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ORIGINS AND AFFINITIES OF THE ANT FAUNA OF MADAGASCAR

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ABSTRACT.- Fifty-two ant genera have been recorded from the Malagasy region, of which 48 are estimated to be indigenous. Four of these genera are endemic to Madagascar and 1 to Mauritius. In Madagascar alone, 41 out of 45 recorded genera are estimated to be indigenous. Currently, there are 318 names of described species-group taxa from Madagascar and 381 names for the Malagasy region. The ant fauna of Madagascar, however, is one of the least understood of all biogeographic regions: 2/3 of the ant species may be undescribed. Associated with Madagascar's long isolation from other land masses, the level of endemism is high at the species level, greater than 90%. The level of 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 Africa than to India and the Oriental region. The striking gaps in the taxonomic composition of the fauna of Madagascar are evaluated in the context of island radiations. The lack of driver ants in Madagascar may have spurred the diversification of Cerapachyinae and may have permitted the persistence of other relic taxa such as the Amblyoponini.

KEY WORDS.- Formicidae, Biogeography, Madagascar, Systematics, Africa, India

RESUME.- Cinquante-deux genres de fourmis, dont 48 considérés comme indigènes, sont connus dans la région Malgache. Quatre d'entr'eux sont endémiques de Madagascar et un seul de l'île Maurice. Parmi les 45 genres malgaches 41 sont considérés comme indigènes. Actuellement 318 espèces et sous-espèces sont décrites de Madagascar et 381 de la région Malgache. La faune des fourmis est pourtant l'une des moins connues de toutes les régions biogéographiques: on estime que 2/3 des espèces n'ont pas été décrites. Lié au long isolement de Madagascar, le taux d'endémisme est très élevé à l'échelle spécifique et pourrait dépasser 90%. Le niveau de diversité générique est comparable à celui des autres régions biogéographiques. Par comparaison, la composition générique ou spécifique de la faune de fourmis malgaches paraît plus étroitement liée à celle de l'Afrique qu'à celle de l'Inde ou de la région orientale. Les lacunes frappantes dans la composition taxinomique de la faune Malgache sont évaluées dans le contexte des radiations insulaires. L'absence des dorylines (fourmis voyageuses) est supposée avoir stimulé la diversification des Cerapachyinae et probablement permis la survie de lignées ancestrales de fourmis comme celle des Amblyoponini.

MOTS-CLES.- Formicidae, Biogéographie, Madagascar, Systématique, Afrique, Inde

INTRODUCTION

Madagascar with its large size and varied topography, offers a diverse array of habitats occupied by a highly endemic and species rich ant fauna. In this manuscript, I discuss the species richness and endemism on the island, and provide a summary of the generic affinities of the Malagasy ant fauna to the Afrotropical and Oriental

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biogeographic 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. I contrast this pattern with that found for India. These themes are further elaborated in FISHER (in press a).

SPECIES DIVERSITY AND ENDEMISM

In the following discussions and analyses, Madagascar includes the coastal islands (*e.g.*, Nossi Bé, St. Marie), and the Malagasy Region refers to Madagascar and neighboring islands of the Indian Ocean: Mauritius, Reunion, Seychelles, Rodrigues, Aldabra, Farquhar, Chagos, and the Comoros Islands. In 1893, DALLA TORRE listed 119 Malagasy species (excluding subspecies), and WHEELER (1922) enumerated 237 species (excluding subspecies) for the Malagasy Region. There are currently a total of 288 species (381 including subspecies) for the Malagasy region and 243 species (318 including subspecific names) in Madagascar alone. The small increase in new species described since 1922 does not reflect a saturation of collecting of a well-known fauna, but the lack of new material. 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 level of endemism is extraordinary, with 90% of the taxa endemic to Madagascar alone, and 96% endemic to the Malagasy region. The level of endemism may even be greater in the eastern forests of 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 b).

AFFINITIES TO AFRICA AND THE ORIENT

To investigate the origin and affinities of the ants of Madagascar, I compared the number of genera in common with neighboring land masses of India and Africa which were all once united in Gondwana (SMITH *et al.*, 1994). To further understand affinities with the African ant fauna, I have compared the genera of Madagascar with geographically distinct subregions within Africa: West Africa (W.A.), East Africa (E.A.), and southern Africa (S.A.) (For a discussion, definition, and the list of genera of these regions and subregions, refer to FISHER, in press a).

In Table I, I list the 52 genera recorded from the Malagasy region. Forty-eight are estimated to be indigenous to the region, of which 4 are endemic to Madagascar and 1 to Mauritius. For the island of Madagascar, 45 genera are recorded, of which 41 are considered to be indigenous. 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.

The richness of 48 genera in Madagascar is comparable with other tropical regions. In a comparison of the log of the total number of genera present in each of the biogeographic regions and subregions, and of the log of the area of each region, the Malagasy region is not depauperate. The slope of the log-log relationship has a z-value of 0.224 ($R^2 = 0.61$) and the log number of genera in the Malagasy region falls very close to this line.

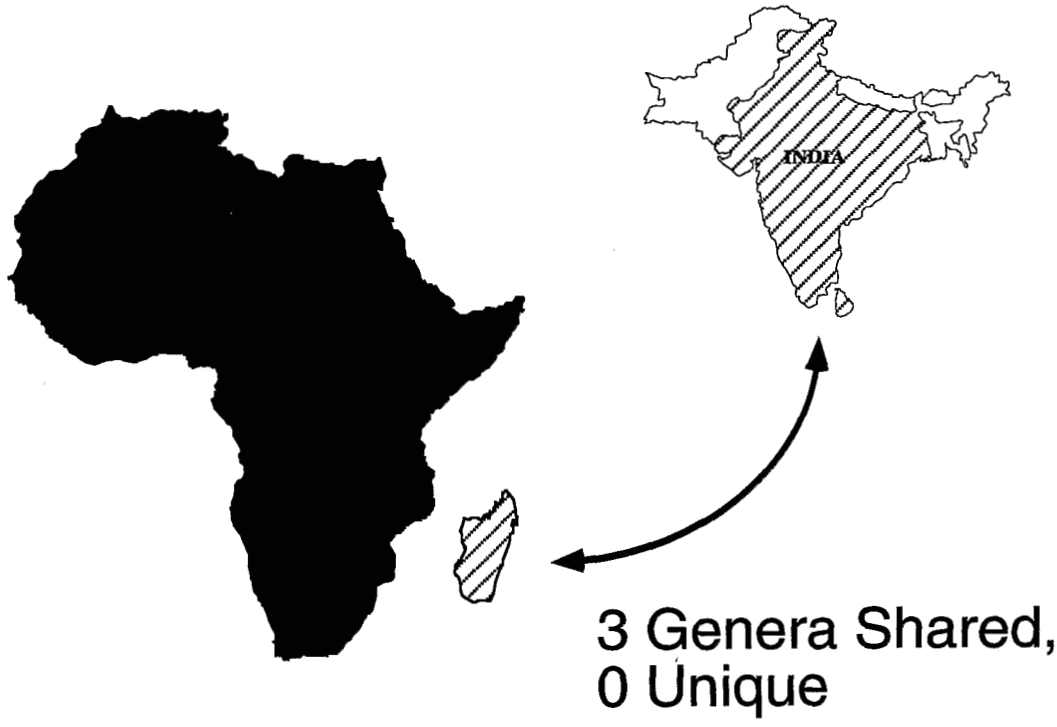

Fig. 1. Three genera are shared between the Malagasy region and Peninsular India (included Sri Lanka, but excludes Bhutan, Nepal, Pakistan, Bangladesh, and Assam) and are not found in the Afrotropical region. These genera are not uniquely shared since they are found in other biogeographic regions.

Three genera, *Aphaenogaster*, *Kyidris*, and *Vollenhovia*, are shared between the Malagasy region and India and are not found in Africa. These three genera are found in other biogeographic regions and thus are not uniquely shared between the Malagasy region and India (Fig. 1).

Nine genera are shared between the Malagasy region and Africa and are not recorded from India:

Anopolepis
Glamyromyrmex
Mystrium
Pristomyrmex
Terataner
Discothyrea
Melissotarsus
Prionopelta
Simopone

Melissotarsus, and *Terataner* are the only genera uniquely shared between the Malagasy region and Africa (Fig. 2). *Simopone*, *Mystrium*, *Prionopelta*, *Discothyrea*, and *Pristomyrmex* are also found in the Oriental biogeographic region and it is possible that these genera may have gone 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 (2 genera uniquely shared with Africa, 0 with India and the Oriental regions). Two additional analyses support the close relationship between Africa and Madagascar. Results from a cluster analysis (single linkage) and an analysis of faunal similarity using the Jaccard Index (MAGURRAN, 1988) of the genera present in each biogeographic region, indicate that the Malagasy and African Regions are most similar (see FISHER, in press a). The Jaccard Index also indicates that within Africa, the southern and East Africa regions are the most similar to Madagascar.

The close relationship of Africa and Madagascar is also supported at the level of species-groups and species. For example, of the 36 described species of *Tetramorium* in the Malagasy region (BOLTON, 1979), 29 are endemic, 4 are shared with Africa, and 3 are pantropical tramp species. Bolton organized the taxa into 8 species groups of which 3 are endemic to Madagascar, 2 are shared with Africa and 3 are widespread. In addition, 3 indigenous species from the Malagasy region are shared with Africa, while none are shared with the Oriental or Indo-Australian regions. Affinities at the species-group and species level with the Oriental and Indo-Australian regions 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 Africa and India or the Orient but not in Madagascar:

Aenictus
Carebara
Centromyrmex
Dorylus
Leptanilla
Myrmicaria
Paedalgus
Polyrhachis
Rhoptromyrmex
Sphinctomyrmex
Calyptomyrmex
Cataglyphis
Cryptopone
Epitritus
Messor
Oecophylla
Pheidologeton
Probolomyrmex
Pseudolasius

If we assume that the ant genera found on Madagascar arrived primarily by dispersal (see discussion of the origin of genera below), the nesting behavior of the nineteen genera listed above may help explain which ant genera successfully colonized the island. These taxa nest in either the ground, in termite mounds, in the leaf litter or in rotten wood, or 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 preformed plant cavities are best suited for surviving long distance dispersal by rafting across an ocean. Ants could weather such a journey for many months by sealing off the entrance of the nest and feeding on their own larvae. A similar method of dispersal could also have been used by a hibernating ancestor of the present day lemurs to raft across the Mozambique Channel. The arrival of the driver ants (*Aenictus and Dorylus*) and *Leptanilla* to Madagascar may also have been hindered by the fact that queens are wingless, and colonies reproduce by budding.

The driver ants which dominate the forest floor, and the weaver ants (*Oecophylla*) which dominant 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 & WILSON, 1990; GOTWALD, 1995).

Because of their absence from Madagascar, the population dynamics of Malagasy ant communities may differ greatly from other Old World ant communities. A comparison of African and Malagasy ant communities provides a natural experiment for evaluating the effect of these dominant African ants.

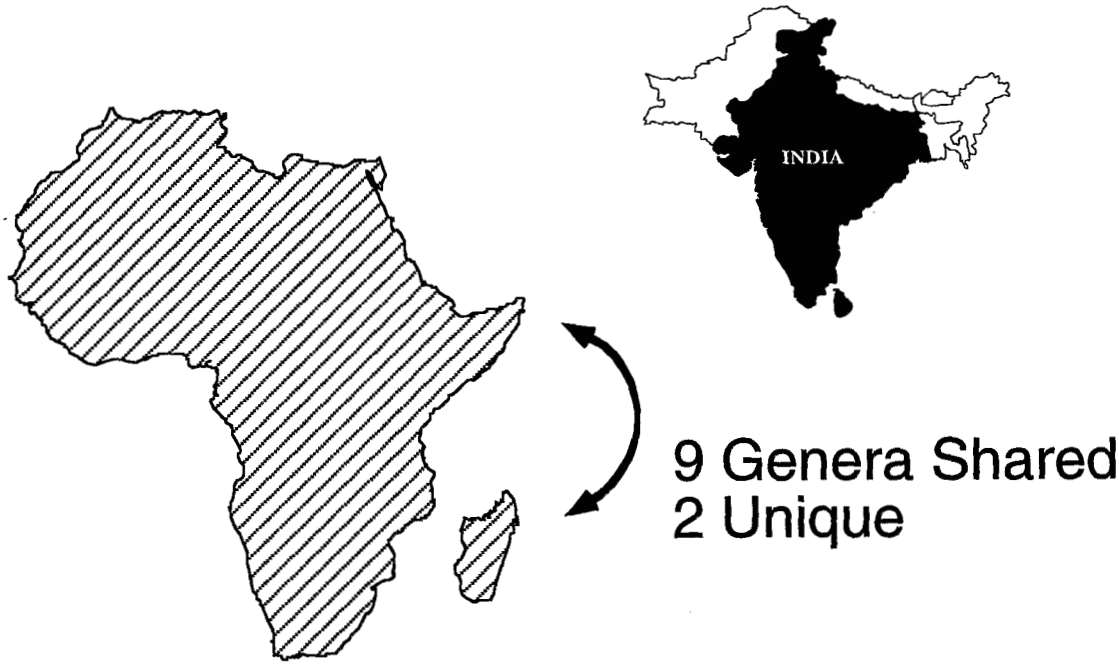

Fig. 2. Nine genera are shared between the Malagasy region and Africa and are not recorded from Peninsular India. Of these, 2 genera are uniquely found in the Malagasy and Afrotropical regions.

The lack of driver ants in Madagascar may have spurred the diversification of the tribe Cerapachyinae (*Cerapachys* and *Simopone*) on the island (HÖLLDOBLER & WILSON, 1990; OLSON & WARD, in press). The morphologically diverse and species rich *Cerapachys* on the island include species that are morphologically convergent to the driver ant genus *Aenictus* found in Africa and exhibit army ant habits of raiding the nests of other ants (BROWN, 1975; pers. obs.). In the absence of Dorylinae, *Cerapachys* may have been free to develop and capitalize on their army ant-like predatory behavior, and thus represent a monophyletic island radiation of species. On the other hand, this clade of *Cerapachys* may have been found once in other biogeographic regions, but now only persists in Madagascar in the absence of driver ants.

Mystrium, in the tribe Amblyoponini which possesses many morphologically primitive characters, 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 6 described species of *Mystrium* from Madagascar,

while only one species from West Africa and one species from the Oriental, Indo-Australian, and Australian regions are known.

ORIGINS OF THE ANT FAUNA

The origin of the ant fauna of Madagascar must be inferred from our understanding of geological history and our limited fossil records of ants. The high number of extant ant genera found in Baltic amber fossils (Oligocene) suggests that many extant genera are at least 35 million years old (HÖLLDOBLER & WILSON, 1990). The almost complete lack of extant genera found in Cretaceous and Eocene deposits implies that most modern taxa may not have been abundant or even extant before the Oligocene. If the fossil data accurately reflects the history of ants, then all modern genera most likely evolved after the complete separation of Madagascar from Africa (around 120 Ma; RABINOWITZ *et al.*, 1983) and after the separation of India from Madagascar (approx. 90 Ma; STOREY *et al.*, 1995).

An alternative hypothesis, though not supported by the fossil record, is that some extant genera are much older and may date back to around the mid-Cretaceous at the time of the break up of Gondwana. BARONI URBANI *et al.* (1992) offer some indirect evidence to support this. They hypothesized that the Old and New World army ants are each others closest relative, and thus, form a monophyletic group. Since all modern taxa have wingless queens and reproduce by budding, it is most parsimonious to assume that the ancestor of this clade also had wingless queens. The present distribution of Ecitoninae in the New World and Dorylinae in the Old World, may be explained by a common ancestor that was 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 Dorylinae are absent from Madagascar, this common ancestor may have evolved after the complete separation of Madagascar from Africa more than 120 Ma (RABINOWITZ *et al.*, 1983). Other genera which have a present day Gondwanaland distribution, such as in the tribe Amblyoponini, may also be much older than predicted from the fossil record.

THE INDIA ENIGMA

In summary, Madagascar can be described as an isolated landmass that has a highly endemic fauna characterized by close affinities to the Afrotropical region with many groups that have apparently undergone unique island radiations, and relict taxa that have numerous plesiomorphic characters. These patterns can be explained by the proximity of Madagascar to Africa and its long history of isolation. Peninsular India, the sister continent of Madagascar, does not follow these predictions. Along with Madagascar, it began separating from Africa 150 Ma and remained joined with Madagascar until around 90 Ma before splitting off, moving northward, reaching its present position approximately 50 Ma (RABINOWITZ *et al.*, 1983; STOREY *et al.*, 1995). Therefore India was isolated with Madagascar for 60 million years and completely isolated for an additional 40 million years. India is over five times as large as Madagascar, but contains only 3 endemic ant genera, *Aneuretus* and *Stereomyrmex* in Sri Lanka, and *Indomyrma* in the Western Ghats in India, two of the most mesic localities in the region.

What happened to the endemic fauna that would be predicted from India's long isolation? Did the endemic taxa go extinct after initial contact with Asia due to the invasion of superior competitors? Did India experience dramatic climatic changes that drove taxa to extinction, leaving the two endemic taxa in the mesic localities? Or was India in contact with other landmasses via land bridges or filters during its sojourn in the Indian Ocean, and therefore not an isolated land mass for 100 million years?

BRIGGS (1989) suggested that during the Cretaceous, India moved northward and became in direct or close contact with Northern Africa. Faunal interchange that occurred during this contact with Africa, or during later contact with Asia could have allowed superior competitors to colonize India, driving endemic taxa to extinction. The mechanism for the absence of endemic ant taxa is not known, but the pattern has been noticed for vertebrate groups (BRIGGS, 1987; SAHNI, 1984).

CONCLUSIONS

Our understanding of the origins and affinities of the ant fauna of Madagascar is far from complete. We understand even less about the biogeographic patterns of ants within the island. Almost every one of the 48 indigenous genera is in need of revision. Nonetheless, evidence does suggest that the Malagasy ant fauna is more closely related to the Afrotropical fauna than to the Oriental or Indo-Australian faunas. The absence of ecologically dominant genera found in Africa, such as weaver and driver ants, may have created unique opportunities for the ants of Madagascar, allowing some to persist and others to radiate. The absence of a high number of endemic genera in India, Madagascar sister landmass for 60 million years, poses interesting biological and geological questions.

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Table I. Ant Genera found in the Malagasy region. Endemic genera are indicated in bold, and genera known only from probable introduced species are noted with an *. Genera that are unique to Mauritius, Seychelles, and Reunion are also indicated.

DOLICHODERINAE
*Ochetellus** [Mauritius]
Tapinoma
Technomyrmex

FORMICINAE
Acropyga [Mauritius]
Anopolepis [Reunion]
*Brachymyrmex**
Camponotus
Lepisiota
Paratrechina
Plagiolepis

PSEUDOMYRMECINAE
Tetraponera

MYRMICINAE
Aphaenogaster
Cardiocondyla
Cataulacus
Crematogaster
Eutetramorium
Glamyromyrmex
Ireneopone [Mauritius]
Kyidris
Leptothorax
Melissotarsus
Meranoplus
Metapone
Monomorium
Oligomyrmex
Pheidole
Pilotrochus
Pristomyrmex [Mauritius]
*Quadristruma** [Seychelles]
Serrastruma
Smithistruma
Solenopsis
Strumigenys
Teratanер
Tetramorium
Undescribed genus

CERAPACHYINAE
Cerapachys
Simopone

PONERINAE
Adetomyrma
Amblyopone
Anochetus
Discothyrea
Hypoponera
Leptogenys
Mystrium
Odontomachus
Pachycondyla
Platythyrea
Platythyrea
*Ponera**
Prionopelta
Proceratium