

## Biogeography and ecology of the ant fauna of Madagascar (Hymenoptera: Formicidae)

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In the Malagasy region, 52 ant genera have been recorded, of which 48 are estimated to be indigenous. On the island of Madagascar, 41 out of 45 recorded genera are considered to be indigenous. Four genera are endemic to Madagascar and one to Mauritius. Currently, there are 383 names of described species-group taxa from the Malagasy region, and 320 from Madagascar. The level of endemism is high at the species level, > 90%. The ant fauna of the Malagasy region, however, is poorly understood; an estimated two thirds of the ant species are undescribed. The diversity of ant genera on the island is comparable to that of other biogeographic regions. On the basis of generic and species level comparisons, the Malagasy fauna shows greater affinities to the Afrotropical region than to peninsular India and the Oriental region. The distinct gaps in the taxonomic and ecological composition of the fauna of Madagascar are evaluated in the context of island radiations and relict taxa. The absence of driver ants in Madagascar may have spurred the diversification of Cerapachyinae and may have permitted the persistence of other relict taxa such as the Amblyoponini.

KEYWORDS: Formicidae, biogeography, Madagascar, systematics, Africa, ecology.

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### Introduction

For the Malagasy region, ant taxonomy had a prolific beginning in the late 1800's and early 1900's. In 1891, and with an additional supplement in 1892, Forel provided the first and only thorough treatment of the ants of the Malagasy region. On the basis of this work, Emery (1920c) evaluated the similarities of the ant genera of Madagascar with Asia and Africa. A few years later, Wheeler (1922c) provided an updated list of the ant fauna of the region. Except for Donisthorpe's work based on the collections of Mamet and Vinson in the Mascarenes (summarized in Mamet 1954), almost 50 years passed without additional work on the ants of Madagascar (Fig. 1). One reason for the lack of taxonomic interest in Madagascar was the paucity of new material since the late 19th and early 20th century collections of Camboué, Sikora, Mocquerys, Voeltzkow, Perrot, Alluaud, and Hildebrandt.

In the late 1960's, Brown provided greatly needed new collections from Madagascar, and returned our attention to the importance of the Malagasy region in understanding ant phylogeny (Brown 1975, 1978a; and see Bolton 1979, 1981). Over the last five years, collections and field observations from Madagascar have greatly increased, improving our understanding of the evolution, taxonomy, and ecology of

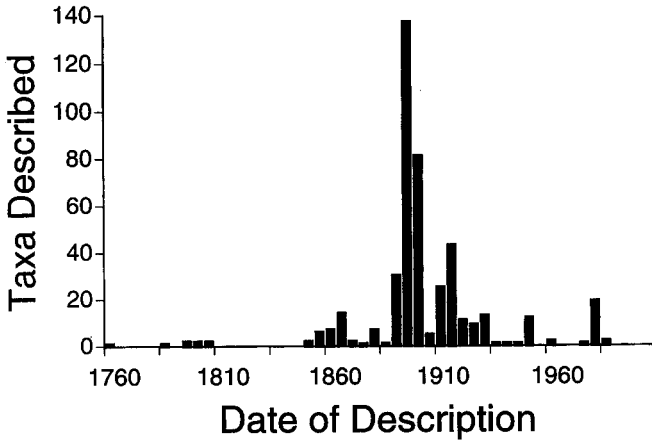


FIG. 1. Date of publication of all named ants from the Malagasy region. The number of described taxa are grouped by five year intervals.

ants of the island, and most of all, have demonstrated that the fauna is incompletely known (Alpert 1992, Ward 1994, Fisher in press, Olson and Ward in press).

The time is right to reassess what we know of the ants of Madagascar, to provide baseline taxonomic data for the resurgence of interest in the region's ant fauna, and to provide a summary of the biogeographic patterns ascertainable from available data. To this end, I add to the early work of Forel, Emery, and Wheeler, and provide an updated species list for the Malagasy region and discuss the generic affinities of the fauna to the Afrotropical and Oriental regions. I propose possible origins for the Malagasy fauna and evaluate the striking gaps in the taxonomic composition of the fauna in the context of island radiations.

## Results and discussion

### *Ant species of the Malagasy region*

Data on the richness and endemism of Malagasy ants are summarized in Appendix 1 which contains a list of all valid species-group names. In all discussions and analyses, Madagascar includes the coastal islands (e.g., Nossi Bé, St. Marie), and the Malagasy Region refers to Madagascar and neighbouring islands of the Indian Ocean: Mauritius, Réunion, Seychelles, Rodrigues, Aldabra, Farquhar, Chagos, and the Comoro Is.

In 1893, Dalla Torre listed 119 Malagasy species (excluding subspecies), and

Table 1. The number of valid specific and subspecific names, and the number of introduced and endemic taxa. Introduced and endemic taxa contain both species and subspecies. Data summarized from the list of ant species-group names of the Malagasy Region in Appendix 1.

	Madagascar	Malagasy Region
Valid specific and subspecific names	320	383
Valid subspecific names	76	93
Introduced taxa	19	33
Endemic taxa	271	331
Per cent endemism	90%	95%

Wheeler (1922c) enumerated 237 species (excluding subspecies) for the Malagasy Region. The present total of 290 species (383 including subspecies) for the Malagasy region is a small increase in described taxa over the last 75 years (Appendix 1. Fig. 1). Recent collections by the author, G. D. Alpert *et al.*, D. M. Olson, and P. S. Ward suggest that there may be over 1000 species in the Malagasy region. The recently collected, undescribed material, indicates that the level of endemism for Madagascar and the Malagasy region is greater than the figures of 90% and 95% presented in Table 1. New and more intense inventory techniques are collecting an amazing number of new species that are cryptic and locally distributed in Madagascar. A recent ant survey of a wet tropical closed forest site in the RNI d'Andringitra found an estimated 100% of the 134 ant species in this mountainous region to be endemic to Madagascar (Fisher, in press).

### *Biogeographical affinities*

Griswold (1991) described two main approaches to understanding historical biogeographic patterns, the phenetic and cladistic methods. The cladistic approach determines the relationship among areas based on sister-group relationships among taxa endemic to those areas. The phenetic approach does not use a phylogeny to determine relationships among areas, but evaluates relationships based on proportion of shared taxa. Though Griswold clearly demonstrates that the cladistic method is the preferred approach, most invertebrate groups lack the necessary phylogenetic information to construct the area cladograms necessary to implement these methods. In these cases, the phenetic approach is appropriate, but with the understanding that historical patterns may need future testing with cladistic methods. For the Malagasy ant fauna, the phenetic comparison must be done at the generic level, since the species level taxonomy is inadequate.

In this paper, the origins and affinities of the ants of Madagascar are investigated by comparing the number of genera in common with neighbouring land masses of India and Africa which were all once united in Gondwana (Briggs, 1987). The ant genera present in Madagascar and other biogeographic regions are presented in Appendix 2. In addition to described taxa and literature records, the list contains data from undescribed material in museum collections.

To further understand affinities with the African ant fauna, I have compared the genera of Madagascar with geographically distinct regions within Africa: West Africa (W.A.), East Africa (E.A.), and southern Africa (S.A.) (see Appendix 2 for area descriptions). Ideally these regions would be equal in size to Madagascar, and contain equal representation of the habitats found on the island. Unfortunately, we lack detailed information on the distribution of the ant genera in Africa. For example, there are insufficient collections records to develop a list of the ant genera of Mozambique, the land mass closest to Madagascar. I am not proposing that these areas of Africa are biogeographically distinct. The regions differ in the proximity to Madagascar with South and East Africa providing closer grounds for dispersal to Madagascar. This division also separates the mostly mesic tropical forest of West Africa from the more xeric habitats of East and southern Africa.

There are 52 ant genera, 48 of which are estimated to be indigenous, in the Malagasy region. The classification of a genus as indigenous or introduced is based on a subjective evaluation of historical distribution records and the biology of the species. There are five endemic genera in the region: *Adetomyrma* [Mad.], *Eutetramorium* [Mad.], *Ireneopone* [Mau.], *Pilotrochus* [Mad.], and an undescribed genus [Mad.].

Is the richness of 48 genera in Madagascar depauperate compared with other

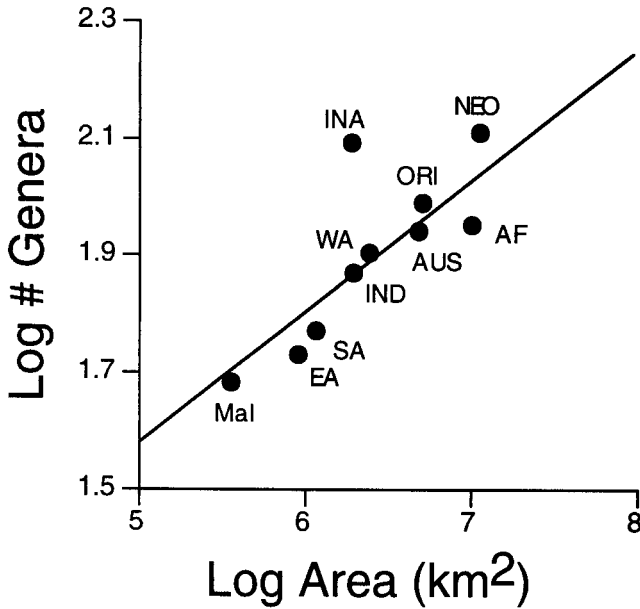


FIG. 2. The log number of genera for each Gondwanaland biogeographic region plotted with respect to the log area of the region. The data fit the equation:  $f(x) = 0.215(x) + 0.52$  with a  $R^2 = 0.60$ . If the subregions EA, SA, WA and IND are removed  $R^2 = 0.553$ . Biogeographic regions: Neotropical (NEO), Afrotropical (AF), Malagasy (MAL), Palaeartic (PAL), Oriental (ORI), Indo-Australian (INA), Australian (AUS), India (IND), West Africa (WA), East Africa, (EA), southern Africa (SA). Regions are defined in Appendix 2.

tropical regions? Ideally, a comparison of diversity would be made at the species level, but these data do not exist. In Fig. 2, I present a genera-area curve for the Gondwanaland regions and subregions. The log of the total number of genera present in each of the regions is plotted in relation to the log of the area of each region. The slope of the log-log relationship has a z-value of 0.215 ( $R^2 = 0.60$ ). The log number of genera in the Malagasy region falls very close to this line. Thus, the ant fauna, at least at the generic level, is not depauperate. The Indo-Australian region is the only visible outlier, showing a highly diverse fauna in a small area. This could be the result of an actual higher generic diversity, or an artifact of a poorly defined biogeographic region. As defined here in Bolton (1995b), the Indo-Australian region includes islands on both sides of the Wallace line. Future work should be directed at clarifying the boundaries of this region.

These genera are shared between the Malagasy region and India but are not found in Africa: *Aphaenogaster*, *Kyidris*, and *Vollenhovia*. These three genera are found in other biogeographic regions and are not uniquely shared between the Malagasy region and India (Appendix 2).

Nine genera are shared between the Malagasy region and Africa and are not recorded from India: *Anoplolepis* [All Africa], *Discothyrea* [S.A., W.A.], *Glamyromyrmex* [W.A., E.A.], *Melissotarsus* [All Africa], *Mystrium* [W.A.], *Prionopelta* [S.A., W.A.], *Pristomyrmex* [All Africa], *Simopone* [S.A., W.A.], and *Terataner* [All Africa]. *Melissotarsus* and *Terataner* are the only genera uniquely shared between the Malagasy region and Africa. *Simopone*, *Mystrium*, *Prionopelta*, *Discothyrea*, and *Pristomyrmex* are also

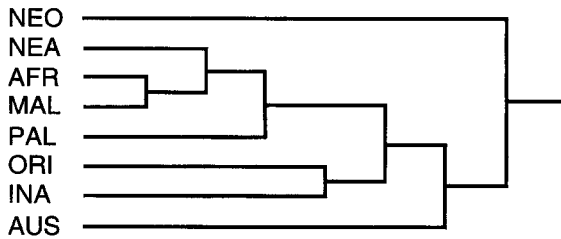


FIG. 3. Dendrogram resulting from a single linkage cluster analysis of the genera present in each biogeographic region: Neotropical (NEO), Nearctic (NEA), Afrotropical (AFR), Malagasy (MAL), Palearctic (PAL), Oriental (ORI), Indo-Australian (INA), and Australian (AUS). Data shown in Appendix 2.

Table 2. Number of genera shared and the Jaccard Index of similarity between biogeographic regions presented in Appendix 2. Higher values represent greater similarity. (Mal. = Malagasy region; Ori. = Oriental Region; Afr. = Afrotropical region; E.A. = East Africa; W.A. = West Africa; S.A. = southern Africa; see Appendix 2 for further explanation of regions.)

	Mal.-Ori.	Mal.-India	Mal.-Afr.	Mal.-W.A.	Mal.-E.A.	Mal.-S.A.
Genera shared	37	33	40	39	36	37
Unique to Mal.	11	15	8	11	15	11
Unique to other	60	41	49	42	19	23
Jaccard index	0.343	0.371	0.412	0.424	0.514	0.521

found in the Oriental biogeographic region and it is possible that these genera may have become locally extinct in India.

The number of uniquely shared genera is very low, but it does suggest that the ant fauna of Madagascar has closer affinities to Africa than to India and the Orient (two genera uniquely shared with Africa, zero with India and the Oriental region). This type of analysis would be more appropriate at the species level, but the poor state of the taxonomy of these regions does not permit it.

A cluster analysis (single linkage; SAS, 1994) of the genera present in each biogeographic region groups the Malagasy and African Regions as most similar (Fig. 3). An analysis of faunal similarity using the Jaccard Index (Magurran, 1988) also indicates that the Malagasy fauna is most similar to the African, and more precisely, to that of the southern and East Africa regions (Table 2; Jaccard Index:  $C_j = j/(a + b - j)$  where  $j$  = number of genera shared by both regions,  $a$  = number of genera in Madagascar, and  $b$  = number of genera in region B).

An examination of the only recent world revision of a genus that included Madagascar (Bolton, 1979) indicates that the Madagascar-Africa relationship is also true at the level of species-groups and species. Of the 36 described species of *Tetramorium* in the Malagasy region, 29 are endemic, four are shared with Africa, and three are pantropical tramp species. The 36 described species represent eight species groups of which three are endemic to Madagascar, two are shared with Africa and three are widespread. In addition, three indigenous species from the Malagasy region are shared with Africa, while none are shared with the Oriental or Indo-Australian regions. Closer affinities with the Oriental and Indo-Australian regions, however, may exist in other pantropical genera, such as *Strumigenys* and *Pheidole* which have numerous undescribed species in collections awaiting revision.

Nineteen genera are found in both Africa and the Oriental region, but not in Madagascar: *Aenictus*, *Calyptomyrmex*, *Carebara*, *Cataglyphis*, *Centromyrmex*, *Cryptopone*, *Dorylus*, *Epitritus*, *Leptanilla*, *Messor*, *Myrmecaria*, *Oecophylla*, *Paedalgus*, *Pheidologeton*, *Polyrhachis*, *Probolomyrmex*, *Rhoptromyrmex*, *Pseudolasius*, and *Sphinctomyrmex*.

Nesting behaviour may help explain which ant genera successfully colonized the island. The following discussion assumes that the ant genera found on Madagascar arrived primarily by dispersal (see discussion of the origin of genera below). The nineteen genera listed above nest either in the ground, with termite, in the leaf litter or in rotten wood, or in self constructed nests. *Polyrhachis* is the only genus that has some species that nest in plant cavities. Brown (1973) suggested that those ants that nest in performed plant cavities are best suited for surviving long distance dispersal by rafting across an ocean. Not surprisingly, however, there are other genera that successfully colonized Madagascar which do not nest in plant cavities. In addition to not nesting in plant cavities, the arrival of the driver ants (*Aenictus* and *Dorylus*) and *Leptanilla* to Madagascar has been hindered by the fact that queens are wingless. The genus, *Aenictus*, however, has managed to establish on the islands beyond the Asian mainland, crossing even the Wallace Line (Gotwald 1995).

The striking gaps in the taxonomic composition of the fauna of Madagascar suggest a disharmonic or unbalanced condition. The driver ants which dominate the forest floor, and the weaver ants (*Oecophylla*) which dominate the forest canopy in Afrotropical and Oriental tropical regions are absent from the Malagasy region. Weaver ants and especially driver ants are important predators of other ants and have been shown to influence ant population structure and the diversity of ant communities (Hölldobler and Wilson, 1990; Gotwald, 1995). Because of the absence of driver ants and weaver ants from Madagascar, the ant population dynamics of Malagasy ant communities may differ greatly from other Old World ant communities. During a raid, driver ants provide a natural disturbance in the ant community. They create a gap, like a treefall for plants, that provides opportunities for successful colonization by foundress queens. Driver ants have also been shown to be the most important predator of termites in Africa (Gotwald, 1995). Even the long legs and leaping ability of certain African shrews are suggested to be adaptations for escape during driver ant attack (Brosset, 1988). Driver ants, because of their affect on ant populations and other insects, have been labelled 'keystone species' (Gotwald, 1995). An investigation of African and Malagasy ant community ecology provides a natural experiment for evaluating the effect of these dominant African ants on ant communities.

Possible consequences of the imbalance in the fauna in Madagascar may include unique island radiations. The lack of driver ants in Madagascar may have spurred the diversification of the tribe Cerapachyini (*Cerapachys* and *Simopone*) on the island (Hölldobler and Wilson, 1990; Olson and Ward, in press). Recent faunal surveys of the ants of Madagascar have revealed an unprecedented morphologically diverse and species rich assemblage of cerapachyine species. Certain *Cerapachys* are morphologically convergent with the driver ant genus *Aenictus* found in Africa. In recent phylogenetic analyses, the cerapachyines appear to be a sister group to the army ants (Cerapachyinae + (Ecitoninae + Dorylinae + Aenictogitoninae + Aenictinae); Bolton, 1990; Baroni Urbani *et al.*, 1992) and have convergently evolved army ant habits of raiding the nests of other ants (Brown, 1975; personal observation). We do not know whether the lack of driver ants in Madagascar has led to the diversification of *Cerapachys* in Madagascar, or has permitted their persistence. *Cerapachys* may have

been free to develop and capitalize on their army ant predatory behaviour or they may have been able to survive despite their less successful behaviour in comparison to driver ants.

Some species of *Cerapachys* and *Simopone* have queens that are winged and both genera are known to nest in preformed plant cavities. It is this combination of nesting in plant cavities and having winged queens that has most likely resulted in their successful colonization of Madagascar. This assumes, that these genera were not present on Madagascar before it separated from Africa (see below).

*Mystrium*, in the morphologically primitive tribe Amblyoponini, represents another genus that may have been able to persist in the absence of competition from more recently evolved genera that failed to colonize Madagascar. Currently there are six described species of *Mystrium* from Madagascar, while only one species from west Africa and one species from the Oriental, Indo-Australian, and Australian regions still exists. *Mystrium*, along with the other genera in the tribe, are specialized arthropod predators and possess many anatomically and behaviourally primitive characters. For example, personal observations of *Mystrium* and parallel observations of the genus *Amblyopone* suggest they lack social food transfer and the queens are exclusively dependent on the hemolymph of their own larvae (Wheeler and Wheeler, 1988).

#### *Origin of the ant genera of Madagascar*

Where did the ant fauna of Madagascar come from? Which taxa were present when Madagascar separated from Africa? We have no fossil records of any ants from Madagascar that could help us understand the Mesozoic or Tertiary ant fauna of Madagascar. The origin of the ant fauna of Madagascar must be inferred from our understanding of the movements of continents and our scant knowledge of the ancestry of ants. The high number of extant ant genera found in Baltic amber fossils (Oligocene) suggests that many extant genera may be at least 35 million years old (Hölldobler and Wilson, 1990). Since only one of 10 genera of ants found in Cretaceous and Eocene deposits are extant genera, most modern taxa may not have been abundant or even extant before the Oligocene. If this is true, then all modern genera probably evolved after the proposed separation of Madagascar from Africa (around 120 million years ago (Ma); Rabinowitz *et al.*, 1983) and the separation of India from Madagascar > 80 Ma; Storey *et al.*, 1995). By the early Cretaceous, Madagascar had reached its present position (Storey *et al.*, 1995).

The tribe Amblyoponini is diverse in Madagascar at the genus and species level. They may represent relic taxa still present in Madagascar that once had a wider distribution. Brown (1960) proposed that the extent Amblyoponini represent surviving species of a much more varied group of ants that date back to the Cretaceous. Even if this ancestral group of ants diversified as early as the Cretaceous, then the amblyoponini genera *Adetomyrma*, *Amblyopone*, *Mystrium* and *Prionopelta* could have arrived only onto Madagascar by queen dispersal of rafting. Dispersal during the Cretaceous, however, may have been easier than during recent times. Briggs (1989) suggested that during the Cretaceous, India was in direct contact with Northern Africa, and the Seychelles had already broken off from India as it moved northward. The proximity of the Seychelles to Madagascar and India could have provided a means of faunal exchange with India and Africa during the Cretaceous.

Recent faunal inventories in Madagascar have shown that the most species-rich and abundant genera of Madagascar are *Pheidole*, *Crematogaster*, *Tetramorium* and

*Camponotus*. Because of their virtual absence in pre-Miocene deposits, Brown (1973) proposed that these genera experienced an explosive radiation since the Miocene, and possible slightly earlier for *Camponotus*. Assuming this is correct, their arrival in Madagascar must be from long distance dispersal. Phylogenetic studies will be needed to show whether the species in Madagascar are derived from an early stock of these genera, or represent species derived from a series of colonizations by these genera. Evidence from *Tetramorium* suggests that a majority of species may have arisen from an old evolutionary stock. Bolton (1976, 1979) observed that *Tetramorium* with 11-segmented antennae dominate in Australia and Madagascar, where they outnumber the 12-segmented forms which dominate elsewhere around the world. Bolton postulated that the 11-merous forms are remnants of an earlier radiation that has been replaced elsewhere by later-evolving 12-segmented forms. As with the genus *Mystrium*, evidence suggests that Madagascar contains taxa with numerous plesiomorphic characters.

The above discussion assumes that the modern ant genera are not older than the Cretaceous. An alternative scenario, though not supported by the fossil record, is to hypothesize that some extant genera are much older and may date back to around the break up of Gondwana, around 100 million years ago (Ma). Bolton (1990) and Baroni Urbani *et al.*, (1992) offer some indirect evidence to support this. They hypothesized that the Old and New World army ants are sister groups, and therefore form a monophyletic clade and share a common ancestor. It is most parsimonious to assume that the ancestor of this clade had wingless queens as do all the modern taxa. The present distribution of Ecitoninae in the New World and Dorylinae in the Old World, may be explained by a common ancestor present before the complete breakup of South America and Africa which is estimated to have occurred between 84 Ma and 106 Ma (Pitman *et al.*, 1993). Since the Dorylinae are absent from Madagascar, this common ancestor may have evolved after the separation of Madagascar from Africa around 120 Ma (Rabinowitz *et al.*, 1983). Other genera, such as in the tribe Amblyoponini which have a Gondwanan distribution, may actually be much older than the Cretaceous.

One of the most perplexing finds in Madagascar was the 1993 discovery of the new genus *Adetomyrma* (Ward 1994). This genus was not only found to belong to a group that has retained many primitive characters, but it also created a seemingly insoluble problem in the reconstruction of the internal phylogeny of the ants. *Adetomyrma* lacks two derived characters, previously thought to be unique and irreversible, of the subfamily Ponerinae in which it is placed (tergosternal fusion of abdominal segments 3 and 4). Despite lacking these two apomorphic characters, it does possess all the other apomorphies of the tribe Amblyoponini. Faunal inventories and the greatly needed revisionary work on the ants of Madagascar, hold great promise to provide new insight and clarification of the higher phylogeny of ants.

#### *Exotic ants*

There are almost 20 ant species that are believed to have been introduced into Madagascar (Table 1). Some of these species were present when Forel (1891), completed the first treatment of the Malagasy ant fauna. Open and disturbed habitats in Madagascar and other islands are the most susceptible to invasion by the exotic species. Some species, such as *Technomyrmex albipes*, have begun to invade undisturbed forest sites near rice fields and villages in the northeast of Madagascar. There is some danger that even though small remnant patches of forest may be



preserved in the region, invasion by aggressive, exotic ants may drive native ants locally extinct. On smaller islands such as Mauritius, this phenomenon is already in its late stages. Exotic ants have followed the advance of invasive weeds and have left the island with little chance for preserving most of the approximately 10 endemic species, including the endemic genus *Ireneopone* (Ward, 1990).

### Conclusions

Our understanding of the ant fauna of Madagascar is far from complete. Almost every one of the 48 indigenous genera is in need of revision. Nonetheless, evidence does suggest that the Malagasy ant fauna shows closer ties with Africa than with the Orient or Indo-Australian regions. The absence of dominant genera found in Africa, such as *Oecophylla*, *Aenictus* and *Dorylus* had posed unique opportunities for the ants of Madagascar, possibly allowing some to persist and others to radiate. The completion of taxonomic revisions of the most important genera of the region, coupled with phylogenetic analysis, will help clarify these hypotheses.

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Appendix 1 continued.....

Genus	Species	Author reference	Additional reference	Nomenclature and distribution notes	Mad.	Mau.	Réu.	Sey.	Com.	Ald.	Far.	Cha.	Rod.
	<i>hova radamae</i>	Forel 1891:31	Wheeler 1922c		1				1				
	<i>legionarium</i>	Santschi 1911b:283	Wheeler 1922c		1								
	<i>maculatus</i>	(Fabricius) 1782:491	Wheeler 1922c	West Africa	1		1		1				
	<i>maculatus lincoemisi</i> var. <i>Emery</i> 1905:30		Wheeler 1922c	Unavailable name; described from Madagascar	1								
	<i>maidecassa</i>												
	<i>maculatus lividior</i> = <i>maculatus</i>	Santschi 1911a:128	Wheeler 1922c										
	<i>maculatus radamooides</i> = <i>maculatus</i>	Forel 1891:213	Wheeler 1922c	Syn. Baroni Urbani 1972:125									
	<i>maculatus strangulatus</i>	Santschi 1911a:129	Wheeler 1922c	Unavailable name; described from Seychelles	1								
	<i>maculatus juba</i> var. <i>Forel</i> 1907a:93		Bolton 1955b	Unavailable name; described from Seychelles									
	<i>fuvoocoronotata</i>	Forel 1897:202	Wheeler 1922c	Unavailable name; described from Seychelles									
	<i>maculatus juba</i> var. <i>ocionotatus</i>												
	<i>nasicus</i>	Forel 1891:67	Wheeler 1922c		1								
	<i>perroti</i>	Forel 1897:202	Wheeler 1922c		1								
	<i>perroti aechylus</i>	Forel 1913a:224	Wheeler 1922c		1								
	<i>radamae becki</i> var. <i>Santschi</i> 1923:292		Bolton 1955b	Unavailable name; described from Madagascar									
	<i>altior</i>												
	<i>roesei</i>	Forel 1910a:20	Wheeler 1922c		1								
<b>Lasini</b>													
<b>Paratrechina</b>													
	<i>amblyops</i>	(Forel) 1892c:240	Wheeler 1922c		1								
	<i>amblyops rubescens</i>	(Forel) 1892b:516	Wheeler 1922c		1								
	<i>bourbonica</i>	(Forel) 1886b:210	Wheeler 1992c; Wilson & Taylor 1967	Pantropical tramp species			1	1				1	
	<i>bourbonica bengalensis</i>	(Forel) 1894b:408	Wheeler 1922c; Wilson & Taylor 1967; Trager 1984	Syn. Wilson & Taylor 1967:88, but see Trager 1984:151; India, Burma									
	<i>bourbonica</i>	(Forel) 1907b:92	Wheeler 1922c						1				
	<i>bourbonica farquharensis</i>	(Forel) 1907b:87	Wheeler 1922c						1				
	<i>bourbonica agassiana</i>	(Forel) 1907b:87	Wheeler 1922c						1				
	<i>comarensis</i>	(Forel) 1891:92	Wheeler 1922c		1								
	<i>glabra</i>	(Forel) 1892b:517	Wheeler 1922c		1								
	<i>gracilis</i>	(Forel) 1891:90	Wheeler 1922c		1								
	<i>humbloti</i>	(Latreille) 1802:113	Wheeler 1922c		1		1		1				1
	<i>longicornis</i>	(Forel) 1886b:212	Wheeler 1922c		1								
	<i>madagascarensis</i>	(Forel) 1891:87	Wheeler 1922c		1								
	<i>madagascarensis ellisi</i>	Wheeler 1922c:1038	Wheeler 1922c										
	<i>madagascarensis</i>												
	<i>refescens</i>	(Forel) 1897:203	Wheeler 1922c		1								
	<i>mixta</i>	(Forel) 1892c:238	Wheeler 1922c										
	<i>sikoroae</i>	(Forel) 1893:342	Wheeler 1922c	Antilles, West Indies									
	<i>steinheili</i>	Nylander 1846a:900	Donisthorpe 1946c; Mamet 1954	Cosmopolitan			1						
	<i>vioidala</i>												
<b>Plagiolepidini</b>													
<b>Acropyga</b>													
	<i>dodo</i>	Donisthorpe 1946a:782	Donisthorpe 1946c; Mamet 1954				1						













Appendix 1 continued.....

Genus	Species	Author reference	Additional reference	Nomenclature and distribution notes	Mad.	Mau.	Réu.	Sey.	Com.	Ald.	Far.	Cha.	Rod.
	<i>mauricei</i> = <i>lanuginosa</i>	(Donisthorpe) 1946a:778	Bolton 1976	Syn. Bolton 1976:351									
	<i>minutum</i> = <i>caldarium</i>	Donisthorpe 1942:30	Bolton 1979	Syn. Bolton 1979:169	1								
	<i>nageum</i>	Bolton 1979:136											
	<i>nasanowii</i> = <i>schaaffussii</i>	Forel 1892b:521	Bolton 1979	Syn. Bolton 1979:137									
	<i>paralela</i> = <i>simillimum</i>	(F. Smith) 1859:147	Bolton 1980	Syn. Forel 1916:421									
	<i>pauper transformans</i> = <i>caldarium</i>	Santschi 1914a:104	Bolton 1980	Syn. Bolton 1980:310									
	<i>pleganon</i>	Bolton 1979:146			1								
	<i>plesiarum</i>	Bolton 1979:150			1								
	<i>proximum</i>	Bolton 1979:137			1								
	<i>pusillum bantouana</i> = <i>simillimum</i>	Santschi 1910:382	Bolton 1980	Syn. Bolton 1980:320									
	<i>pusillum exoleta</i> = <i>simillimum</i>	Santschi 1914b:366	Bolton 1980	Syn. Bolton 1980:320									
	<i>pusillum henisti</i> = <i>caldarium</i>	Wheeler 1922a:193	Bolton 1979	Syn. Bolton 1979:169									
	<i>quadrifiduosum</i>	Emery 1886:362	Bolton 1979	Widespread in southern Africa, fairly common on Aldabra and Cosmoledo Atoll	1					1			
	<i>quadratum</i>	Bolton 1979:150			1								
	<i>roazanum</i>	Forel 1895c:486	Bolton 1979		1								
	<i>robustior</i>	Forel 1892b:521	Bolton 1979		1								
	<i>schaaffussii</i>	Forel 1891:138	Bolton 1979		1								
	<i>scytalum</i>	Bolton 1979:157			1								
	<i>sericeiventre</i>	Emery 1877:370	Bolton 1979	Common and widespread in Africa	1								
	<i>severini</i>	(Emery) 1895a:343	Bolton 1979		1								
	<i>sikaroe</i>	Forel 1892b:522	Bolton 1979		1								
	<i>simillimum</i>	(F. Smith) 1851:118	Bolton 1979, 1980	Pantropical tramp species	1								
	<i>simillimum denticulatum</i>	Forel 1902:235	Bolton 1980	Syn. Bolton 1977:131									
	= <i>simillimum</i>												
	<i>simillimum insulare</i> = <i>simillimum</i>	Santschi 1928a:69	Bolton 1980	Syn. Bolton 1977:131									
	<i>simillimum</i>												
	<i>simillimum madecassum</i>	Forel 1895b:248	Bolton 1979	Syn. Bolton 1979:156									
	= <i>delagoense</i>												
	<i>simillimum opacior</i> = <i>simillimum</i>	Forel 1913b:81	Bolton 1980	Syn. Bolton 1980:320									
	<i>steinheiti</i>	Forel 1892b:520	Bolton 1979		1								
	<i>tanitillum</i>	Bolton 1979:152			1								
	<i>tosii</i>	Emery 1899:284	Bolton 1979		1								
	<i>xanthogaster</i>	Santschi 1911a:124	Bolton 1979		1								
	<i>zenatum</i>	Bolton 1979:151			1								
	<i>venatrix</i>	Ward 1994:159											
	<i>besucheti</i>	Baroni Urbani 1978:49											

PONERINAE

- Amblyoponini*
- Adicomyrma*
- Amblyopone*









## /Appendix 2 continued.....

	NEO	NEA	PAL	AFR	(S.A.)	(W.A)	(E.A)	MAL	(India)	ORI	INA	AUS
<i>Basiceros</i>	1											
<i>Belonopelta</i>	1											
<i>Blepharidatta</i>	1											
<i>Bondroitia</i>				1		1						
<i>Bothriomyrmex</i>			1						1	1	1	1
<i>Brachymyrmex</i>	1	1	1					[1]				
<i>Bregmatomyrma</i>											1	
<i>Calomyrmex</i>											1	1
<i>Calyptomyrmex</i>				1	1	1	1		1	1	1	
<i>Camponotus</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cardiocondyla</i>	1	1	1	1	1	1	1	1	1	1	1	
<i>Carebara</i>	1			1	1	1	1			1	1	
<i>Carebarella</i>	1											
<i>Cataglyphis</i>			1						1	1		
<i>Cataulacus</i>				1	1	1	1	1	1	1	1	
<i>Centromyrmex</i>	1			1	1	1			1	1	1	
<i>Cephalotes</i>	1											
<i>Cerapachys</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Chalepoxenus</i>			1									
<i>Cheliomyrmex</i>	1											
<i>Chelystruma</i>	1											
<i>Chimaeridris</i>											1	
<i>Cladrogenys</i>				1		1						
<i>Cladomyrma</i>											1	
<i>Codiomyrmex</i>	1											
<i>Codioxenus</i>	1											
<i>Colobostruma</i>											1	1
<i>Concoctio</i>				1		1	1					
<i>Creightonidris</i>	1											
<i>Crematogaster</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Cryptopone</i>	1	1	1	1	1	1			1	1	1	1
<i>Cylindromyrmex</i>	1											
<i>Cyphoidris</i>				1		1						
<i>Cyphomyrmex</i>	1	1										
<i>Dacatria</i>			1									
<i>Dacatinops</i>											1	
<i>Daceton</i>	1											
<i>Decamorium</i>				1	1	1						
<i>Dendromyrmex</i>	1											
<i>Diacamma</i>									1	1	1	1
<i>Dicroaspis</i>				1		1						
<i>Dilobocondyla</i>									1	1	1	
<i>Dinoponera</i>	1											
<i>Diplomorium</i>				1		1						
<i>Discothyrea</i>	1	1		1	1	1		1		1	1	1
<i>Doleromyrma</i>												1
<i>Dolichoderus</i>	1	1	1						1	1	1	1
<i>Doloponera</i>				1		1						
<i>Dorisidris</i>	1											
<i>Doronomyrmex</i>		1	1									
<i>Dorylus</i>				1	1	1	1		1	1	1	
<i>Dorymyrmex</i>	1	1										
<i>Dysedrognathus</i>										1	1	
<i>Echinopla</i>											1	1
<i>Eciton</i>	1											
<i>Ecphorella</i>				1								
<i>Ectatomma</i>	1											
<i>Emeryopone</i>			1							1	1	
<i>Epelysidris</i>											1	
<i>Epimyрма</i>			1									
<i>Epitritus</i>			1	1		1				1	1	
<i>Epopostruma</i>												1
<i>Eucryptocerus</i>	1											
<i>Euprenolepis</i>											1	
<i>Eurhopalothrix</i>	1	1									1	1
<i>Eutetramorium</i>								1				
<i>Forelius</i>	1	1										
<i>Forelophilus</i>											1	
<i>Formica</i>	1	1	1						(1)	1		







/Appendix 2 continued.....

	NEO	NEA	PAL	AFR	(S.A.)	(W.A)	(E.A)	MAL	(India)	ORI	INA	AUS
<i>Rhoptromyrmex</i>			1	1	1	1			1	1	1	
<i>Rhytidoponera</i>											1	1
<i>Rogeria</i>	1	1									1	
<i>Romblonella</i>											1	1
<i>Rossomyrmex</i>			1									
<i>Rostromyrmex</i>										1		
<i>Rotastruma</i>										1	1	
<i>Santschiella</i>				1		1						
<i>Scyphodon</i>											1	
<i>Secostruma</i>											1	
<i>Sericomyrmex</i>	1											
<i>Serrastruma</i>				1	1	1	1	1				
<i>Simopelta</i>	1											
<i>Simopone</i>				1	1	1		1		1	1	
<i>Smithistruma</i>	1	1	1	1	1	1	1	1	1	1	1	
<i>Solenopsis</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Sphinctomyrmex</i>	1			1		1			1	1	1	1
<i>Stegomyrmex</i>	1											
<i>Stenamma</i>	1	1	1						(1)	1		
<i>Stereomyrmex</i>									1	1		
<i>Stigmacros</i>												1
<i>Streblognathus</i>				1	1							
<i>Strongylognathus</i>			1									
<i>Strumigenys</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Talaridris</i>	1											
<i>Tapinoma</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Tatuidris</i>	1											
<i>Technomyrmex</i>	1		1	1	1	1	1	1	1	1	1	1
<i>Teleutomyrmex</i>			1									
<i>Terataner</i>				1	1	1	1	1				
<i>Teratomyrmex</i>												1
<i>Tetheamyрма</i>											1	
<i>Tetramorium</i>	1	1	1	1	1	1	1	1	1	1	1	1
<i>Tetraoponera</i>			1	1	1	1	1	1	1	1	1	1
<i>Thaumatomyrmex</i>	1											
<i>Tingimyrmex</i>	1											
<i>Trachomyrmex</i>	1	1										
<i>Tranopelta</i>	1											
<i>Trichoscapa</i>		[1]	1	[1]		[1]						
<i>Tricytarus</i>											1	
<i>Turneria</i>											1	1
<i>Typhlomyrmex</i>	1											
<i>Vollenhovia</i>			1						1	1	1	1
<i>Vombisidris</i>									1	1	1	1
<i>Wasmannia</i>	1	[1]										
<i>Willowskiella</i>											1	1
<i>Xenomyrmex</i>	1	1										
<i>Yavnella</i>			1						1	1		
<i>Zacryptocerus</i>	1	1										
undescribed myrmicine genus								1				
undescribed ponerine genus				1		1						
Total	128	63	73	89	60	83	55	48	74	97	123	88

*Anillomyrma* and *Decamorium* have recently been recorded from E.A.