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ON THE BIOGEOGRAPHY OF ATTINI (HYMENOPTERA: FORMICIDAE)

SOBRE LA BIOGEOGRAFÍA DE LOS ATTINI (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

An analysis of the distribution of 209 species in the tribe Attini shows that about half of these species are only known from the type locality, suggesting that this group is still largely undersampled. The tribe is exclusively American, with 95% of the species reported from the neotropical region and only 5% from the neartic. The genera of the tribe can be divided in two groups according to their centers of species richness. In northern South America *Apterostigma, Cyphomyrmex* (*rimosus* group), *Mycocepurus, Myrmicocrypta, Sericomyrmex* and *Trachymyrmex*; and in southern South America *Acromyrmex, Atta, Cyphomyrmex* (*strigatus* group), *Mycetarotes*, *Mycetophylax* and *Mycetosoritis*. The Amazon region has less species richness compared to other areas, although it contains most of the "palaeoattini". Regarding the ecological range or ecological plasticity, the genera of Attini may be divided in: Highly plastic - *Acromyrmex, Atta, Cyphomyrmex* (*rimosus* group) and *Trachymyrmex*; plastic - *Cyphomyrmex* (*strigatus* group) *Mycetarotes, Mycetosoritis* and *Sericomyrmex;* and specialized on arid and open areas - *Mycetophylax* and *Mycocepurus*. We suggest examples for allopatric diversification of the Attini through both, dispersal and vicariance. The data are congruent with a scenario in which the Attini appeared in the Amazon basin after separation of America and Africa, and had a large dispersion in the Tertiary, in at least two historically separated events.

Key-words: Attini, biogeography, distribution

RESUMEN

Un análisis de la distribución de 209 especies de la tribu Attini muestra que alrededor de la mitad de estas especies son conocidas sólo de la localidad típica, lo que sugiere que este grupo todavía está sub-muestreado. La tribu es exclusivamente americana, con 95% de las especies reportadas para la región neotropical y solo el 5% de la neártica. Los géneros de la tribu pueden dividirse en dos grupos de acuerdo a sus centros de riqueza de especies. En el norte de Sur América estarían *Apterostigma, Cyphomyrmex* (grupo *rimosus*), *Mycocepurus, Myrmicocrypta, Sericomyrmex* y *Trachymyrmex*; y en el sur de Sur América *Acromyrmex, Atta, Cyphomyrmex* (grupo *strigatus*), *Mycetarotes*, *Mycetophylax* y *Mycetosoritis*. La región Amazónica tiene menos riqueza de especies comparada con otras áreas, aunque contiene a la mayoría de los "palaeoattini". Con respecto al rango ecológico o plasticidad ecológica, los géneros de Attini pueden dividirse en: Muy plásticos - *Acromyrmex, Atta, Cyphomyrmex* (grupo *rimosus*) y *Trachymyrmex*; plásticos - *Cyphomyrmex* (grupo *strigatus*) *Mycetarotes, Mycetosoritis y Sericomyrmex; y* especializados a ambientes áridos y abiertos - *Mycetophylax y Mycocepurus*. Sugerimos ejemplos para diversificación alopátrica de los Attini a través de dispersión y de vicarianza. Los datos apoyan un escenario en el que los Attini aparecen en la cuenca del Amazonas después de la separación de América y África, tuvieron una gran dispersión en la era Terciaria en al menos dos eventos históricos separados.

Palabras clave: Attini, biogeografía, distribución

INTRODUCTION

The tribe Attini, which includes all known fungus growing ants, is exclusively American. It occurs all over tropical and sub-tropical America except for Chile. Weber (1972) postulated that the absence of Attini in Chile is due to the fact that they were not able to cross the northern coastal desert of Atacama nor the Andes in the south.The evidence cited by Weber is the presence of other species of ants in similar latitudes in Chile and Argentina, which were probably in place before the formation of the Andes. Kusnezov (1949) and later Weber (1972) report the latitudinal extremes of attine distribution as those of *Trachymyrmex septentrionalis* (40° N) and *Mycetosoritis asper* (44° S).

Wheeler (1923) proposed that the Attini originated in humid tropical areas of America due to the fact that at the beginning of the century most of the species considered as 'primitive' were collected in tropical rain forests. Zoogeographic studies of South American ants by Kusnezov (1963) suggested that some areas in Argentina (Litoral, Tucuman), Brazil (Rio Grande do Sul to Rio de Janeiro), Paraguay (East) and Uruguay form a secondary centre of evolution for ants, together with another centre around the Amazon basin, and a third one west of the Patagonia and south of Chile. He did not discard other centres in intertropical Andean areas. Regarding the Attini, and especially *Acromyrmex*, he suggested that their nesting habits indicate a progressive adaptation from humid areas to more arid environments in southern Brazil and Argentina. He placed great importance on the central plains of Brazil for the evolution of *Acromyrmex*, among other more or less specialized ant species, due to the diversity of microhabitats existing there. Kusnezov (1963) suggested that the three most 'primitive' Attini genera, *Apterostigma, Mycocepurus* and *Myrmicocrypta*, which he called palaeoattini, are mesophilic and more abundant in tropical rain forests, which he proposed as the areas from which the Attini expanded. Kusnezov also suggested that the genus *Mycetophylax*, which occurs in arid extra-tropical area of South America, probably represents a lateral ramification of the ancestral trunk of the tribe, secondarily adapted to drier habitats.

Weber (1972) indicated possible migratory

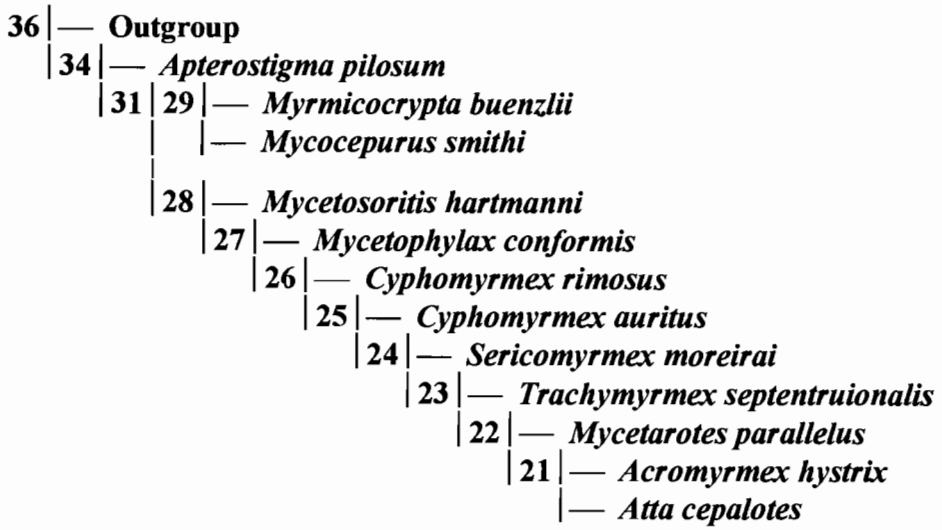

Figure 1. Cladogram of 12 Attini species with 9 outgroup species produced with the Henning 86 program run with equal weight for the 42 characters used (commands IE-1 232, ic = 53, ir = 72). Taken from Mayhé-Nunes (1995).

routes used during the expansion of the Attini. He postulated that they originated in the tropical lowlands (0 to 200 m) in northern South America. He justified his hypothesis by assuming that areas of South America, from sea level up to 200 m, may have remained sufficiently warm and humid during the periods of past climatic changes, allowing the survival of the ants and their fungus. Since the Amazon basin is the largest area in the continent with such a climate, he suggested the following migratory routes of the Attini expanding from the Amazon:

a. To the north through the river basins of the Amazon, Rio Negro and Orinoco.

b. To the north through the continental coast of the Atlantic.

c. To the south through the basin of the Parana river.

In addition, Weber suggested that the opening and closing of the Panama strait caused geographical isolation and possible expansions to Central and North America, and eventually to the Major Antilles, of several Attini and other ants.

Recent quantitative phylogenetic analyses of the attine genera using different techniques (Chapela *et al.* 1994, Mayhé-Nunes 1995, Shultz and Meier 1995) revealed the first detailed possible phylogenetic relations among them (for example, Figure 1). Thus, the group seems to be ready for a first tentative detailed biogeographical analysis. Here we present an update of the present geographical distribution of the Attini, allowing comparisons of species richness and endemisms of the various genera, in order to clarify the biogeography of this group of fungus growing ants.

MATERIALS AND METHODS

Geographical data were obtained from the ant species catalogues of Uruguay (Zolessi *et al.* 1989), the neotropical (Kempf 1972, Brandão 1991) and neartic regions (Smith 1979). Other data came from entomological collections at the Museo del Instituto Agrícola - Universidad Central de Venezuela, Maracay, and Museo de Ciencias Naturales - Universidad Simón Bolívar, Caracas, in Venezuela and Museu de Zoologia da Universidade de São Paulo, Museu Nacional and Instituto de Biologia da Universidade Federal Rural do Rio de Janeiro, in Brazil. Collection by the authors with new relevant reports are given in Tables 2 and 3. The geographical data from locations of 209 species of 11 genera were plotted on maps.

The concept of neotropical region used throughout this paper follows Kempf (1972). We divided this region into: Southern South America (SSA) = south of latitude 10^0 S, except for humid forests in the north of Bolivia and the west of Brazil. Northern South America (NSA) = between latitude 10^0 N and 10^0 S, including the northern coasts of Venezuela and Colombia, and the northern forests of Bolivia and west of Brazil. Central America (CA) = Central America from Panama to the south of Mexico. Islands = the West-Indies, Bahamas and Galapagos. Neartic (NA) = northern Mexico and southern USA.

RESULTS

95% of the species of the tribe Attini are reported from the neotropical region and only 5% from the neartic. Nearly 43% of the species are known only from type localities; new, formerly unpublished reports are summarized in Table 1.

The genera *Acromyrmex* and *Atta* have the best known distributions with the highest species richness between latitude 20^0 S and 40^0 S. *Acromyrmex* (Table 3) has a relatively low number of species in the Amazon basin and north of it. In CA only a few *Acromyrmex* species occur. *Acromyrmex coronatus, Acromyrmex niger, Acromyrmex nigrosetosus, Acromyrmex rugosus* and *Acromyrmex subterraneus* are the species of the genus with the widest distribution regarding range in latitude. In the subgenus *Moellerius* only *Acromyrmex versicolor* is endemic in NA and the rest, except *Acromyrmex landolti,* are reported only from SSA.

Table 1. New reports of localities for Attini species.

SPECIES	LOCALITIES
Acromyrmex hystrix (Latreille)	Venezuela
Acromyrmex nigrosetosus Forel	Venezuela
Apterostigma auriculatum Wheeler	Venezuela (Lattke det.)
Apterostigma dentigerum Wheeler	Venezuela (Lattke det.)
Apterostigma epinotale Weber *	Venezuela (Lattke det.)
Apterostigma gibbum Weber *	Venezuela (Lattke det.)
Apterostigma manni Weber *	Venezuela (Lattke det.)
Apterostigma peruvianum Wheeler *	Venezuela (Lattke det.)
Apterostigma mayri Forel	Venezuela (Lattke det.)
Apterostigma robustum Emery	Venezuela (Lattke det.)
Apterostigma urichi Forel	Venezuela
Cyphomyrmex auritus Mayr	Brazil, Minas Gerais
Cyphomyrmex bigibbosus Emery	Venezuela
Cyphomyrmex costatus Mann	Ecuador; Venezuela
Cyphomyrmex faunulus Wheeler	Brazil, Pará; Venezuela
Cyphomyrmex laevigatus Weber	Venezuela
Mycetarotes parallelus (Emery)	Brazil, Amazonas and Minas Gerais
Mycetarotes carinatus Mayhé-Nunes *	Brazil, Minas Gerais
Mycocepurus obsoletus Emery *	Venezuela
Mycocepurus smithi Forel	Venezuela
Trachymyrmex bugnioni Forel	Venezuela
Trachymyrmex dichrous Kempf	Brazil, Minas Gerais
Trachymyrmex farinosus Emery	Venezuela
Trachymyrmex holmgreni Wheeler *	Brazil, Rio Grande do Sul
Trachymyrmex levis Weber *	Venezuela
Trachymyrmex mandibularis Weber *	Brazil, Amazonas; Venezuela
Trachymyrmex oetkeri Forel	Brazil, Bahia
Trachymyrmex opulentus (Mann) *	Brazil, Amazonas; Colombia; Venezuela
Trachymyrmex phaleratus Wheeler *	Venezuela
Trachymyrmex relictus Borgmeier	Venezuela
Trachymyrmex wheeleri (Weber) *	Brazil, Amazonas; Venezuela

When not indicated, Mayhé det.
Species marked with * were known only from type localities.

Although the genus *Atta* (Table 3) contains only three Amazonian species, it is more diverse in CA than *Acromyrmex*. The subgenus *Archeatta* ranges up to NA with the endemic *Atta texana* and *Atta mexicana*. A widely distributed species in the subgenus *Atta* is *Atta cephalotes* with a range from latitude 20° N to 20° S. Most of the species in the subgenera *Paleoatta* and *Neoatta* occur in SSA, except for *Atta* (*Neoatta*) *laevigata* and *Atta* (*Neoatta*) *sexdens* which have a wide distribution between 10° N and 25° S. The genus *Apterostigma* occurs mainly between the equator and 10° N (Table 3), with some species in CA and SSA. Among these species, 56% are only known from the type locality. *Apterostigma auriculatum, Apterostigma mayri, Apterostigma pilosum* and *Apterostigma robustum* show the widest distributions and only *Apterostigma scutellare* occurs in NA. The genus *Cyphomyrmex* has two centres of species richness (Table 3). Species of the *rimosus* group concentrate around 10° N, whereas the majority of the *strigatus* group are restricted to ranges between 20° S and 30° S. This last group lacks species with wide distributions. Species in the genus *Mycetarotes* have been found only south of the equator up to about 28° S (Table 3). *Mycetarotes parallelus*

is the species with the widest distribution and three of the four species in the genus occur in south-east Brazil. *Mycetophylax* is a genus with many infra-specific descriptions of *Mycetophylax emeryi* from Sierra Nevada, Colombia and from Argentina (Table 3). Most species occur between 15° S and 42° S. The most common species is a quantitative analysis of species richness (Table 2) shows that three genera have more than 50% of their species in the Amazon basin: *Mycocepurus, Apterostigma* and *Myrmicocrypta.* Only the last two have high endemism in that area. A global analysis of the tribe, however, shows that only 76 species occur in the Amazon basin with 49 endemic species. When analyzing the species richness according to our south-north division, both show similar values. In SSA we recorded 96 species with 73 endemic species; whereas in NSA we found 98 species with 63 endemics. The genera *Acromyrmex, Atta* and *Cyphomyrmex* (*strigatus* group) clearly have their highest species richness and endemism in SSA, followed by *Mycetarotes, Mycetophylax* and *Mycetosoritis.*

DISCUSSION

We still have incomplete knowledge about the distribution of many of the Attini species. These species usually have very small workers, cryptic coloration and behaviour, and are not attracted to baited traps. Their collection thus depends on the skills of the collector and they are rarely sampled (Mayhé-Nunes 1995). In addition, many areas of tropical America are poorly sampled (especially Bolivia, Peru, Ecuador, Colombia, Venezuela and

Table 2. Percentage of species in each genera reported for each of the biogeographical regions studied. The percentage of species of that genus endemic to that region is given in parenthesis. The percentage of species distributed in a wide latitudinal range and of species which are known only from one locality, are also given.

	% of Species and (% Endemics) by region							
GENERA(nr of spp.)	**SSA**	**NSA**	**Amazon**	**CA**	**Islands**	**NA**	**% wide distrib.**	**% types only**
Acromyrmex (28)	82 (57)	39 (11)	32 (11)	4 (0)	4 (0)	7 (4)	29	7
Apterostigma (27)	30 (22)	56 (44)	52 (41)	30 (15)	0 (0)	4 (4)	15	56
Atta (15)	73 (47)	33 (0)	20 (0)	27 (0)	13 (7)	20 (7)	40	13
Cyphomyrmex								
gr. *rimosus* (22)	23 (9)	59 (23)	32 (9)	41 (5)	23 (14)	18 (9)	41	27
gr. *strigatus* (15)	87 (87)	13 (13)	13 (13)	0 (0)	0 (0)	0 (0)	0	13
Mycetarotes (4)	75 (50)	50 (25)	50 (25)	0 (0)	0 (0)	0 (0)	25	50
Mycetophylax (6)	83 (50)	50 (17)	0 (0)	0 (0)	17 (0)	0 (0)	33	50
Mycetosoritis (4)	75 (75)	0 (0)	0 (0)	0 (0)	0 (0)	25 (25)	0	25
Mycocepurus (4)	50 (0)	75 (25)	75 (25)	50 (25)	25 (0)	25 (0)	50	25
Myrmicocrypta (24)	13 (8)	75 (67)	71 (63)	21 (13)	0 (0)	4 (0)	13	79
Sericomyrmex (19)	47 (42)	42 (37)	32 (26)	11 (11)	0 (0)	5 (5)	5	95
Trachymyrmex (41)	27 (27)	44 (37)	32 (22)	15 (7)	5 (2)	20 (17)	10	44
TOTAL (209)	46 (35)	47 (30)	36 (23)	18 (7)	6 (2)	11 (7)	20	44

SSA= Southern South America, south of latitude 10° S, except for humid forest in the north of Bolivia and the west of Brazil. NSA= Northern South America between latitude 10° N and 10° S, including the northern coasts of Venezuela and Colombia, and the northern forest of Bolivia and west of Brazil. CA= Central America from Panama to the south of Mexico. Islands= the West-Indies, Bahamas and Galapagos. NA= Neartic, northern Mexico and Southern USA.

Table 3. Geographical distribution of Attini species.

Taxon	SSA	NSA	CA	Islands	NA
Acromyrmex (s. str.)					
ambiguus	x				
aspersus	x				
carli		x			
coronatus	x	x			
crassispinus	x				
diasi	x				
disciger	x				
gallardoi	x				
hispidus	x				
hystrix		x			
laticeps	x				
lobicornis	x				
lundi	x				
niger	x	x			
nigrosetosus	x	x			
nobilis		x			
octospinosus		x	x	x	x
rochai	x	x			
rugosus	x	x			
subterraneus	x	x			
Acromyrmex (Mollerius)					
balzani	x				
fracticornis	x				
heyeri	x				
landolti	x	x			
pulvereus	x				
silvestri	x				
striatus	x				
versicolor					x
Atta (Atta)					
cephalotes	x	x	x	x	x
colombica		x	x		
Atta (Archeatta)					
insularis				x	
mexicana			x		x
texana					x
Atta (Neoatta)					
capiguara	x				
laevigata	x	x			
opaciceps	x	x			
robusta	x				
sexdens	x	x	x		
silvai	x				
vollenweideri	x				
Atta (Palaeatta)					
bisphaerica	x				
goiana	x				
saltensis	x				
Apterostigma					
affinis	x				
auriculatum		x	x		
billi		x			
bolivianum		x			
bruchi	x				
calverti			x		
collare			x		
dentigerum			x		

continuación

Taxon	SSA	NSA	CA	Islands	NA
dorotheae		x			
epinotale		x			
fallax		x			
fusinodum		x			
gibbum		x			
ierense		x			
luederwaldti	x				
madidiense		x			
manni		x			
mayri	x	x	x		
moelleri	x				
peruvianum		x			
pilosum	x	?	x		
robustum		x	x		
scutellare					x
steigeri	x				
tramitis			x		
urichi		x			
wasmanni	x				
Cyphomyrmex (rimosus)					
bicarinatus		x			
bicornis	x				
castagnei		x			
cornutus		x	x		
costatus		x	x		
dixus			x		
flavidus					x
foxi				x	
hamulatus		x	x		
kirbyi		x			
laevigatus		x			
longiscapus		x	x		
major	x	?	x		
minutus		x	x	x	x
nesiotus				Galapagos	
peltatus	x				
podargus				x	
rimosus	x	x	x	x	x
salvini		x	x		
transversus	x	x			
vorticis		x			
wheeleri					x
Cyphomyrmex (strigatus)					
auritus	x				
bigibbosus		x			
bruchi	x				
daguerri	x				
faunulus		x			
lectus	x				
lilloanus	x				
morchi	x				
nemei	x				
occultus	x				
olitor	x				
paniscus	x				
plaumanni	x				
strigatus	x				
vallensis	x				

Table 3. Continuación

Taxon	SSA	NSA	CA	Islands	NA
Mycetarotes					
parallelus	x				
senticosus	x				
sp.n.AM		x			
sp.n.RJ	x				
Mycetophylax					
bruchi	x				
conformis	x	x		x	
cristulatus	x				
emeryi	x	x			
glaber	x				
simplex	x				
Mycetosoritis					
asper	x				
clorindae	x				
explicata	x				
hartmanni					x
Mycocepurus					
goeldii	x	x			
obsoletus		x			
smithi	x	x	x	x	x
tardus			x		
Myrmicocrypta					
boliviana		x			
bruchi	x				
buenzlii		x			
collaris		x			
dilacerata			x		x
ednaella			x		
elizabethae		x			
foreli		x			
godmani			x		
guianensis		x			
infuscata		x			
longinoda		x			
microphthalma		x			
occipitalis		x			
ogloblini	x				
rudiscapus		x			
spinosa		x			
squamosa	x	x			
subnitida			x		
triangulata		x	x		
tuberculata		x			
unidentata		x			
urichi		x			
weyrauchi		x			
Sericomyrmex					
amabilis			x		
aztecus					x
beniensis		x			
bondari	x				
burchelli	x				
diego		x			
karekulli		x			

continuación

Taxon	SSA	NSA	CA	Islands	NA
impexus		x			
luederwaldti	x				
lutzi		x			
mayri	x				
moreirai	x				
myersi		x			
opacus	x				
parvulus	x	x			
saussurei	x				
scrobifer	x				
urichi		x			
zacapanus			x		
Trachymyrmex					
agudensis	x				
arizonensis					x
bugnioni		x	x		
carib		x			
cornetzi		x	x		
desertorum					x
dichrous	x				
diversus		x			
echinus		x			
farinosus		x			
fiebrigi	x				
fuscus	x				
gaigei		x			
guianensis		x			
holmgreni	x				
internedius			x		
irmgardae		x			
isthmiscus			x		
jamaicensis				x	x
jheringi	x				
kempfi	x				
levis		x			
mandibularis		x			
nogalensis					x
oetkeri	x				
opulentus		x	x		
papulatus	x				
phaleratus		x			
pruinosus	x				
relictus		x			
ruthae		x			
saussurei					x
septentrionalis					x
sharpii				x	
smithi					x
squamulifer			x		
tucumanus	x				
turrifex					x
urichi		x			
verrucosus		x			
wheeleri		x			

SSA= Southern South America, south of latitude 10° S, except for humid forest in the north of Bolivia and the west of Brazil. NSA= Northern South America between latitude 10° N and 10° S, including the northern coasts of Venezuela and Colombia, and the northern forest of Bolivia and west of Brazil. CA= Central America from Panama to the south of Mexico. Islands= the West-Indies, Bahamas and Galapagos. NA= Neartic, northern Mexico and Southern USA.

the north-east of Brazil), which adds to the lack of knowledge about this group. Despite these shortcomings, our survey indicates the following:

The attini in geological time

Holldobler and Wilson (1990) reported that the only fossils of the tribe are from the Oligocene-Miocene (nearly 30-20 million years old). One of them belongs to a relatively modern genus, *Trachymyrmex*, whilst the other, *Cyphomyrmex* is regarded as 'primitive' (Weber 1982). Neither fossils nor extant species exist in the Old World, suggesting that the tribe originated after the splitting of West Gondwana some 80-65 million years ago. Alternative hypotheses are not likely, such as: 1 - the ancestor was distributed between the two continents of West Gondwana (America and Africa) and, after separation, the African population became extinct; 2 - initially the ancestor was restricted to Africa, and then it migrated to America, and after the splitting of West Gondwana the African population became extinct. The absence of Attini in Chile indicate that the dispersion of these species occurred after the formation of the Andes (Tertiary). Therefore, likely dates for the origin of the Attini are between the end of the Cretaceous and the Oligocene-Miocene (between 80 and 20 million years ago), probably at the beginning of the Tertiary (Palaeocene-Eocene).

Centres of species richness

Our data suggest at least two centers of species richness for the group. The more phylogenetically derived genera *Acromyrmex* and *Atta* have species adapted to various environments, although their centre of species richness is located in SSA. *Trachymyrmex* and *Cyphomyrmex* (*rimosus* group) have widely distributed species, but not *Mycocepurus*, their centre of species richness lay in NSA. Species of the latter genus normally build their nests in open land, usually avoiding forests. Species of the genera *Apterostigma* and *Myrmicocrypta* seem to be more restricted to forest habitats and also have their centres of species richness in the NSA. Most species of *Mycetophylax* occur in South America and the genus has its centre of species richness in the SSA, with many species adapted to arid conditions in the interior of Argentina (Kusnezov 1963). The *strigatus* group of *Cyphomyrmex* also concentrates in SSA, possessing one species, *Cyphomyrmex morschi*, which lives on the shores of South America and has behaviour similar to that of *Mycetophylax conformis* (Gonçalves and Mayhé-Nunes 1984). This species of the *strigatus* group is very close to the latter (Kempf 1962) and seems to represent the link between these two genera. *Mycetarotes* is a rare genus and exclusively South American, with a centre of species richness in the south of the continent. *Mycetosoritis*, the rarest genus of the tribe, has a unusual distribution, concentrating in SSA with one species in North America. *Sericomyrmex* is the genus with the poorest records on the distribution of its species. Our data suggest two centres of species richness, one in NSA and another in SSA.

The origin of the attini

Our results support previous suggestions that the centre of origin of the tribe is the Amazon basin (Kusnezov 1963, Weber 1972). This region seems to have had a relatively stable humid climate starting from the Mesozoic (Cretaceous) to the present (Rivero 1980). Our data show that genera with a majority of species in SSA seem to be more adapted to arid environments at present. Therefore, migrations from the Amazon basin seem to be related to adaptation to open habitats.

Although Croizat *et al.* (1974) criticised the concept of centres of origin, here we follow the criteria for the assessment of a centre of origin given by Cranston and Naumann (1991). The arguments favouring the hypothesis that the Attini

originated in the Amazon are:

a. Ecologically, the Amazon forests represents the most appropriate area for the 'primitive' Attini and their symbiotic fungus, as it provides relatively constant humidity and temperature throughout the year and the day.

b. The Amazon is the area with the largest number of 'primitive' forms (the palaeoattini: *Apterostigma, Mycocepurus* and *Myrmicocrypta*) and the most derived genera (*Atta* and *Acromyrmex*) occur mostly outside this area.

Contradicting this suggestion however, our results also show that only 34% of the species of the tribe occur in the Amazon basin, with 21% of endemism. These numbers may increase with more sampling efforts, but in general the species richness between NSA and SSA are similar. The derived genera do not compete with the palaeoattini for food or territory, and their nests occur in the same habitats without any signs of aggression (Weber 1941, 1946). Consequently, displacement of one group by other does not seem to be likely in modern times.

Since all palaeoattini, the most 'primitive' genera, are more common in the Amazon area, this area can safely be assumed as the place where the tribe originated. *Trachymyrmex* and, possibly, *Sericomyrmex* originated also in NSA, not necessarily in the Amazon. From the phylogenetic relationship shown in Figure 1 we know that these two taxa are among the closest relatives of the advanced Attini (*Atta* and *Acromyrmex*). Their relationship and distribution suggest a migration from the humid north to the south, but clearly at a different evolutionary moment, suggesting at least two bio-historical events for the biogeographical distribution of Attini. The genera *Acromyrmex* and *Atta* probably appeared in the south from a common ancestor close to *Trachymyrmex* and *Sericomyrmex*. After their appearance in the south, some of the species of *Acromyrmex* and *Atta* colonised the north.

Species in the Caribbean, such as the endemic *Trachymyrmex sharpii* from St. Vincent, may represent an example of allopatric speciation by dispersal, due to the fact that the islands where they occur are of volcanic origin (Coney 1983). Another example is *Cyphomyrmex nesiotus*, endemic in Galapagos (Snelling and Longino 1992). Some species of the genera *Acromyrmex*, *Atta*, *Cyphomyrmex*, *Mycetophylax*, *Mycocepurus* and *Trachymyrmex* that occur in the islands are widely distributed species, showing the migratory potential of these ants. Dispersal by humans is known to have occurred in the case of *Acromyrmex octospinousus* which was introduced to the island of Guadeloupe, Carriacou and Curacao (Cherrett 1968).

Examples which can be explained by the tectonic model for the biogeography of the Caribbean (Rosen 1985) may be found among the endemics in *Atta* and *Cyphomyrmex*. *Atta insularis*, from Cuba, could have arisen through vicariance together with *Atta mexicana*, of Central America, which are members of the same subgenus and share a common ancestor. In the genus *Cyphomyrmex* there are two species exclusively

found in Jamaica, *Cyphomyrmex foxi* and *Cyphomyrmex podargus*, but the relationships with other species of the *rimosus* group are not clear (Snelling and Longino 1992).

Our data also support cases of vicariant distribution as proposed by Croizat *et al.* (1974) in South America. Perhaps, the best example is *Cyphomyrmex laevigatus*, a species restricted to NSA. This species is closer phylogenetically to *Cyphomyrmex bicornis*, know only from the type locality (Rio de Janeiro), than to any other member of the *rimosus* group from NSA. Although future revisions may change the present taxonomic status of some Attini (Kempf 1972), other possible examples of vicariance are:

a. *Mycetophylax emeryi*, which is restricted to Colombia and Venezuela, has many infraspecies reported in Argentina.

b. *Acromyrmex lundi*, supposedly endemic to SSA is taxonomically very close to *Acromyrmex*

carli from the Amazon.

c. *Mycetosoritis*, although showing a strange distribution, may also be explained by vicariant phenomena, assuming that the taxon is adapted to cold climates. A future taxonomic revision may divide this poorly studied group.

These examples may be explained by the appearance of biogeographical barriers in the Cenozoic. During the cold glacial periods, the climatic conditions in South America were supposedly drier, with vast areas surrounding the contracting forests in the Amazon (Vanzolini 1973). During the interglacial periods in the Tertiary and Quaternary the Amazonian forests expanded, favoring the dispersion of the Attini.

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