505	SIBR	no data	Brazil	DF	Minas Brasília Tênis Club, Brasília	12 Jul 2003	-15.75305556	-47.86875	1017	This study
Atta	sexdens	9956	C.A. Barrera	E673	ethanol	worker	ASU-SIBR00000506	SIBR	no data	Brazil	Goiás	Jatãl Termas Club , Jatãl	2003	-18.05113611	-51.70050833	714	This study
Atta	sexdens	9957	C.A. Barrera	E685	ethanol	worker	ASU-SIBR00000507	SIBR	no data	Brazil	Goiás	Vitória Farm, Itapaci	2003	-14.91383333	-49.98969444	582	This study
Atta	sexdens	9958	A. Rodrigues	AR091021-01	ethanol	worker	ASU-SIBR00000510	SIBR	A. Rodrigues	Brazil	Tocantins	Palmas	21 Oct 2009	-10.17718333	-48.30566667	330	This study
Atta	sexdens	9959	C.A. Barrera	CAB170704-01	ethanol	worker	ASU-SIBR00000511	SIBR	C.A. Barrera	Brazil	São Paulo	Recife Campus, Rio Claro	4 Jul 2017	-22.39593056	-47.54388889	627	This study
Atta	sexdens	9960	A. Rodrigues	AR090323-01	ethanol	worker	ASU-SIBR00000512	SIBR	A. Rodrigues	Brazil	São Paulo	Corumbatai	23 Mar 2009	-22.29085	-47.65298333	650	This study
Atta	sexdens	9961	M. Bacci Jr	E892	ethanol	worker	ASU-SIBR00000513	SIBR	M. Bacci Jr	Brazil	Pernambuco	Recife	4 Oct 2004	-8.06033056	-34.90165933	23	This study
Atta	sexdens	9962	M. Nicklele	ANTC46325	ethanol	worker	ASU-SIBR00000515	SIBR	M. Nicklele	Brazil	Paraná	Arapoti	1 Jul 2014	-24.13505556	-50.08647222	812	This study
Atta	sexdens	9964	A. Arnhold	ANTC46326	ethanol	worker	ASU-SIBR00000517	SIBR	A. Arnhold	Brazil	Minas Gerais	João pinheiro	9 Apr 2014	-17.66143	-46.57152	555	This study
Atta	sexdens	9965	A. Arnhold	ANTC46328	ethanol	worker	ASU-SIBR00000519	SIBR	A. Arnhold	Brazil	Minas Gerais	Augusto de Lima	4 Apr 2014	-17.84226	-44.43163	1099	This study
Atta	sexdens	9966	A. Arnhold	ANTC46329	ethanol	worker	ASU-SIBR00000520	SIBR	A. Arnhold	Brazil	Minas Gerais	Bocaiúva	31 Mar 2014	-17.27651	-43.72079	811	This study
Atta	sexdens	9967	H. Vasconcelos	no data	ethanol	worker	ASU-SIBR00000521	SIBR	H. Vasconcelos	Brazil	Minas Gerais	Linear do Rio Uberabinha Park, Uberlândia	Jul 2018	-18.91505556	-48.305	788	This study
Atta	sexdens	9968	G. Santiago	PQ31A3-A	ethanol	worker	ASU-SIBR00000522	SIBR	G. Santiago	Brazil	Minas Gerais	Pandeirois	7 Jan 2016	-15.49948611	-44.76109444	509	This study
Atta	sexdens	9969	G. Santiago	PQ21A15-B	ethanol	worker	ASU-SIBR00000523	SIBR	G. Santiago	Brazil	Minas Gerais	Pandeirois	7 Jan 2016	-15.49948611	-44.76109444	509	This study
Atta	sexdens	9971	C.A. Barrera	E482	ethanol	worker	ASU-SIBR00000527	SIBR	no data	Panama	no data	no data	2002	no data	no data	no data	This study
Atta	sexdens	9972	M. Nicklele	ANTC46330	ethanol	worker	ASU-SIBR00000528	SIBR	M. Nicklele, W. Reis	Brazil	Pará	São Domingos do Araguaia	14 Oct 2012	-5.597083333	-48.46544444	149	This study
Atta	sexdens	9973	J. Martins	JM061010-03	ethanol	worker	ASU-SIBR00000529	SIBR	J. Martins	Brazil	Rio Grande do S	Santa Maria	10 Oct 2006	-29.70947222	-53.79838333	284	This study
Atta	sexdens	9974	J. Martins	JM061010-11	ethanol	worker	ASU-SIBR00000530	SIBR	J. Martins	Brazil	Rio Grande do S	Restinga Seca	10 Oct 2006	-28.220875	-54.33870556	284	This study
Atta	sexdens	9976	R.M. Louzada	RML010405-02	ethanol	worker	ASU-SIBR00000533	SIBR	R.M. Louzada	Brazil	Paraná	INPACEL, Arapoti	5 Apr 2001	-24.04035833	-50.45619444	763	This study
Atta	sexdens	9977	M. Nicklele	ANTC46331	ethanol	worker	ASU-SIBR00000534	SIBR	M. Nicklele, W. Reis	Brazil	Paraná	São Mateus do Sul	2018	-24.24052778	-50.50496667	935	This study
Atta	sexdens	9978	S.L. Arcuri	SLA111012-01	ethanol	worker	ASU-SIBR00000535	SIBR	S.L. Arcuri	Brazil	São Paulo	Botucatu	12 Oct 2011	-22.84405	-48.43476667	803	This study
Atta	sexdens	9979	M. Nicklele	T190	ethanol	worker	ASU-SIBR00000536	SIBR	M. Nicklele	Brazil	Mato Grosso do	Dois Irmãos, Inocência	12 Agu 2016	-19.93056667	-51.65348611	495	This study
Atta	sexdens	9980	M. Nicklele	ANTC46332	ethanol	worker	ASU-SIBR00000537	SIBR	M. Nicklele	Brazil	Paraná	Arapoti	1 Jul 2014	-24.14241667	-50.09591667	847	This study
Atta	sexdens	9981	M. Nicklele	AI177F1	ethanol	worker	ASU-SIBR00000538	SIBR	M. Nicklele	Brazil	Paraná	Foz do Iguaçu	9 Jan 2017	-25.24694444	-54.42277778	241	This study
Atta	sexdens	9982	M. Nicklele	CAB180220-01	ethanol	worker	ASU-SIBR00000539	SIBR	M. Nicklele, W. Reis	Brazil	Paraná	Telemarc Borba	20 Feb 2018	-24.24052778	-50.50496667	935	This study
Atta	sexdens	9989	M. Nicklele	ANTC46333	ethanol	worker	ASU-SIBR00000554	SIBR	M. Nicklele	Brazil	Santa Catarina	Campos Belo do Sul	1 Nov 2014	-27.96010833	-50.81311944	949	This study
Atta	sexdens	9995	L.D.M. Rodriguez	no data	ethanol	worker	ASU-SIBR00000560	SIBR	G. Melo	Brazil	Pará	Enxada de Moraes square, Belém	6 Sep 2017	-1.437577778	-48.4787	14	This study
Atta	sexdens	10001	C.A. Barrera	PS181009-02	ethanol	worker	ASU-SIBR00000566	SIBR	P. Sena, M.Pessoa	Brazil	Pernambuco	UFPR Campus, Recife	9 Oct 2018	-8.013888889	-34.94972222	16	This study
Atta	sexdens	10002	C.A. Barrera	PS181029-01	ethanol	worker	ASU-SIBR00000567	SIBR	P. Sena, M.Pessoa	Brazil	Pernambuco	UFPR Campus, Recife	29 Oct 2018	-8.016666667	-34.94638889	22	This study
Atta	sexdens	10010	L.D.M. Rodriguez	no data	ethanol	worker	ASU-SIBR00000575	SIBR	J. Chaul	Perú	Madre de Dios	Tambopata Nat. Reserve, Sachavacayoc	31 Jul 2012	-12.85583333	-69.36194444	201	This study
Atta	sexdens	10011	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000576	SIBR	G. Alarcon	Perú	Junin, Chanchar	San José Farm, La Merced	27 Dec 2018	-11.06863333	-75.34540833	974	This study
Atta	sexdens	10022	L.C. Forti	5183	point-mounted	worker	ASU-SIBR00000582	CPDC	L.C. Forti	Brazil	Mato Grosso	Barra das Garças	Oct 1996	-15.77666667	-52.56222222	402	This study
Atta	sexdens	10049	C.A. Barrera	A10P1	ethanol	worker	ASU-SIBR00000598	MZUSP	no data	Brazil	Rondonia	Abunã A10P1 area, Porto Velho	12 Jan 2014	-9.59666667	-65.36555556	109	This study
Atta	sexdens	10051	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000600	MZUSP	Brandão, Diniz, Oliv	Brazil	Bahia	M. Indica Farm, Maracás	29 Nov 1990	-13.529175	-40.55308611	719	This study
Atta	sexdens	10054	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000603	MZUSP	C.R.F. Brandão et. I	Brazil	São Paulo	P. E. Serra do Mar, Picinguaba, Ubatuba	4 Apr 2001	-23.33611111	-44.83758333	101	This study
Atta	sexdens	10057	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000606	MZUSP	B.H. Dietz	Brazil	São Paulo	Iporanga	10 Sep 2000	-24.58648611	-49.59787778	120	This study
Atta	sexdens	10060	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000608	MZUSP	R.R. Silva, F. Eberh	Brazil	Paraná	João Pinheiro	2 Aug 2002	-27.14019444	-54.85922222	38	This study
Atta	sexdens	10062	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000610	MZUSP	Gilverson, Dietz, Car	Brazil	Goiás	Serra da Mesa, Colinas do Sul	15 Dec 1995	-14.01666667	-48.2	447	This study
Atta	sexdens	10063	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000611	MZUSP	R. Silva, R.M. Feito	Brazil	Tocantins	Cerrado and mata, Araguacema	30 Nov 2005	-8.810788889	-49.55468333	169	This study
Atta	sexdens	10064	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000612	MZUSP	R. Silva, R.M. Feito	Brazil	Tocantins	Cerrado and mata, Araguacema	30 Nov 2005	-8.810788889	-49.55468333	169	This study
Atta	sexdens	10067	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000615	MZUSP	F.A. Esteve	Brazil	Mato Grosso do	Rio Brilhante	20 Jan 2008	-21.81641667	-54.53066389	306	This study
Atta	sexdens	10068	C.A. Barrera	P19-60-8	ethanol	worker	ASU-SIBR00000616	MZUSP	N. Aristizábal, E. Rc	Brazil	Minas Gerais	Guaxupé	28 Mar 2015	-21.32611111	-46.68055556	925	This study
Atta	sexdens	10079	C.A. Barrera	no data	ethanol	worker	ASU-SIBR00000624	MZUSP	no data	Peru	Loreto	Lenora Herrera Station, Iquitos	23 Jan 2011	-4.898611111	-73.65011111	123	This study
Atta	sexdens	10082	C.A. Barrera	11004	ethanol	worker	ASU-SIBR00000627	INPA	no data	Brazil	Roraima	Viruá National Park, Caracará	28 Feb 2007	1.293752778	-61.15564722	55	This study
Atta	sexdens	10701	C. Rabeling	CR170928-04	ethanol	worker	ASU-SIBR00000498	SIBR	C. Rabeling	Brazil	Mato Grosso	Forest path 9.35 km SW Juara	28 Sep 2017	-11.30233	-57.5781	266	This study
Atta	sexdens	10702	C. Rabeling	CR171015-01	ethanol	worker	ASU-SIBR00000499	SIBR	C. Rabeling	Brazil	Mato Grosso	54.5 km N Canarana, Tanguro Farm	15 Oct 2017	-13.07648	-52.38057	398	This study
Atta	sexdens	10706	A. Arnhold	ANTC46327	ethanol	worker	ASU-SIBR00000518	SIBR	A. Arnhold	Brazil	Minas Gerais	Augusto de Lima	4 Apr 2014	-17.97251	-44.387	1143	This study
Atta	sexdens	10709	C.A. Barrera	Pit CVM 16 Mata	ethanol	worker	ASU-SIBR00000563	SIBR	no data	Brazil	Pará	Jari	23 Feb	-0.920186111	-52.46953056	20	This study
Atta	sexdens	10714	J. Chaul	UFV000937	point-mounted	worker	UFV-LABECOL-000937	UFV	J. Chaul	Brazil	Espírito Santo	Anchieta	5 May 2012	-20.74642194	-40.65481611	18	This study
Atta	sexdens	10715	J. Chaul	no data	point-mounted	worker	INTVVB1038266	UFV	J.L.B. Lopez	Brazil	Espírito Santo	Ouro Preto Farm, Sooretama	13 May 2014	-19.08333333	-40.16666667	83	This study
Atta	sexdens	10724	C.A. Barrera	no data	point-mounted	worker	ASU-SIBR00000635	MPEG	R.R. Silva, R.M. Fei	Brazil	Maranhão	Planalto Farm, Estreito	22 Feb 2006	-6.59805556	-47.414	206	This study
Atta	sexdens	10726	C.A. Barrera	no data	point-mounted	worker	ASU-SIBR00000637	MPEG	F.V. Silva	Brazil	Maranhão	Imperatriz	13 Jul 2015	-5.51055556	-47.47944444	139	This study
Atta	sexdens	10737	C. Rabeling	no data	point-mounted												

Mycetagroicus	triangularis	1493					USNMMENT00529392	USNM		Brazil								Branstetter et al. (2017)
Mycetagroicus	triangularis	5365	C. Rabeling	CR131122-09	point-mounted	worker	ASU-SIBR00000806	SIBR	C. Rabeling	Brazil	DF	IBGE RECOR Ecological Reserve, Campo Sujo at Ponte do Corujão next to Viveiro, Brasília	22 Nov 2013	-15.9381	-47.8961	1055	This study	
Mycetomoellerius	cf. relictus	1497					USNMMENT01125244	USNM		Peru							Ješovnik et al. (2016); Branstetter et al. (2017)	
Mycetomoellerius	opulentus	1469					USNMMENT00443295	USNM		Panama							Ješovnik et al. (2016); Branstetter et al. (2017)	
Mycetomoellerius	opulentus	8120	S.E. Solomon	SES090117-04	point-mounted	worker	USNMMENT00923166	USNM	S.E. Solomon	Brazil	Amazonas	Dimona, 1 ha fragment, 2801 along principal trail, Manaus	17 Jan 2009	-2.33866	-60.10271	85	This study	
Mycetomoellerius	papulatus	1485					USNMMENT00444749	USNM		Argentina							Ješovnik et al. (2016); Branstetter et al. (2017)	
Mycetomoellerius	ruthae	DNAex608	S.E. Solomon	SES090109-07	point-mounted	worker	USNMMENT01130073	USNM	S.E. Solomon	Brazil	Amazonas	km 41, Manaus	9 Jan 2009	-2.44894	-59.7702	115	This study	
Mycetomoellerius	zeteki	1538					USNMMENT01125246	USNM		Panama							Ješovnik et al. (2016); Branstetter et al. (2017)	
Paratrachymyrmex	bugnioni	1472					USNMMENT00308176	USNM		Brazil							Branstetter et al. (2017)	
Paratrachymyrmex	bugnioni	8167	S.E. Solomon	SES090212-03	point-mounted	queen	USNMMENT00923219	USNM	S.E. Solomon	Brazil	Pará	Parauapebas	12 Feb 2009	-6.41503	-49.94954	295	This study	
Paratrachymyrmex	cornetzi	1537					USNMMENT00439347	USNM		Costa Rica							Branstetter et al. (2017)	
Paratrachymyrmex	diversus	1471					USNMMENT00410919	USNM		Brazil							Branstetter et al. (2017)	
Paratrachymyrmex	diversus	8127	S.E. Solomon	SES090115-03	point-mounted	worker	USNMMENT00923164	USNM	S.E. Solomon	Brazil	Amazonas	Dimona, 1 ha fragment, 2801 along principal trail, Manaus	15 Jan 2009	-2.33866	-60.10271	85	This study	
Paratrachymyrmex	intermedius	1470					USNMMENT00304784	USNM		Guyana							Branstetter et al. (2017)	
Sericomyrmex	amabilis	1556					USNMMENT00302294	USNM		Panama							Ješovnik et al. (2016); Branstetter et al. (2017)	
Sericomyrmex	bondari	1551					USNMMENT00921156	USNM		Brazil							Ješovnik et al. (2016); Branstetter et al. (2017)	
Sericomyrmex	mayri	1549					USNMMENT00521938	USNM		Guyana							Ješovnik et al. (2016); Branstetter et al. (2017)	
Sericomyrmex	parvulus	1467					USNMMENT00526245	USNM		Peru							Ješovnik et al. (2016); Branstetter et al. (2017)	
Sericomyrmex	parvulus	1552					USNMMENT00759412	USNM		Brazil							Ješovnik et al. (2016); Branstetter et al. (2017)	
Sericomyrmex	scrobifer	1567					USNMMENT01125115	USNM		Brazil							Ješovnik et al. (2016); Branstetter et al. (2017)	
Sericomyrmex	sp	8178	J. Sosa-Calvo	JSC071001-22	point-mounted	worker	USNMMENT00923215	USNM	J. Sosa-Calvo, T.R.	Colombia	Meta	El Caduceo Farm, San Martín	1 Oct 2007	3.629283333	-73.62568333	364	This study	
Sericomyrmex	sp	8346	J. Sosa-Calvo	JSC170923-10	point-mounted	worker	USNMMENT00923242	USNM	J. Sosa-Calvo, T.R.	Brazil	Pará	Parque Zoolobotânico do Carajás, Parauapebas	23 Sep 2017	-6.06352	-50.05769	684	This study	
Sericomyrmex	sp	8464	J. Sosa-Calvo	JSC170920-08	point-mounted	worker	USNMMENT00923181	USNM	J. Sosa-Calvo, T.R.	Brazil	Pará	Parque Zoolobotânico do Carajás, Parauapebas	20 Sep 2017	-6.04258	-50.0888	678	This study	
Trachymyrmex	arizonensis	1473					CASENT0106047	UCDC		USA							Branstetter et al. (2017)	
Trachymyrmex	arizonensis	5368	C. Rabeling	CR050808-34	point-mounted	worker	ASU-SIBR00000698	SIBR	C. Rabeling	USA	Arizona	Cochise County, Southwestern Research Station, oak-pine-juniper woodland	08 Aug 2005	31.8846	-109.2063	1652	This study	
Trachymyrmex	septentrionalis	1486					USNMMENT00439001	USNM		USA							Branstetter et al. (2017)	
Trachymyrmex	septentrionalis	8341	S.J. Messer	SJM170718-08	point-mounted	worker	USNMMENT00923241	USNM	S.J. Messer	USA	Florida	Highlands County, Archbold Biological Station	17 Sep 2018	27.1825148	-81.339022	0	This study	
Trachymyrmex	smithi	1503					USNMMENT00924133	USNM		USA							Branstetter et al. (2017)	
Xeroltor	explicatus	3767	C. Rabeling	CR151031-07	point-mounted	worker	ASU-SIBR00000700	SIBR	C. Rabeling, T.R. Schultz, J. Sosa-Calvo, A. Jesovnik, R. Dahan	Paraguay	Boquerón	Teniente Enciso Nacional Park	31 Oct 2015	-21.20601	-61.65737	264	This study	

*Voucher Repositories: CPDC: Centro de Pesquisas do Cacau; ICBS: Instituto de Ciências Biológicas e da Saúde; MPEG: Museu Paraense "Emílio Goeldi"; MZUSP: Museum of Zoology at the University of São Paulo; SIBR: Social Insect Biodiversity Repository; UFV: Universidade Federal de Viçosa.

*UCDC: University of California-Davis Collection; USNM: National Museum of Natural History-Smithsonian Institution

***Italic GPS coordinates were estimated in google Earth*

Supplementary Table S2 Summary statistics for the final alignment matrices analyzed.

Alignment	N° of taxa	N° of UCE loci	Alignment length (pb)	Mean length	95% CI	min	max	N° of partitions	PIS	InL	S.E.	Tree length	% missing data	Distinct patterns
Atta273t-70per-unpartitioned	273	2340	2308679	986.61	10.35	202	2354	1	441234	-11485086.98	11889.3292	0.9493	10.68	1386996
Atta273t-70per-byLocus	273	2340	2308679					2340	441234	-11289495.17	11217.0833	1.335	10.68	1386996
Atta273t-70per-SWSC-EN	273	2340	2308679					1520	441234	-10984439.4	10724.0321	1.2819	4.54	1386996
Atta273t-90per-unpartitioned	273	1038	1064781	1025.8	14.59	265	1792	1	208343	-5407481.704	7798.5208	0.8512	6.12	648340
Atta273t-90per-byLocus	273	1038	1064781					1038	208343	-5332952.575	7518.6565	1.0187	6.12	648340
Atta273t-90per-SWSC-EN	273	1038	1064781					774	208343	-5203140.785	7250.2222	1.0793	2.45	648340
Atta73t-70per-unpartitioned	73	2274	2168673	953.68	9.58	208	2260	1	342571	-8263520.933	6325.8231	0.6318	16.79	848122
Atta73t-70per-SWSC-EN-Dati	73	2274	2168673					1039	342571	-7951260.01	6094.2953	0.6771	7.09	848122

Supplementary Table S3 Bioregions data matrix used as input for biogeographical analysis.

Species	North America	Caribbean	Central / NW South America	Guiana Shield	Amazonia	Cerrado	Caatinga	Atlantic Forest	Chaco	Pampas	N° areas		
<i>Atta texana</i>	1	0	0	0	0	0	0	0	0	0	1	A	North America
<i>Atta insularis</i>	0	1	0	0	0	0	0	0	0	0	1	B	Caribbean
<i>Atta mexicana</i>	1	0	1	0	0	0	0	0	0	0	2	C	Central America
<i>Atta colombica</i>	0	0	1	0	1	0	0	0	0	0	2	D	Guiana Shield
<i>Atta cephalotes</i>	1	1	1	1	1	0	0	1	0	0	6	E	Amazonia
<i>Atta saltensis</i>	0	0	0	0	0	1	0	0	1	0	2	F	Cerrado
<i>Atta vollenweideri</i>	0	0	0	0	0	1	0	0	1	1	3	G	Caatinga
<i>Atta goiana</i>	0	0	0	0	0	1	0	0	0	0	1	H	Atlantic Forest
<i>Atta bisphaerica</i>	0	0	0	0	0	1	0	1	0	0	2	I	Chaco
<i>Atta capiguara</i>	0	0	0	0	0	1	0	1	0	0	2	J	Pampas
<i>Atta opaciceps</i>	0	0	0	0	0	1	1	1	0	0	3		
<i>Atta laevigata</i>	0	0	0	1	1	1	1	1	1	0	6	1	Occurrence
<i>Atta robusta</i>	0	0	0	0	0	0	0	1	0	0	1	0	No occurrence
<i>Atta sexdens</i>	0	0	1	1	1	1	1	1	1	1	8		
<i>Acromyrmex ambiguus</i>	0	0	0	0	0	1	0	1	1	1	4		
<i>Acromyrmex aspersus</i>	0	0	0	0	1	1	0	1	1	1	5		
<i>Acromyrmex balzani</i>	0	0	0	0	0	1	0	1	1	1	4		
<i>Acromyrmex coronatus</i>	1	0	1	1	1	1	1	1	1	1	9		
<i>Acromyrmex crassispinus</i>	0	0	0	0	0	1	0	1	1	1	4		
<i>Acromyrmex echinator</i>	1	0	1	0	0	0	0	0	0	0	2		
<i>Acromyrmex insinuator</i>	0	0	1	0	0	0	0	0	0	0	1		
<i>Acromyrmex lundii</i>	0	0	0	0	1	0	0	1	1	1	4		
<i>Acromyrmex octospinosus</i>	1	1	1	1	1	0	0	0	0	0	5		
<i>Amoimymex silvestrii</i>	0	0	0	0	0	0	0	1	1	1	3		
<i>Amoimymex striatus</i>	0	0	0	0	0	0	0	1	1	1	3		
<i>Acromyrmex versicolor</i>	1	0	0	0	0	0	0	0	0	0	1		
<i>Acromyrmex volcanus</i>	0	0	1	0	0	0	0	0	0	0	1		
<i>Mycetagroicus cerradensis</i>	0	0	0	0	0	1	0	1	0	0	2		
<i>Mycetagroicus inflatus</i>	0	0	0	0	1	0	0	0	0	0	1		
<i>Mycetagroicus triangularis</i>	0	0	0	0	0	1	0	1	0	0	2		
<i>Sericomyrmex amabilis</i>	1	0	1	0	1	0	0	0	0	0	3		
<i>Sericomyrmex bondari</i>	0	0	0	1	1	0	0	1	0	0	3		
<i>Sericomyrmex scrobifer</i>	0	0	0	0	0	1	0	1	0	0	2		
<i>Paratrachymyrmex bugnioni</i>	0	1	1	1	1	1	1	0	0	0	6		
<i>Paratrachymyrmex cornetzi</i>	1	1	1	1	1	0	0	1	0	0	6		
<i>Paratrachymyrmex diversus</i>	0	0	0	1	1	0	0	0	0	0	2		
<i>Paratrachymyrmex intermedius</i>	1	0	1	1	0	0	0	0	0	0	3		
<i>Mycetomoellerius cf. relictus</i>	0	1	0	1	1	1	0	1	0	0	5		
<i>Mycetomoellerius opulentus</i>	1	0	1	1	1	0	0	0	0	0	4		
<i>Mycetomoellerius papulatus</i>	0	0	0	0	0	1	0	0	1	0	2		
<i>Mycetomoellerius ruthae</i>	0	1	0	1	1	1	0	0	0	0	4		
<i>Mycetomoellerius zeteki</i>	0	0	1	0	0	0	0	0	0	0	1		
<i>Trachymyrmex arizonensis</i>	1	0	0	0	0	0	0	0	0	0	1		
<i>Trachymyrmex septentrionalis</i>	1	0	0	0	0	0	0	0	0	0	1		
<i>Trachymyrmex smithi</i>	1	0	0	0	0	0	0	0	0	0	1		
<i>Xerolitor explicatus</i>	0	0	0	0	0	1	0	0	1	0	2		

Supplementary Table S4 List of *Atta* species and their distribution in the Americas.

Species	Known distribution	Reference
<i>A. mexicana</i> (Smith, 1858)	Southern USA (southern Arizona, Texas), Mexico, Guatemala, Belize, Honduras, El Salvador, Nicaragua	Borgmeier, 1959; Kempf, 1972; Wilson, 1986; Holldobler & Wilson, 1990; Maes & MacKay, 1993; Fernández & Sendoya, 2004
<i>A. texana</i> (Buckley, 1860)	Southern USA (central and eastern Texas, central northern Louisiana), northeastern Mexico	Borgmeier, 1959; Gonçalves, 1960; Moser, 2006; Sanchez-Peña, 2010; Schowalter & Ring, 2017
<i>A. insularis</i> Guérin, 1844	Cuba	Borgmeier, 1959; Kempf, 1972; Wilson, 1986; Holldobler & Wilson, 1990; Fernández & Sendoya, 2004; Antmap; AntWeb
<i>A. cubana</i> Fontenla, 1995	Cuba	Fontenla Rizo, 1995
<i>A. cephalotes</i> (Linnaeus, 1758)	México (Oaxaca, Vera Cruz, Yucatan), Belize, Honduras, Guatemala, Honduras, Costa Rica, Isla de Cocos, Panama, Trinidad and Tobago, Lesser Antilles, Barbados, Guyana, French Guiana, Suriname, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil (AM, AP, RR, AC, RO, PA, MA, MT, PE, AL, BA)	Borgmeier, 1959; Kempf, 1972; Gonçalves, 1960, 1967; Weber, 1966, 1969; Wilson, 1986; Holldobler & Wilson, 1990; Fernández & Sendoya, 2004; Forti <i>et al.</i> , 2020; Antmap; AntWeb
<i>A. colombica</i> Guérin, 1844	Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia	Borgmeier, 1959; Kempf, 1972; Wilson, 1986; Holldobler & Wilson, 1990; Fernández & Sendoya, 2004; Fernández & Serna, 2019; Antmap; AntWeb
<i>A. saltensis</i> Forel, 1913	Bolivia, Paraguay, Central western and northern Argentina, Brazil (MS)	Daguerre, 1945; Borgmeier, 1959; Weber, 1966 ("A. laevigata"); Kempf, 1972; Wilson, 1986; Holldobler & Wilson, 1990; Farji-Brener & Ruggiero, 1994; Fernández & Sendoya, 2004; Demetrio <i>et al.</i> , 2017
<i>A. vollenweideri</i> Forel, 1893	Bolivia, central and western Paraguay, central northern and northeast Argentina, western Uruguay, western Brazil (RS, MS)	Gonçalves, 1942, 1960, 1971; Daguerre, 1945; Weber, 1966, 1969; Borgmeier, 1959; Kempf, 1972; Kusnezov 1978; Wilson, 1986; Holldobler & Wilson, 1990; Farji-Brener & Ruggiero, 1994; Fernández & Sendoya, 2004
<i>A. goiana</i> Gonçalves, 1942	Brazil (GO, MT, MG)	Gonçalves, 1942, 1971; Borgmeier, 1950, 1959
<i>A. bisphaerica</i> Forel, 1908	Brazil (GO, MG, RJ, SP, BA, PB)	Gonçalves, 1942, 1971; Borgmeier, 1950, 1959; Wilson, 1986; Forti <i>et al.</i> , 2020
<i>A. capiguara</i> Gonçalves, 1944	Paraguay, Brazil (MT, GO, MG, SP, PR, MS)	Gonçalves, 1942, 1960, 1971; Borgmeier, 1950, 1959; Fowler, 1985; Wilson, 1986; Brandão, 1991; Forti <i>et al.</i> , 2020

<i>A. opaciceps</i> Borgmeier, 1939	Brazil (MA, PI, CE, RN, PB, PE, AL, SE, BA)	Borgmeier, 1959; Kempf, 1972; Pires do Prado <i>et al.</i> , 2019; Forti <i>et al.</i> , 2020
<i>A. laevigata</i> (Smith, 1858)	Colombia, Venezuela, French Guiana, Guyana, Suriname, Brazil (AM, RR, AC, RO, PA, TO, MA, PI, CE, PE, AL, SE, BA, MT, GO, MG, RJ, SP, PR), northern Bolivia, Paraguay	Borgmeier, 1959; Kempf, 1972; Wilson, 1986; Holldobler & Wilson, 1990; Fernández & Sendoya, 2004; Forti <i>et al.</i> , 2020
<i>A. robusta</i> Borgmeier, 1939	Brazil (restingas of ES and RJ)	Borgmeier, 1959; Kempf, 1972; Wilson, 1986; Holldobler & Wilson, 1990; Fernández & Sendoya, 2004
<i>A. sexdens</i> (Linnaeus, 1758)	Costa Rica, Panama, Venezuela, Colombia, French Guiana, Guyana, Suriname, Ecuador, Peru, Brazil (AM, RR, AC, RO, AP, PA, MA, PI, CE, RN, PB, PE, AL, SE, BA, GO, MT, MS, MG, ES, RJ, SP, PR, SC, RS), Bolivia, Paraguay, northwestern Argentina, Uruguay	Borgmeier, 1959; Gonçalves, 1967; Kempf, 1972; Wilson, 1986; Holldobler & Wilson, 1990; Fernández & Sendoya, 2004; Forti <i>et al.</i> , 2020
<i>Atta sexdens sexdens</i> (Linnaeus, 1758)	Costa Rica, Panama, Colombia, Venezuela, Guianas, Ecuador, Peru, northern Bolivia, Brazil (AC, RO, RR, AP, AM, PA, MA, PI, CE, RN, PB, PE, AL, SE, BA, MT, GO, MG), Paraguay	Borgmeier, 1959; Gonçalves, 1961, 1967; Kempf, 1972; Forti <i>et al.</i> , 2020
<i>Atta sexdens rubropilosa</i> Forel, 1908	Paraguay, southern Bolivia, Brazil (south MT, GO, MG, ES, RJ, SP, PR), northern Argentina (Misiones)	Borgmeier, 1959; Kempf, 1972; Arruda <i>et al.</i> , 2020 (central GO); Forti <i>et al.</i> , 2020
<i>Atta sexdens piriventris</i> Santschi 1919	Brazil (PR, SC, RS), Argentina (Chaco, Misiones, Tucuman, Santa Fe, northern Corrientes), northwestern Uruguay.	Borgmeier, 1959; Kempf, 1972; Forti <i>et al.</i> , 2020

Supplementary Table S5 List of UCE data collection and sequencing statistics of all taxa sequenced for this study.

Extraction code	Taxon name	Extraction Qubit (ng/μL)	Post PCR Lib Qubit (ng/μL)	Raw reads	n50	n50 length	Total contigs	UCE loci
3501	<i>Acromyrmex ambiguus</i> 3501 UR	4.080	41.60	217507	1074	475	3337	1906
3669	<i>Acromyrmex aspersus</i> 3669 CO	3.770	43.40	819195	1769	726	7880	2362
3524	<i>Acromyrmex coronatus</i> 3524 HO	2.840	50.80	1430762	5174	370	21466	2349
3679	<i>Acromyrmex crassispinus</i> 3679 BR:SP	2.750	24.20	2400772	14887	271	45990	2195
3545	<i>Acromyrmex echinator</i> 3545 GU	4.740	7.00	351278	1643	390	5275	1331
3553	<i>Acromyrmex heyeri</i> 3553 AR	5.710	26.00	2766101	24486	319	78787	2072
3720	<i>Acromyrmex insinuator</i> 3720 PN	12.40	20.10	1249238	10360	278	32992	2396
3593	<i>Acromyrmex lundii</i> 3593 AR	2.040	11.30	655284	2262	388	7083	1687
3851	<i>Amoimyrmex silvestrii</i> 3851 PR	4.20	44.00	2108111	30463	273	84530	2349
3900	<i>Amoimyrmex silvestrii</i> 3900 AR	5.960	36.70	1448659	2998	529	14856	2330
3622	<i>Amoimyrmex striatus</i> 3622 BR:RS	2.790	24.50	416785	1306	399	3840	1723
3644	<i>Acromyrmex volcanus</i> 3644 NI	4.830	53.00	409019	1641	380	5121	1545
3711	<i>Atta bisphaerica</i> 3711 BR:SP	21.90	40.30	2252369	14470	277	46251	2348
9901	<i>Atta bisphaerica</i> 9901 BR:MG	4.190	14.80	1194471	1981	861	10218	2325
9903	<i>Atta bisphaerica</i> 9903 BR:SP	1.060	17.30	1597102	4378	385	20257	2336
10097	<i>Atta bisphaerica</i> 10097 BR:SP	5.870	27.90	2536876	13807	298	50181	2267
10711	<i>Atta bisphaerica</i> 10711 BR:SP	7.590	23.80	3225816	19456	299	67112	2272
9904	<i>Atta capiguara</i> 9904 BR:SP	0.265	7.64	2759960	20078	278	59427	2411
9951	<i>Atta capiguara</i> 9951 BR:MT	0.411	35.40	2221738	11673	290	40500	2347
10750	<i>Atta capiguara</i> 10750 BR:DF	low	16.30	853710	1956	275	5039	2105
9905	<i>Atta cephalotes</i> 9905 BR:PA	3.690	22.80	1802132	4575	379	22937	2304
9906	<i>Atta cephalotes</i> 9906 BR:BA	1.010	9.43	965212	2305	534	9625	2392
9907	<i>Atta cephalotes</i> 9907 BR:BA	1.090	19.70	1279713	2280	754	12359	2344
9909	<i>Atta cephalotes</i> 9909 BR:MT	1.490	18.40	1738252	4738	372	22532	2332
9910	<i>Atta cephalotes</i> 9910 BR:MT	1.490	17.80	2101753	7735	325	32023	2304
9911	<i>Atta cephalotes</i> 9911 CO	0.832	12.80	1299138	2662	585	13230	2362
9912	<i>Atta cephalotes</i> 9912 CO	1.340	15.90	1978519	5377	337	25274	2285
9913	<i>Atta cephalotes</i> 9913 CO	0.174	13.60	2213859	6352	329	29973	2366
9914	<i>Atta cephalotes</i> 9914 CR	1.050	18.40	2334535	10133	303	38517	2298
9915	<i>Atta cephalotes</i> 9915 FG	0.544	15.70	1906096	4853	358	23465	2292
9916	<i>Atta cephalotes</i> 9916 FG	0.994	25.60	2087595	6267	331	27633	2317
9990	<i>Atta cephalotes</i> 9990 BR:AM	0.216	18.80	1417811	4213	317	15706	2381
9991	<i>Atta cephalotes</i> 9991 BR:AM	0.155	14.00	1500809	5621	290	18331	2385
9992	<i>Atta cephalotes</i> 9992 BR:AC	6.970	30.60	2370353	12346	299	44164	2302
9993	<i>Atta cephalotes</i> 9993 BR:AC	1.880	29.00	1319646	2313	735	12267	2337
9994	<i>Atta cephalotes</i> 9994 BR:AP	4.620	34.30	2620929	16953	300	60516	2310
9996	<i>Atta cephalotes</i> 9996 BR:PA	2.030	34.90	2320460	11306	302	41175	2305
9997	<i>Atta cephalotes</i> 9997 BR:PA	1.150	28.90	1831680	5247	344	23704	2313
9999	<i>Atta cephalotes</i> 9999 BR:PA	0.161	5.82	632588	3010	289	8450	2349
10004	<i>Atta cephalotes</i> 10004 EC	4.840	33.00	2006140	6825	325	28698	2313
10005	<i>Atta cephalotes</i> 10005 EC	1.320	32.00	1504597	4523	344	19576	2355
10006	<i>Atta cephalotes</i> 10006 CR	2.020	27.90	2070672	7779	319	32131	2306
10008	<i>Atta cephalotes</i> 10008 PE	4.940	26.00	2328534	12541	296	44433	2286
10009	<i>Atta cephalotes</i> 10009 PE	1.450	11.90	1964370	7284	320	29609	2320
10012	<i>Atta cephalotes</i> 10012 BR:AP	1.010	30.80	3087335	17667	290	59936	2256
10013	<i>Atta cephalotes</i> 10013 CO	1.590	28.80	2067923	4391	375	22247	2274
10015	<i>Atta cephalotes</i> 10015 MX	3.620	25.30	2143951	4112	406	22211	2283
10016	<i>Atta cephalotes</i> 10016 PN	4.110	24.40	2831542	10779	303	42054	2273
10017	<i>Atta cephalotes</i> 10017 CR	2.520	31.30	3204999	19470	290	64908	2285
10018	<i>Atta cephalotes</i> 10018 CR	0.995	21.30	2026971	6662	325	26504	2378
10019	<i>Atta cephalotes</i> 10019 CR	0.098	8.25	1274955	3287	354	13024	2421
10020	<i>Atta cephalotes</i> 10020 NI	1.660	33.30	2649448	8572	306	35094	2283
10028	<i>Atta cephalotes</i> 10028 BR:MT	1.920	23.40	4178131	32329	301	104201	2252
10048	<i>Atta cephalotes</i> 10048 BR:RO	6.060	34.50	1455659	3286	459	15766	2355
10083	<i>Atta cephalotes</i> 10083 BR:RR	1.280	20.50	3089394	22599	272	62494	2430
10084	<i>Atta cephalotes</i> 10084 BR:RR	2.720	24.20	2995115	24205	280	70021	2421
10087	<i>Atta cephalotes</i> 10087 CR	4.270	21.60	6413625	74788	335	236430	2221
10088	<i>Atta cephalotes</i> 10088 NI	2.430	19.30	5025406	48534	310	151461	2262
10089	<i>Atta cephalotes</i> 10089 GU	2.240	18.70	2044689	7478	323	29979	2332

10091	Atta cephalotes 10091 PE	0.596	19.70	1463675	4443	373	18387	2368
10710	Atta cephalotes 10710 BR:PA	0.302	18.50	845723	1904	422	6200	2384
10717	Atta cephalotes 10717 EC	16.10	19.30	1823290	5260	384	24366	2385
10718	Atta cephalotes 10718 EC	9.580	33.60	2555853	16296	289	51599	2368
10723	Atta cephalotes 10723 BR:AL	1.030	15.30	608749	1913	362	5857	2254
10727	Atta cephalotes 10727 BR:MT	8.180	25.00	3213446	22197	298	70961	2367
10746	Atta cephalotes 10746 HO	3.110	32.30	2474216	8956	319	36750	2284
10748	Atta cephalotes 10748 GY	3.060	26.70	1536672	6397	282	19804	2430
10771	Atta cephalotes 10771 MX	1.260	27.50	3198046	22414	297	73338	2334
3781	Atta colombica 3781	20.00	38.00	3246845	27878	281	84600	2301
9917	Atta colombica 9917	0.268	21.50	3007918	20751	286	65784	2315
9918	Atta colombica 9918 PN	1.350	17.10	2841756	16892	293	57270	2298
9954	Atta colombica 9954	0.882	34.60	2490251	12242	292	44501	2275
10007	Atta colombica 10007 PN	1.750	33.00	2127446	9535	305	36920	2301
10021	Atta colombica 10021 CR	1.160	24.60	1863891	4296	371	20062	2362
10744	Atta colombica 10744 CO	1.600	28.70	1961447	7690	313	27926	2386
10745	Atta colombica 10745 CR	9.170	32.90	2959928	19471	295	65637	2328
9900	Atta goiana 9900 BR:MG	0.471	25.60	1794539	5570	352	25541	2331
10025	Atta insularis 10025 CU	2.530	28.90	1900001	4591	358	20928	2366
10026	Atta insularis 10026 CU	1.20	27.60	2611080	12257	291	42332	2350
10027	Atta insularis 10027 CU	2.870	35.80	2505285	9845	302	37957	2316
3842	Atta laevigata 3842 BR:DF	20.50	28.30	1682183	22264	273	62135	2388
9902	Atta laevigata 9902 BR:MG	0.360	7.20	2471967	14193	277	43163	2409
9919	Atta laevigata 9919 BR:MG	0.372	19.90	2546541	11934	296	42351	2330
9920	Atta laevigata 9920 BR:MG	0.096	9.05	795214	1845	498	6732	2389
9921	Atta laevigata 9921 BR:MG	0.375	12.00	1008785	2360	511	9772	2404
9922	Atta laevigata 9922 BR:MG	0.664	21.50	3077318	23427	289	74436	2308
9923	Atta laevigata 9923 BR:MG	0.175	12.10	1479787	3052	480	14829	2348
9924	Atta laevigata 9924 BR:SP	0.288	19.30	1771181	3862	451	20390	2320
9925	Atta laevigata 9925 BR:PR	0.618	13.00	542243	3067	593	15695	1679
9926	Atta laevigata 9926 BR:MS	0.998	17.50	1565254	2994	520	16226	2334
9927	Atta laevigata 9927 BR:MS	0.221	11.90	1012187	2263	573	10341	2378
9928	Atta laevigata 9928 BR:PE	4.520	15.30	2084919	6809	335	29779	2301
9929	Atta laevigata 9929 BR:AM	0.729	14.70	2842698	23656	286	73275	2361
9930	Atta laevigata 9930 BR:AM	0.352	15.80	2389273	13880	297	48001	2325
9931	Atta laevigata 9931 VN	0.110	7.30	1804907	8333	260	22664	2447
9963	Atta laevigata 9963 BR:MG	4.310	33.80	3045172	24344	291	78132	2290
10000	Atta laevigata 10000 BR:MG	0.946	29.40	1766699	6074	341	25672	2321
10014	Atta laevigata 10014 BR:MG	0.448	17.00	1297943	2679	483	11602	2410
10039	Atta laevigata 10039 BR:SP	3.010	19.10	1880493	1714	1271	20198	2383
10040	Atta laevigata 10040 BR:SP	7.750	26.90	1841389	4568	372	22589	2277
10041	Atta laevigata 10041 BR:SP	3.440	30.80	1419021	2193	833	12793	2314
10042	Atta laevigata 10042 BR:SP	7.990	29.40	1825780	4561	377	23052	2282
10043	Atta laevigata 10043 BR:SP	2.910	41.00	1677997	3997	405	20586	2330
10044	Atta laevigata 10044 BR:SP	7.690	35.50	1687570	4086	414	20771	2296
10045	Atta laevigata 10045 BR:SP	3.850	36.00	1679098	3411	475	18986	2289
10052	Atta laevigata 10052 BR:BA	0.153	22.80	839626	2331	375	7915	2361
10058	Atta laevigata 10058 BR:SP	0.479	18.70	1552151	6332	298	20743	2416
10065	Atta laevigata 10065 BR:TO	0.626	18.80	1225417	4229	353	15445	2396
10075	Atta laevigata 10075 BR:SP	0.181	19.50	1120053	3995	322	13403	2392
10080	Atta laevigata 10080 BR:MT	1.250	20.00	2913350	22655	273	64165	2414
10081	Atta laevigata 10081 BR:RR	3.030	27.50	4149832	40930	300	123123	2343
10085	Atta laevigata 10085 BR:SP	4.070	19.60	3829170	21998	311	75422	2273
10094	Atta laevigata 10094 BR:DF	4.050	34.60	2653118	12791	305	48114	2230
10095	Atta laevigata 10095 BR:PI	12.50	45.20	1333968	599	1074	3359	2243
10096	Atta laevigata 10096 BR:PI	2.370	25.30	2841257	19283	293	64495	2272
10099	Atta laevigata 10099 BR:MT	6.240	27.50	2940209	21659	290	71234	2268
10100	Atta laevigata 10100 BR:MT	4.160	34.50	2298891	8584	321	35782	2259
10703	Atta laevigata 10703 BR:MG	1.530	22.60	1639913	6566	304	23098	2389
10704	Atta laevigata 10704 BR:MG	2.570	21.70	1906636	7396	312	27145	2387
10705	Atta laevigata 10705 VN	0.296	16.70	1194506	3746	289	11218	2408
10716	Atta laevigata 10716 BR:MG	1.540	15.70	918165	2648	462	10248	2383
10730	Atta laevigata 10730 BR:MS	1.160	17.70	1516792	4262	375	17082	2371
10736	Atta laevigata 10736 BR:GO	3.560	25.10	3167304	21745	293	68380	2348
10047	Atta mexicana 10047 MX	5.350	32.00	2205433	9646	310	37396	2288

10090	<i>Atta mexicana</i> 10090 HO	1.880	28.90	2447899	9752	312	37918	2244
10731	<i>Atta mexicana</i> 10731 MX	0.272	21.00	1830741	7540	279	22573	2432
10732	<i>Atta mexicana</i> 10732 MX	0.310	19.50	1149083	2715	405	11230	2395
10733	<i>Atta mexicana</i> 10733 MX	0.759	19.20	1863259	6725	319	24793	2390
10734	<i>Atta mexicana</i> 10734 GU	3.90	38.40	3090907	16734	302	56261	2311
10735	<i>Atta mexicana</i> 10735 HO	3.370	31.90	1879146	5746	349	23710	2317
3782	<i>Atta opaciceps</i> 3782 BR:SE	2.540	41.90	4254913	60987	300	177664	2300
9932	<i>Atta opaciceps</i> 9932 BR:CE	0.457	21.10	1306521	3739	374	15555	2410
9933	<i>Atta opaciceps</i> 9933 BR:PE	2.210	18.90	1447392	3157	473	15736	2381
9934	<i>Atta opaciceps</i> 9934 BR:PE	2.440	17.50	1643724	4376	389	20036	2369
9953	<i>Atta opaciceps</i> 9953 BR:AL	0.075	19.00	1208603	2054	673	10522	2376
9970	<i>Atta opaciceps</i> 9970 BR:CE	0.736	23.60	3847233	43091	299	129924	2332
10003	<i>Atta opaciceps</i> 10003 BR:CE	0.550	34.20	1865017	7590	301	29217	2329
10719	<i>Atta opaciceps</i> 10719 BR:BA	0.590	22.20	1288232	4454	280	13063	2406
10720	<i>Atta opaciceps</i> 10720 BR:BA	0.194	22.40	1540236	5352	271	14949	2398
10721	<i>Atta opaciceps</i> 10721 BR:AL	0.361	19.70	1949621	11320	270	32379	2432
10722	<i>Atta opaciceps</i> 10722 BR:SE	0.579	17.30	791681	2174	291	5959	2195
3785	<i>Atta robusta</i> 3785 BR:ES	27.40	34.00	3409345	32022	283	95814	2330
3786	<i>Atta robusta</i> 3786 BR:ES	14.10	35.40	3531666	39380	287	115670	2321
9935	<i>Atta robusta</i> 9935 BR:ES	0.643	21.20	1659446	4270	385	19921	2355
9936	<i>Atta robusta</i> 9936 BR:ES	0.666	22.00	2243115	11214	300	40900	2328
9937	<i>Atta robusta</i> 9937 BR:ES	3.720	21.00	2159468	7865	325	32557	2310
9938	<i>Atta robusta</i> 9938 BR:ES	3.440	19.50	2123808	6196	346	28530	2273
9939	<i>Atta robusta</i> 9939 BR:ES	0.520	19.10	5289892	72149	322	219200	2263
9940	<i>Atta robusta</i> 9940 BR:ES	3.080	20.20	2876697	17238	296	59162	2284
9947	<i>Atta saltensis</i> 9947 BO	0.252	9.67	3667395	26979	288	79534	2392
10092	<i>Atta cf. saltensis</i> 10092 PR	1.710	24.30	3178847	23379	295	77293	2254
10707	<i>Atta saltensis</i> 10707 BO	1.690	26.00	2758013	16697	292	54137	2377
3714	<i>Atta sexdens</i> 3714 BR:SP	31.30	36.90	2651620	18876	278	59182	2324
3715	<i>Atta sexdens</i> 3715 UR	21.50	35.30	1492415	4424	320	18891	2367
3783	<i>Atta sexdens</i> 3783 BR:AM	12.40	39.50	2781543	23194	281	70779	2335
3784	<i>Atta sexdens</i> 3784 BR:SP	10.50	33.20	2687399	19616	277	60290	2326
3787	<i>Atta sexdens</i> 3787 BR:RS	9.950	33.10	3083123	30585	278	90331	2309
3788	<i>Atta sexdens</i> 3788 BR:RS	17.90	33.10	2866092	25765	271	73809	2360
8168	<i>Atta sexdens</i> 8168 BR:MS	3.090	38.40	3682686	26276	283	80624	2305
9945	<i>Atta sexdens</i> 9945 BR:MS	0.070	4.360	300654	1553	318	4179	2234
9948	<i>Atta sexdens</i> 9948 BR:RJ	1.250	34.60	2282884	8579	301	34001	2283
9949	<i>Atta sexdens</i> 9949 BR:MT	1.350	29.60	2839367	19474	283	62449	2287
9950	<i>Atta sexdens</i> 9950 BR:MT	2.180	30.60	2254683	10751	293	39059	2297
9952	<i>Atta sexdens</i> 9952 BR:AM	1.600	38.30	2051158	7763	307	31652	2284
9955	<i>Atta sexdens</i> 9955 BR:DF	0.572	39.40	1665782	3968	368	19684	2321
9956	<i>Atta sexdens</i> 9956 BR:GO	0.138	27.20	1724182	3903	383	19018	2306
9957	<i>Atta sexdens</i> 9957 BR:GO	0.389	27.10	1411233	2388	651	12913	2331
9958	<i>Atta sexdens</i> 9958 BR:TO	0.325	20.50	1832815	6634	317	25766	2366
9959	<i>Atta sexdens</i> 9959 BR:SP	0.974	31.00	1507265	2417	711	14037	2305
9960	<i>Atta sexdens</i> 9960 BR:SP	0.913	25.40	2671410	16694	293	54881	2333
9961	<i>Atta sexdens</i> 9961 BR:PE	1.40	29.70	780636	513	3359	6818	2330
9962	<i>Atta sexdens</i> 9962 BR:PR	1.720	26.00	2987649	23926	293	75301	2336
9964	<i>Atta sexdens</i> 9964 BR:MG	0.169	13.10	1755986	7142	303	24760	2384
9965	<i>Atta sexdens</i> 9965 BR:MG	0.059	7.65	3866942	34336	284	98814	2399
9966	<i>Atta sexdens</i> 9966 BR:MG	1.280	15.00	1785164	8561	286	26871	2418
9967	<i>Atta sexdens</i> 9967 BR:MG	1.450	35.50	3235997	28365	292	88292	2290
9968	<i>Atta sexdens</i> 9968 BR:MG	0.20	12.00	2539996	15845	290	47944	2418
9969	<i>Atta sexdens</i> 9969 BR:MG	0.424	18.30	1252458	2747	499	12830	2393
9971	<i>Atta sexdens</i> 9971 PN	3.110	39.80	2875745	6982	462	54904	2346
9972	<i>Atta sexdens</i> 9972 BR:PA	0.804	21.30	1932322	8824	297	30349	2376
9973	<i>Atta sexdens</i> 9973 BR:RS	0.555	19.40	2648045	14677	295	50093	2330
9974	<i>Atta sexdens</i> 9974 BR:RS	0.682	26.80	3025294	26106	289	81280	2300
9976	<i>Atta sexdens</i> 9976 BR:PR	0.158	18.70	656368	4561	546	22450	1088
9977	<i>Atta sexdens</i> 9977 BR:PR	2.520	30.10	2694298	12459	318	51289	2328
9978	<i>Atta sexdens</i> 9978 BR:SP	0.919	18.70	1759680	8309	286	26414	2418
9979	<i>Atta sexdens</i> 9979 BR:MS	0.367	28.50	2307860	12846	293	43813	2322
9980	<i>Atta sexdens</i> 9980 BR:PR	2.170	21.30	2490845	18147	286	55604	2370
9981	<i>Atta sexdens</i> 9981 BR:PR	1.560	18.30	1667600	4227	379	18830	2351
9982	<i>Atta sexdens</i> 9982 BR:PR	1.160	24.90	2912227	21303	293	69275	2298

9989	<i>Atta sexdens</i> 9989 BR:SC	0.857	26.10	1956577	8074	308	30519	2351
9995	<i>Atta sexdens</i> 9995 BR:PA	3.280	33.20	1952117	7454	317	30264	2297
10001	<i>Atta sexdens</i> 10001 BR:PE	2.570	37.30	2534456	16725	294	56075	2336
10002	<i>Atta sexdens</i> 10002 BR:PE	2.240	29.70	1980186	6620	337	28238	2304
10010	<i>Atta sexdens</i> 10010 PE	0.196	11.20	277557	965	445	2808	2050
10011	<i>Atta sexdens</i> 10011 PE	0.227	31.40	1818875	7622	325	29249	2333
10022	<i>Atta sexdens</i> 10022 BR:MT	0.914	19.40	857964	1953	327	5556	2354
10049	<i>Atta sexdens</i> 10049 BR:RO	0.618	13.50	593006	1662	413	5533	2222
10051	<i>Atta sexdens</i> 10051 BR:BA	0.176	20.50	1064320	2974	328	9641	2376
10054	<i>Atta sexdens</i> 10054 BR:SP	0.116	10.00	914187	2732	361	9054	2392
10057	<i>Atta sexdens</i> 10057 BR:SP	0.244	19.30	1460971	5790	293	18414	2420
10060	<i>Atta sexdens</i> 10060 BR:PB	low	5.72	7307553	47102	278	127962	2447
10062	<i>Atta sexdens</i> 10062 BR:GO	2.840	12.90	2848164	20412	288	61819	2386
10063	<i>Atta sexdens</i> 10063 BR:TO	0.214	16.20	1291353	5152	313	17500	2405
10064	<i>Atta sexdens</i> 10064 BR:TO	0.193	15.50	705550	2146	460	7756	2376
10067	<i>Atta sexdens</i> 10067 BR:MS	3.520	23.30	2897048	17564	299	56819	2353
10068	<i>Atta sexdens</i> 10068 BR:MG	2.20	28.50	2482942	11542	317	42194	2307
10079	<i>Atta sexdens</i> 10079 PE	4.120	26.90	3206655	21343	311	69769	2362
10082	<i>Atta sexdens</i> 10082 BR:RR	0.378	17.20	1613761	5162	283	15866	2410
10701	<i>Atta sexdens</i> 10701 BR:MT	2.840	35.00	2620746	10299	312	40448	2264
10702	<i>Atta sexdens</i> 10702 BR:MT	2.720	28.50	3293257	20515	293	69665	2226
10706	<i>Atta sexdens</i> 10706 BR:MG	0.795	17.00	1779487	7745	278	23911	2403
10709	<i>Atta sexdens</i> 10709 BR:PA	3.660	19.30	1594746	6838	292	21711	2416
10714	<i>Atta sexdens</i> 10714 BR:ES	3.970	14.70	1204439	3420	384	13183	2381
10715	<i>Atta sexdens</i> 10715 BR:ES	1.740	15.30	1784492	6438	292	20857	2441
10724	<i>Atta sexdens</i> 10724 BR:MA	2.170	23.80	1752651	8773	268	24781	2412
10726	<i>Atta sexdens</i> 10726 BR:MA	1.520	27.30	912211	198	12926	6465	2387
10737	<i>Atta sexdens</i> 10737 BR:SP	0.627	21.40	1384525	5275	294	16526	2399
9983	<i>Atta texana</i> 9983 US	1.260	25.90	1852849	5495	348	24923	2325
10738	<i>Atta texana</i> 10738 US	4.280	25.60	1253939	3597	392	14372	2400
10739	<i>Atta texana</i> 10739 US	1.060	22.80	950289	2602	411	9713	2385
10740	<i>Atta texana</i> 10740 US	1.410	21.90	78145	493	317	1276	1175
10741	<i>Atta texana</i> 10741 US	8.710	26.30	2467776	11273	309	42423	2335
9941	<i>Atta vollenweideri</i> 9941 BR:MS	0.799	10.60	1827504	7014	312	24105	2406
9942	<i>Atta vollenweideri</i> 9942 BR:MS	0.129	7.34	1427540	6932	281	21314	2440
9943	<i>Atta vollenweideri</i> 9943 BR:MS	0.651	8.39	2507930	14933	285	46051	2410
9944	<i>Atta vollenweideri</i> 9944 BR:MS	0.848	10.70	2273932	11968	288	37414	2412
9984	<i>Atta vollenweideri</i> 9984 AR	5.270	19.90	2469490	14005	296	48772	2319
9985	<i>Atta vollenweideri</i> 9985 AR	4.710	26.60	1687710	3508	427	18313	2316
9986	<i>Atta vollenweideri</i> 9986 AR	4.460	34.10	2274877	12438	297	44540	2297
9987	<i>Atta vollenweideri</i> 9987 AR	4.420	36.90	2020391	7538	312	31420	2281
9988	<i>Atta vollenweideri</i> 9988 UR	4.380	33.30	2207032	10019	306	37960	2300
10093	<i>Atta vollenweideri</i> 10093 PR	2.00	33.90	1914265	4755	374	23742	2285
10742	<i>Atta vollenweideri</i> 10742 AR	4.950	27.50	1097474	3083	404	12178	2404
10743	<i>Atta vollenweideri</i> 10743 UR	5.170	30.10	2122474	8807	313	32768	2354
5364	<i>Mycetagioicus cerradensis</i> 5364 BR:MG	1.740	28.10	2411523	9481	381	40173	2322
5365	<i>Mycetagioicus triangularis</i> 5365 BR:DF	1.130	34.30	2328087	6181	461	30859	2251
8120	<i>Mycetomoellerius opulentus</i> 8120 BR:AM	0.451	19.80	3043653	13686	310	49506	2308
DNAex608	<i>Mycetomoellerius ruthae</i> DNAex608 BR:AM	5.340	17.50	4663798	18299	315	68836	2226
8167	<i>Paratrachymyrmex bugnioni</i> 8167 BR:PA	0.657	23.90	3011077	13549	355	52655	2309
8127	<i>Paratrachymyrmex diversus</i> 8127 BR:AM	0.581	27.80	1590244	4141	466	19292	2352
8178	<i>Sericomyrmex</i> sp 8178 CO	2.44	29.70	1078211	2305	722	10566	2321
8346	<i>Sericomyrmex</i> sp 8346 BR:PA	0.559	27.60	2945947	9566	375	43069	2268
8464	<i>Sericomyrmex</i> sp 8464 BR:PA	9.780	35.20	2795016	8448	412	39954	2250
5368	<i>Trachymyrmex arizonensis</i> 5368 US	1.610	15.60	738392	2497	353	8033	2314
8341	<i>Trachymyrmex septentrionalis</i> 8341 US	2.170	17.00	1528665	1604	974	12961	2346
3767	<i>Xerolitor explicatus</i> 3767 PR	0.102	22.10	1090397	7295	346	27987	2343
AVERAGE		3.01	24.21	2083262.20	11100.23	423.78	38133.73	2307.45
min		0.06	4.36	78145.00	198.00	260.00	1276.00	1088.00
max		31.30	53.00	7307553.00	74788.00	12926.00	236430.00	2447.00
SD		4.40	9.00	984256.78	11109.16	833.26	32721.06	164.38

Supplementary Table S5b List of UCE data collection and sequencing statistics of the taxa included in this study from another reference.

Extraction code	Taxon name	Reference	Total contigs	UCE loci
1487	<i>Acromyrmex balzani</i> 1487 GY	Branstetter et al. (2017)	13960	765
1477	<i>Acromyrmex heyeri</i> 1477 AR	Branstetter et al. (2017)	20615	795
1476	<i>Acromyrmex lundii</i> 1476 AR	Branstetter et al. (2017)	42590	825
1475	<i>Acromyrmex octospinosus</i> 1475 PN	Branstetter et al. (2017)	53988	858
1490	<i>Amoimyrmex striatus</i> 1490 BR	Branstetter et al. (2017)	45174	804
1474	<i>Acromyrmex versicolor</i> 1474 US	Branstetter et al. (2017)	33173	857
3779	<i>Atta cephalotes</i> 3779 BR:BA	Li et al. (2018)	186993	2293
3712	<i>Atta insularis</i> 3712 CU	Li et al. (2018)	126749	2333
1465	<i>Mycetagroicus inflatus</i> 1465 BR	Branstetter et al. (2017)	12597	776
1493	<i>Mycetagroicus triangularis</i> 1493 BR	Branstetter et al. (2017)	4258	719
1497	<i>Mycetomoellerius cf. relictus</i> 1497 PE	Ješovnik et al. (2016); Branstetter et al. (2017)	9529	763
1469	<i>Mycetomoellerius opulentus</i> 1469 PN	Ješovnik et al. (2016); Branstetter et al. (2017)	31317	838
1485	<i>Mycetomoellerius papulatus</i> 1485 AR	Ješovnik et al. (2016); Branstetter et al. (2017)	8953	766
1538	<i>Mycetomoellerius zeteki</i> 1538 PN	Ješovnik et al. (2016); Branstetter et al. (2017)	53100	901
1472	<i>Paratrachymyrmex bugnioni</i> 1472 BR	Branstetter et al. (2017)	12780	768
1537	<i>Paratrachymyrmex cornetzi</i> 1537 CR	Branstetter et al. (2017)	32042	835
1471	<i>Paratrachymyrmex diversus</i> 1471 BR	Branstetter et al. (2017)	12559	768
1470	<i>Paratrachymyrmex intermedius</i> 1470 GY	Branstetter et al. (2017)	10289	776
1556	<i>Sericomyrmex amabilis</i> 1556 PN	Ješovnik et al. (2016); Branstetter et al. (2017)	19050	821
1551	<i>Sericomyrmex bondari</i> 1551 BR	Ješovnik et al. (2016); Branstetter et al. (2017)	17151	828
1549	<i>Sericomyrmex mayri</i> 1549 GY	Ješovnik et al. (2016); Branstetter et al. (2017)	33462	855
1467	<i>Sericomyrmex parvulus</i> 1467 PE	Ješovnik et al. (2016); Branstetter et al. (2017)	15942	754
1552	<i>Sericomyrmex parvulus</i> 1552 BR	Ješovnik et al. (2016); Branstetter et al. (2017)	38926	859
1567	<i>Sericomyrmex scrobifer</i> 1567 BR	Ješovnik et al. (2016); Branstetter et al. (2017)	20560	843
1473	<i>Trachymyrmex arizonensis</i> 1473 US	Branstetter et al. (2017)	20415	786
1486	<i>Trachymyrmex septentrionalis</i> 1486 US	Branstetter et al. (2017)	31232	845
1503	<i>Trachymyrmex smithi</i> 1503 US	Branstetter et al. (2017)	29487	859
AVERAGE			34699.67	921.85
min			4258.00	719.00
max			186993.00	2333.00
SD			38652.19	403.32

Supplementary Table S6 Divergence date estimates for clades of ingroup and outgroup taxa.

Clade	This study	Schultz & Brady (2008)	Nygaard et al. (2016)	Jesovnik et al. (2016)	Branstetter et al. (2017)	Li et al. 2018
<i>Mycetagroicus</i> + higher attines ants (root)	33.81 (27.8–37.9)	20.0 (17.0–24.0)	26.6 (19.6–33.8)	33.3 (31.3–35.1)	31.4 (25.9–37.2)	25.9 (20.9–31.6)
Higher attines crown	23.24 (16.4–30.6)	16.0 (13.0–19.0)	22.9 (17.7–28.5)	29.2 (27.4–31.3)	27.3 (22.0–32.6)	21.9 (17.6–27.0)
<i>Mycetomoellerius</i> stem	19.04 (12.7–25.3)	10.5	22.9 (17.7–28.5)	22.6 (20.4–25.3)	18.6 (12.6–24.5)	14.6
<i>Mycetomoellerius</i> crown	14.8 (9.3–20.6)	7.50	na	na	12.3 (7.3–18.7)	7.2
<i>Xerolitor</i> stem	15.82 (10.0–22.0)	na	na	na	16.8 (10.5–21.8)	13.1
<i>Sericomyrmex</i> stem	15.82 (10.0–22.0)	10.5	na	22.6 (20.4–25.3)	16.8 (10.5–21.8)	13.1
<i>Sericomyrmex</i> crown	6.1 (3.2–9.6)	na	na	4.9 (3.4–7.1)	4.7 (2.5–11.6)	3.1
<i>Paratrachymyrmex</i> stem	20.51 (14.2–27.0)	11.5	19.2 (14.7–23.6)	22.3 (20.1–25.1)	21.6 (17.5–26.1)	16.1
<i>Paratrachymyrmex</i> crown	18.42 (12.5–24.7)	10.0	na	na	20.1 (15.7–24.7)	15.2
<i>Trachymyrmex</i> stem	18.91 (12.9–24.9)	9.0 (7.0–11.0)	17.8 (13.7–21.7)	19.9 (17.7–22.5)	19.3 (15.2–23.7)	14.3
<i>Trachymyrmex</i> crown	9.6 (4.8–14.7)	2.5	na	na	7.3 (4.2–12.5)	5.4
Leaf cutting ants stem	18.91 (12.9–24.9)	9.0 (7.0–11.0)	17.8 (13.7–21.7)	19.9 (17.7–22.5)	19.3 (15.2–23.7)	14.8 (11.6–17.6)
Leaf cutting ants crown	18.21 (12.4–24.1)	8.0 (10.0–6.0)	16.2 (11.0–20.0)	17.9 (15.6–20.4)	18.1 (14.2–22.2)	13.7 (11.1–16.9)
<i>Amoimyrmex</i> stem	18.21 (12.4–24.1)	na	na	na	18.1 (14.2–22.2)	13.7 (11.1–16.9)
<i>Amoimyrmex</i> crown	6.9 (2.6–12.0)	na	na	na	na	na
<i>Acromyrmex</i> stem	16.74 (11.3–22.3)	8.0 (10.0–6.0)	16.2 (11.0–20.0)	17.9 (15.6–20.4)	17.0 (13.2–20.8)	12.6 (10.1–15.6)
<i>Acromyrmex</i> crown	13.51 (8.8–18.5)	6.0	na	na	12.5 (8.4–16.5)	8.8
<i>Atta</i> stem	16.74 (11.3–22.3)	8.0 (10.0–6.0)	16.2 (11.0–20.0)	17.9 (15.6–20.4)	17.0 (13.2–20.8)	12.6 (10.1–15.6)
<i>Atta</i> crown	8.5 (4.9–12.5)	3.5	7.05 (5.5–9.0)	na	6.79 (4.0–10.0)	5.05
Archeatta stem	8.5 (4.9–12.5)					
Archeatta crown	4.76 (2.3–7.8)					
<i>Atta</i> s.s. + <i>Epiatta</i> + <i>Neoatta</i> crown	7.46 (4.2–11.2)					
<i>Atta</i> s.s. crown	3.27 (1.5–5.5)					
<i>Epiatta</i> + <i>Neoatta</i> crown	3.72 (2.0–5.7)					
<i>Epiatta</i> crown	2.2 (1.3–3.3)					
<i>Neoatta</i> crown	2.23 (1.1–3.5)					
<i>A. mexicana</i> crown	1.76 (0.6–3.3)					
<i>A. texana</i> + <i>A. insularis</i>	1.21 (0.5–2.1)					
<i>A. texana</i> crown	0.51 (0.1–0.9)					
<i>A. insularis</i> crown	0.52 (0.2–1.0)					
<i>A. colombica</i> + <i>A. cephalotes</i>	3.27 (1.5–5.8)					
<i>A. colombica</i> crown	0.61 (0.2–1.2)					
<i>A. cephalotes</i> crown	1.11 (0.6–1.7)					
<i>A. saltensis</i> + <i>A. vollenweideri</i>	1.74 (0.9–2.7)					
<i>A. saltensis</i> crown	1.51 (0.7–2.4)					
<i>A. vollenweideri</i> crown	0.94 (0.3–1.7)					
<i>A. goiana</i> + <i>A. bisphaerica</i>	1.66 (0.8–2.6)					
<i>A. bisphaerica</i> crown	0.39 (0.1–0.8)					
<i>A. opaciceps</i> + <i>A. capiguara</i>	1.67 (0.9–2.6)					
<i>A. opaciceps</i> crown	0.82 (0.3–1.4)					
<i>A. capiguara</i> crown	1.2 (0.6–2.0)					
<i>A. laevigata</i> stem	2.02 (1.2–3.1)					
<i>A. laevigata</i> crown	1.18 (0.5–2.0)					
<i>A. robusta</i> + <i>A. sexdens</i>	2.23 (1.1–3.5)					
<i>A. robusta</i> crown	0.26 (0.1–0.5)					
<i>A. sexdens</i> crown	1.38 (0.7–2.1)					

3. CONSIDERAÇÕES FINAIS

Pela sua grande importância ecológica e econômica, o gênero *Atta* é um dos grupos de formigas protagonistas em diversos tipos de estudos envolvendo biologia, comportamento, ecologia, controle e as interações entre elas, outros organismos e o meio ambiente. No entanto, este gênero era considerado um dos grupos de formigas mais carentes de uma melhor compreensão da filogenia e da evolução das espécies.

Realizamos um estudo das relações filogenéticas, datação de divergência e biogeográfica do gênero *Atta* usando Elementos Ultra-conservados (UCEs). Nossos resultados representam a filogenia e o estudo sobre a evolução de *Atta* mais completo até o momento, com implicações para a história evolutiva e filogenia das formigas cultivadoras de fungos no geral e para as formigas cortadeiras em particular. Proporcionamos um estudo mais robusto que os estudos anteriores na mesma área devido a que envolvemos um maior número de espécies de *Atta* e abrangemos em grande proporção a área geográfica de cada uma delas, particularmente espécies de ampla distribuição, incluindo uma quantidade superior de espécimes. Além disso, recuperamos uma maior quantidade de loci de UCE como marcadores filogenéticos e as 14 espécies estudadas com o maior suporte. Assim, nossa ampla amostragem de táxons e os métodos filogenéticos aplicados permitem uma maior resolução na história evolutiva dessas espécies e um melhor conhecimento da sistemática, biogeografia e evolução de *Atta* fornecendo, ademais, uma sólida base para futuros estudos taxonômicos.

A partir da definição das relações filogenéticas entre as espécies e uma combinação entre as estimativas das datas de divergência e o cenário biogeográfico envolvido ao longo da evolução, o nosso estudo revela importante informação que permite reconstruir a história evolutiva de *Atta*. A recente e rápida radiação das espécies de *Atta* é uma das conclusões mais interessantes, e quiçá a mais importante, deste trabalho. Estamos na presença de um grupo de formigas muito jovem que tem abarcado uma enorme distribuição e conquistando os diversos ambientes com muito sucesso, tendo começado sua diversificação há pouco tempo (8.5 milhões de anos) e alcançando o máximo da sua especiação em apenas os últimos 2.0 milhões de anos. Além disso, embora o gênero *Atta* tenha uma origem norte-americana, sua expansão pelo resto do continente foi muito rápida e é na América Central e do Sul onde atualmente sua distribuição e diversidade de espécies predominam. Desta forma, resulta muito previsível pensar que a adaptação ao clima tropical e aos ambientes abertos que essas formigas possuem contribuíram ao sucesso de colonização, obtendo posteriormente uma maior diversificação na América do Sul, e principalmente no Brasil, como consequência da expansão dos Cerrados. Por fim, que

espécies de *Atta* amplamente distribuídas tenham condicionado a reconstrução biogeográfica do gênero, sugere que essas espécies podem reter informações históricas sobre as distribuições ancestrais. Este é um ponto muito interessante ao observar que cada uma destas espécies forma parte de um subgrupo filogeneticamente semelhante junto a espécies de distribuição restrita.

Considerando as novas evidências levantadas acima sobre este grupo de formigas tão importante e popular, acreditamos que nossa investigação será de interesse não apenas para cientistas interessados em sistemática, filogenética molecular e biogeografia, senão também para aqueles interessados em ecologia, controle de pragas e entomologia aplicada no geral, incluindo, especificamente, aqueles interessados em mirmecologia aplicada, ou seja, o estudo das formigas de alta importância biológica e econômica.