

BIOGEOGRAPHY OF ANTS IN EASTERN MADAGASCAR

Brian L. FISHER¹ & Derek J. GIRMAN²

¹ Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA : e-mail : bfisher@calacademy.org

² Department of Biology, Sonoma State University, 1801 E. Cotati Ave., Rohnert Park, California 94928, USA : e-mail : girman@sonoma.edu

ABSTRACT.- Parsimony Analysis of Endemism (PAE) is used to determine the relationship among 20 sites in eastern Madagascar based on the distribution of 69 species of dacetone ants. The single most parsimonious cladogram suggests 4 major regions of endemism: littoral forest, south-central, a northern lowland, and a northern montane. Disjunct montane distributions suggest a model of climate-induced vicariance driven by the dynamic environmental history of the island during the Pleistocene. The division of eastern Madagascar into a northern and south-central region is supported in part with area cladograms based on the molecular phylogeny of the ant genus *Mystrium*. The phylogenetic structure among *Mystrium* species and among populations of these species was inferred from DNA sequences from the COI gene. Overall, results demonstrate the historical importance of elevation, latitude, and geological substrate in delimitating areas of endemism in eastern Madagascar.

KEY-WORDS.- Formicidae, Dacetone, Amblyoponini, Endemism, Parsimony Analysis of Endemism, Mitochondrial DNA

RESUME.- L'analyse parcimonieuse de l'endémisme a été utilisée pour déterminer la relation biogéographique entre 20 sites de la région Est de Madagascar. L'analyse est basée sur la distribution des 69 espèces de fourmis dacétonines. Le plus parcimonieux des cladogrammes suggère l'existence de quatre régions d'endémisme : notamment la forêt littorale, le sud central, la région basse du Nord et la région montagneuse du nord. Les distributions des montagnes disjointes suggèrent le modèle de vicariance induit par le climat et par l'histoire de la dynamique environnementale de l'île pendant le Pléistocène. La division de l'Est de Madagascar en région Nord et Sud-Central est confirmée en partie par les cladogrammes des régions biogéographiques basées sur l'analyse phylogénétique moléculaire des fourmis du genre *Mystrium*. La structure phylogénétique entre les espèces des fourmis de ce genre et entre les populations de ces espèces a été obtenue à partir de la séquence de l'ADN du gène COI. En résumé, les résultats illustrent l'importance historique de l'altitude de la latitude et du substrat géologique pour délimiter les régions d'endémismes de l'Est de Madagascar.

MOTS-CLES.- Formicidae, Dacetone, Amblyoponini, Endémisme, Parcimonie Analyse de l'endémisme, ADN mitochondrial

INTRODUCTION

Delimitating areas of endemism is fundamental to both studies in historical biogeography and conservation planning. The majority of data available for analyzing patterns of endemism within Madagascar are restricted to selected vertebrate and plant groups (Lourenço 1996, Ganzhorn *et al.* 1997). Although insects make up the vast majority of animal species in Madagascar, few studies have addressed the biogeographic structure of insects (Paulian 1961, 1972). This inability to clearly define patterns of

endemism within Madagascar for these major taxonomic groups is one of the principal obstacles to establishing priorities for conservation within the island and is the first step to understanding historical events that have shaped the evolution of the island's flora and fauna. Recent progress in ant taxonomy and research permits, for the first time, an analysis of endemism of selected groups of ants in eastern Madagascar.

Ants are one of the most ecologically and numerically dominant families of organisms in almost every terrestrial habitat throughout the world. This dominance is even more remarkable since ants include only about 1% of all described insects species. Over the last 7 years, collections and field observations in Madagascar by Fisher and others have provided important collections necessary for research on the taxonomy, biogeography and origin of the ants of Madagascar. These studies have suggested that ants are well suited for analyzing historical patterns in Madagascar. The group is highly diverse, with an estimated 1000 species in the Malagasy region of which 96% are endemic to the island (Fisher 1996b, 1997). In addition, the ranges of many ant species are « fine-grained, » exhibiting restricted elevational and regional distributions (Fisher 1996a, 1998, 1999a).

The objective of this study is to evaluate the biogeographic structure of ants in eastern Madagascar based on two data sets. First we will analyze patterns of endemism of the ant tribe Dacetoniini from 20 sites based on the recently completed revision of this group in Madagascar. Second, as part of a larger study on the origin and evolution of the amblyoponine ants, we present results that pertain to the biogeography of the genus *Mystrium* within eastern Madagascar. We examine phylogenetic structure among *Mystrium* species and among populations of these species using DNA sequences from the COI gene.

METHODS

ENDEMISM OF DACETONINE ANTS

Background

The ant tribe Dacetoniini is composed of two genera in Madagascar, *Strumigenys* and *Pyramica*, which are hypothesized to form a monophyletic clade within this tribe (Bolton 1999). Distribution data for the analysis of endemism is based on the revision of *Strumigenys* by Fisher and *Pyramica* by B. Bolton which is now approaching publication. Dacetonine ants are predatory ants that rely on the trap-like action of their often long mandibles to secure food. Previous studies in Madagascar have shown *Strumigenys* to be a useful indicator species. This genus is an accurate predictor of total ant species richness at a locality and is useful for assessing patterns of similarity and diversity among localities (Fisher 1999b). The *Strumigenys* revision includes 71 endemic species to Madagascar of which 70 are newly described. The revision of *Pyramica* includes 12 endemic species to Madagascar, all of which are newly described. The high number of new species described in this revision underscores the importance of biodiversity studies and modern collection methods for systematic research. Large series of most of the undescribed species were accumulated during quantitative faunistic inventories conducted by Fisher and colleagues during the last 7 years.

Based on the distribution of dacetone species-groups throughout the world, the Malagasy *Strumigenys* show a mix of African and Asian influence, while the island's *Pyramica* species show a strong Asian influence. There are 50 species of *Strumigenys* in Africa, while there are 74 in Madagascar. The Malagasy taxa are divided into 9 species groups: 4 species-groups are endemic to Madagascar (19 spp.), 2 species-groups are shared with Asia (2 spp.), while 3 of the largest species-groups are shared with Africa (53 spp.). In contrast, there are 81 *Pyramica* species in Africa, while there are only 15 total in Madagascar. The 12 endemic *Pyramica* species are divided into 4 species groups, with none shared with Africa, 1 species group is endemic to Madagascar (1 sp.), and the 3 remaining species-groups are shared with Asia (11 spp.). It is unclear why *Strumigenys* has undergone this diverse island radiation while *Pyramica* has not.

Parsimony Analysis of Endemism

Parsimony Analysis of Endemism (or endemism) (PAE) classifies areas by their shared endemic taxa according to the most parsimonious solution (Rosen 1988; Rosen & Smith 1988). Areas are treated as taxa and taxon distributions are treated as characters in a standard cladistic analysis. PAE data consists of area x taxon matrices. The presence or absence of each taxon at a site provides the basis for the binary (0,1) character data in the matrix. PAE does not require data on the phylogenetic relationships among the taxa, but it does rely on the assumption that each taxon is monophyletic. The resulting cladograms from parsimony analysis represent nested sets of areas based on their shared endemic taxa.

For the present study, we restricted our analysis to the 19 localities that have received a comparable level of collecting effort (Fig. 1). The majority of the records from these localities are based on collections by Fisher (1996a, 1998, 1999a; Fisher & Razafimandimby 1997; Fisher *et al.* 1998), but additional records are from collections by Alpert, Betsch, Brown, Peyrieras, Ratsirarson, Razafimandimby, and Ward. At these 19 localities 69 species of dacetone endemics to Madagascar were collected.

Treating different elevations from within each of the 19 localities as one area in the analysis could obscure important biogeographic structure. On the other hand, keeping each collection from a different elevation separate would result in over 150 separate areas and would make meaningful generalizations of biogeographic history impractical using PAE analysis. This would be especially true in this study because of the unequal sampling in each of the 150 areas. To evaluate which elevations within a locality should be kept separate, we performed an initial PAE with collection sites grouped into 400 m elevation ranges. Elevation sites from the same locality that nested together («sister» areas) in the preliminary analysis were combined in the final analysis. This preliminary analysis suggested that high and low elevation sites in Manongarivo, Anjanaharibe-Sud, and Masoala should be analyzed as separate areas. The three nearby littoral forest blocks near Tolagnaro (Ste. Luce, Mandena, and Petriky) contained the same species so they were combined into one site for the final analysis. For final analysis, we used a matrix with the 20 sites and elevations listed in figure 2.

PAE was performed using the software program PAUP* version 4.0 (Swofford 1999) with the following options: character-state optimization = ACCTRAN, search = HEURISTIC, with 10 replications for stepwise addition. Trees were rooted using a hypothetical outgroup area devoid of all species. All characters were analyzed without differential character weighting.

PHYLOGENY OF *MYSTRIMUM*

Background

We present results from a larger study to examine the phylogeny, of the tribe Amblyoponini, which may include the sister group to all or most ants (Wilson 1971; Sullender & Johnson 1998). These ants are specialized arthropod predators and are thought to possess many plesiomorphic anatomical and behavioral character states (Hölldobler & Wilson 1990). Faunistic studies conducted in Madagascar have resulted in the collection of the rarest members of the tribe and the discovery of a new genus and a number of new species (Ward 1994; Fisher unpublished data). For the first time, a detailed morphological and molecular phylogenetic study of this group is possible.

The hallmark of the Amblyoponini is the broad attachment of the second abdominal segment (petiole) to the third segment (gaster) which is similar to extant vespid and tiphiid wasps. This striking similarity has driven the acceptance of the petiole structure of the Amblyoponini as the ancestral condition of the Formicidae (but see Ward 1994; Hashimoto 1996). In addition to its remarkable morphology, Amblyoponini exhibits many striking behaviors that have been hypothesized to be primitive within ants. Queens of *Mystrium* and *Amblyopone* practice a form of nondestructive cannibalism (Masuko 1986; Wheeler & Wheeler 1988; Fisher, pers. obs.). Queens of *Mystrium* cut holes in the integument of the larvae and feed upon the exuding hemolymph. Unlike other ants which practice social food transfer, *Mystrium* are exclusively dependent on the hemolymph of their own larvae as a food source. In this contribution we present results on *Mystrium*, one of the 7 Amblyoponini genera known from the worker cast and the most diverse in Madagascar with possibly 6 species. Outside of Madagascar, *M. silvestrii* is known from a single collection on Mount Cameroon, West Africa, an undescribed species is known from Sulawesi and *M. camillae* is known from South-east Asia.

Molecular methods

Acquisition of molecular data was directed at inferring the phylogeny of the amblyoponine genera, and addressing the origin of these genera in Madagascar. The analysis includes three species of *Mystrium* that are restricted to eastern Madagascar (species A, B, and C), one *Mystrium* species from Borneo (*M. camillae*), and two outgroup taxa from the same subfamily Ponerinae, *Discothyrea* (Ectatommini) and *Hypoponera* (Ponerini). The taxa from Madagascar can not be named until taxonomic revision is completed.

The polymerase chain reaction (PCR) was used to isolate and amplify a 790 base pair region of the COI gene from *Mystrium* populations in eastern Madagascar (Saiki *et al.* 1980). Primers for this region included published primers Ben and Jerry (Simon *et al.* 1994; Lunt *et al.* 1996; Schultz 1998) and recently developed unpublished primers (Hasegawa, unpublished data). Either an m13 reverse or m13 forward 5' tail was attached to each primer. Double-stranded PCR products were generated in 50 μ l reactions consisting of buffer (100 mM Tris-HCl, pH 9.0, 500 mM KCl, 1% Triton X-100), 2.5mM MgCl₂, 0.8 mM dNTPs, 0.1 mM of each primer, 1.25 units of Promega Taq DNA polymerase, 20-60 ng of genomic DNA in a Perkin Elmer Cetus model 2400 thermocycler. Products were isolated using a Qiagen PCR product isolation kit and then used in a cycle sequencing reaction using fluorescently labeled m13 forward and reverse primers (Thermosequense Kit - Amersham). The sequencing products were run in a 6%

acrylamide gel on a Licor 2-laser automated DNA sequencer in the core sequencing facility at Sonoma State University. Sequences were initially aligned and manipulated using Sequencher 3.0, however, all sequences and alignments were confirmed and adjusted by visual inspection of chromatograms. Further confirmation of the COI sequence was established by comparison to published sequences from this region as reported in Genbank.

Phylogenetic analysis of the resulting sequences included a parsimony analysis to obtain trees via heuristic searches using TBR branch swapping with ten random taxon addition replicates to reduce the chance of missing the most optimal solution due to being isolated within a tree island (Maddison 1991; Page 1993). We used the non-parametric bootstrap to assess support of individual nodes in our trees. The bootstrap estimates sample variance through random resampling with replacement (Felsenstein 1985). In addition, we constructed a neighbor-joining tree using the Kimura two-parameter distance model (Kimura 1980; Saitou & Nei 1987).

RESULTS

PAE OF DACETONINE ANTS

Of the 19 localities shown in figure 1, the most species rich were in the north: Masoala (5 - 825 m) with 25 spp. and Anjanaharibe-Sud (875 - 1995m) with 24 species. Andohahela (420 - 1250 m) and Ivohibe (900 - 1575 m) in the south had 14 and 13 species, respectively. The number of unique taxa at each of these localities was positively correlated with the number of species at the locality. For example, 4 unique species were recorded at both Masoala and Anjanaharibe-Sud, while in Andohahela, and Ivohibe only 1 and 0 species, respectively, were unique.

The PAE data matrix included 69 species and 20 sites (Table I). A single most parsimonious cladogram of length 138 was found with consistency index of 0.50 (Fig. 2). Of the 69 species included in the analysis, 23 are uninformative (single site endemics). At least one unique species was found at 15 of the 20 sites.

In eastern Madagascar, four major regions were identified: (1) a littoral forest area supported by 2 endemic species; (2) a south-central area supported by 13 endemic species; (3) a northern lowland area supported by 12 endemic species; and (4) a northern montane area supported by 5 endemic species.

PHYLOGENY OF *MYSTRIMUM*

The three most parsimonious trees had a length of 620 steps with 199 informative characters (consistency index 0.65, retention index 0.626). The levels of sequence divergence within Malagasy species ranged from 0.2% to 8.0%, whereas between Malagasy species sequence divergences ranged between 11.5% and 14% (Table II). For comparison, the sequence divergence between any *Mystrimum* species and the outgroup species ranged between 16.7% and 21.6%. Phylogenetic analyses with the third codon position weighted at one-tenth other codon positions or eliminated altogether did not alter the arrangement of taxa in the cladogram. Moreover, the neighbor-joining tree based on Kimura 2-parameter distances also agreed with the parsimony analysis. A strict consensus tree based on 1000 bootstrap replicates shows a division between northern and southern populations of *Mystrimum* species B and C (Fig. 3). Populations of species

A are associated in a single clade in two of the three parsimony trees and in the neighbor-joining tree. However, this association did not appear in more than 50% of the bootstrap replicates and so was reduced to a polytomy.

The three *Mystrium* species examined from Madagascar do not appear to form a monophyletic group. Taxa A and C are equally or more closely related to *M. camillae* from Borneo than they are to group B from Madagascar. The bootstrap values that support the association of species A and C and *M. camillae* increases when the third codon is excluded, from 61 to 67. Moreover, the levels of sequence divergence between *M. camillae* and Malagasy *Mystrium* samples are equivalent to those among Malagasy *Mystrium* species, 12.1% to 14.0% (Table II).

DISCUSSION

The distribution of 69 dacetone species from PAE analysis suggest 4 major areas of endemism in eastern Madagascar: littoral forest, south-central, northern lowland, and northern montane. This pattern demonstrates the importance of elevation, latitude, and geological substrate in the delimitation of areas of endemism in eastern Madagascar.

Littoral forest

The littoral forest sites are narrowly restricted blocks of coastal forest. Botanists have stressed their unique plant assemblages (Du Puy & Moat 1998; Schatz, this volume) and this study suggests insect assemblages in littoral forests are also distinct from the adjacent lowland forest insect assemblages. The remaining restricted blocks of littoral forests are under sever threat from mining and human pressures and most are without protective status (Du Puy & Moat 1998). Even if we are to preserve the remaining blocks, the survival of the native populations in these blocks is not certain. The presence of exotic ant species in disturbed and fragmented littoral forest blocks may reduce native ant populations (Fisher *et al.* 1998). The long-term effects of invasion of exotic ants in the Malagasy region could lead to the extinction of a large component of the endemic arthropod fauna.

Northern montane

The northern montane sites exhibit a disjunct distribution of endemic species. The montane forests of Manongarivo and Anjanaharibe-Sud group as a separate region from the adjacent lowland sites from these same mountains. A measure of the strength of these regions is the number of additional steps necessary to group the montane sites with their adjacent lowland sites. To group the 875 m site in Anjanaharibe-Sud with the higher elevation site in Anjanaharibe-Sud, 6 additional steps are required. To group the Manongarivo sites together, 5 or 6 additional steps are required, depending on which site is moved.

There are two plausible hypotheses to explain these disjunct distributions: (1) long distance dispersal or (2) vicariance. Though dispersal can not be ruled out as an explanation, the dynamic environmental history of the island during the Pleistocene may explain the current distributions. During cooler periods, montane forests belts may have lowered, forming a contiguous zone of montane forests between these mountains (Burney 1997 and refs therein). Montane vicariance occurred when the climate warmed and montane ant populations became isolated on mountain tops. This model of climate-

induced vicariance was also suggested by Raxworthy and Nussbaum (1997) to explain disjunct montane distributions of reptiles. Alternatively, montane vicariance could have occurred by the following scenario. Manongarivo and Anjanaharibe-Sud are separated by the highest massif in Madagascar, Tsaratanana, which reaches 2874 m and dominates the landscape in north-central Madagascar. Species originally restricted to montane forest on Tsaratanana could have colonized Manongarivo and Anjanaharibe-Sud during cooler periods when montane forest sites were contiguous across these mountains. When the climate warmed, the montane ant populations became isolated on Manongarivo and Anjanaharibe-Sud.

Northern lowland and South-central

The northern lowland sites formed a distinct region from the south-central sites. The adjacent boundaries of these areas of endemism occurs in the region of Andriantantely, Didy and Périnet. The southern-most northern site, Andriantantely (430 m), is adjacent to the south-central sites of Didy (960 m) and Périnet (900 m). Though the division between a southern and northern region is supported by many endemic species to each region, this pattern could be explained by a lack of collections from low elevation sites in the south-central region. The northern lowland sites may be distinct only because there are almost no lowland southern sites. Currently, the only inventory conducted below 700 m in the southern region is in Andohahela. Therefore, equal effort sampling of elevations from the north and south will be necessary to evaluate the distinction between lowland areas in the north and south.

Sambirano region

Biogeographic divisions in Madagascar based on plant data have often included a distinct Sambirano region in the north-west (reviewed in Lowry *et al.* 1997). The Sambirano region is defined as low elevation (< 800 m) forest in a narrow portion of the northwestern coast where the moist climatic conditions typical of the east extend to the west coast. The only site included in the analysis from the Sambirano region is Manongarivo. Our results tentatively support this region. First, the montane forest sites of Manongarivo grouped with the montane sites of Anjanaharibe-Sud. Second, the lowland Manongarivo forest sites (< 800 m), however, did not group with the other lowland sites in the east but formed an isolated area. The lowland Manongarivo site did share two unique species with Vohibasia, Mt. d'Ambre, and Isalo, suggesting that additional inventories in the west may demonstrate that they are more closely related to western than to eastern forests. Additional surveys within the Sambirano region and in the west are necessary before we can fully evaluate the presence of a Sambirano region of endemism for ants.

Concordance with *Mystrium*

The division of southern and northern forest sites in the PAE cladogram for dacetone ants agrees in part with the area cladogram for *Mystrium* (Fig. 3). The PAE reveals a north-south split among groups of endemic species; while within *Mystrium* species C and B, northern and southern populations form distinct clades and suggest an intraspecific « phylogeographic » north-south split. The relationship between distributional change of biotas as indicated by patterns of congruent distributions (PAE of dacetone ants) and the history of areas as implied by population and species histories

(*Mystrium* area cladogram) may suggest that these patterns have been influenced by the same events (Cracraft 1994; Silva & Oren 1996). Alternatively, there could be two different events, from different time scales that have produced these similar patterns.

The genetic data may further support the distinction between the littoral forest sites and neighboring lowland sites. Samples from Mandena and Ste. Luce are very closely related (0.6% sequence divergence) and are clearly more distantly related to a sample from the southern 900 m forest site in Ivohibe (6.4% to 6.7% sequence divergence). Thus, with further genetic sampling, we may elucidate fine-scaled patterns of genetic subdivision among sites. Moreover, it appears that these divisions may support the areas identified by PAE. However, area cladograms based on phylogenies of additional samples within *Mystrium* and with additional taxa are necessary to evaluate the generality of these biogeographic patterns.

Finally, the genetic data suggest that the historic patterns of dispersal of *Mystrium* to and from Madagascar may be more complex than a single colonization event leading to an isolated radiation on Madagascar. Though our analyses are not conclusive (weak bootstrap support), the close relationship of *M. camillae* from Borneo to the three Malagasy species examined suggests two possibilities. First, there may have been multiple colonizations of Madagascar by *Mystrium* to provide the diversity of *Mystrium* species seen on Madagascar today. Alternatively, the *Mystrium* species found in Borneo is derived from *Mystrium* species that evolved in Madagascar. This latter scenario suggests a dispersal route that perhaps relied on the movement of India across the Indian Ocean. In either case, it opens the door to a complex and old relationship between ants on Madagascar and those found in other regions of the world.

CONCLUSION

The analysis of patterns of endemism of ants in eastern Madagascar suggests the following. Ants have highly restricted distributions and most (75%) of the sites had at least one unique taxon. Though it is impossible to conserve every site in Madagascar, the PAE analysis suggest 4 major areas of endemism that deserve conservation priority in eastern Madagascar: littoral forest, south-central, northern lowland, and northern montane. The phylogenetic analysis of *Mystrium* also supports a division of eastern Madagascar into a northern and southern clade.

These results are based on a single tribe of ants and a preliminary phylogenetic analysis of a genus in a second tribe. The north-south division and the disjunct populations on mountains suggested by the ant data, however, are supported in part by the PAE analysis of reptiles conducted by Raxworthy and Nussbaum (1997). This corroboration may suggest that a general pattern of endemism may be present in Madagascar and that this pattern may be on a much finer scale than that discerned from previous analyses of selected lemur, bird and plant groups. Additional congruent PAE cladograms based on additional distributional records and taxa, and congruent area cladograms from cladistic biogeographic studies are needed before we can be confident that a general pattern of endemism exists in eastern Madagascar.

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Table I. Data set for Parsimony Analysis of Endemism of dacetone ants in eastern Madagascar.

	1	11	21	31	41	51	61
Mnt. Ambre 1000-1100 m	0000000100	0000000000	0000001000	0000000001	0000001000	0010000000	0000000000
Manongarivo 1175-1860 m	0100100100	0000001001	0001001010	0100000000	1100001100	0000000000	001011100
Manongarivo 400-780 m	0100010000	0000000001	0001001000	0100000000	0000001000	0010000010	010010000
Anjanaharibe 1180-1995 m	0110000100	0000101000	1010000000	0100010000	1000001100	0001010001	001001110
Anjanaharibe 875 m	0100000000	0000100010	0000000000	1011000000	0000001000	0001010000	010000000
Marojejy 375 m	0000000000	0000000000	0000001000	0100000000	0000010000	0001000000	010001000
Masoala 5-500 m	1100001000	0010000010	0000110110	0101000100	0000001000	0001000001	010001010
Masoala 825 m	0100001000	0001100010	0000000000	1101000000	0110001101	0000000001	010000010
Tampolo 10 m	0000000000	0010000000	0000010000	1100000000	0000000000	0001100000	000000000
Andriantantely 430 m	0100001000	0000000000	0000111000	1100000000	0000000010	0001000000	011101011
Didy 960 m	0100000000	0000010000	0000011100	0100000000	0000000000	0001000000	010001001
Sandranantitra 450 m	0100001000	0000000000	0000010000	1100000000	0000100010	0001000001	000000010
Perinet 900 m	0000000000	0100011000	0010010000	0100000000	0001001001	0001001000	010001001
Ranomafana 700-1350 m	0101000001	0100010100	0000011000	1100000000	0001000000	0000000100	010001000
Vohibasia 750 m	0100000000	0000000000	0000001000	0000100000	0000001000	0110000000	000000000
Isalo 490-800 m	0000000000	0000010000	0000001000	0000000000	0000000000	0000000000	000000000
Andringitra 785-1995 m	0101000101	1100000100	0000010001	1100001010	0000001000	1000000100	110001110
Ivohibe 900-1575 m	0100000000	0100000000	0000010000	1000000000	0001001000	1000000100	010001111
Andohahela 420-1250 m	0101000000	0000000000	0100010001	1100000000	0001000000	0100000000	010001111
St. Luce, Mandena, Petriky 15 m	0000000010	0000000000	0000010001	0000000000	0000000000	0000100000	010000100

Table II. Pairwise sequence divergence (percent) between samples. Collection site and elevation are indicated for *Mystrium* species A, B, and C.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
1. <i>Discothyrea</i>	-												
2. <i>Hypoponera</i>	15.6	-											
3. <i>M. sp. C</i> Andohahela 330 m	19.3	19.0	-										
4. <i>M. sp. C</i> Andringitra 785 m	20.3	18.9	1.7	-									
5. <i>M. sp. C</i> Andringitra 835 m	20.2	19.0	1.9	0.3	-								
6. <i>M. sp. B</i> Mandena 20 m	19.6	19.6	13.7	13.6	13.6	-							
7. <i>M. sp. C</i> Manongarivo 1175 m	20.0	18.8	7.2	6.5	6.5	13.9	-						
8. <i>M. sp. B</i> Anjanaharibe 875 m	17.6	16.8	11.9	11.6	11.8	7.6	12.5	-					
9. <i>M. sp. B</i> Manongarivo 400 m	19.6	18.2	13.3	12.8	12.8	8.5	14.0	5.1	-				
10. <i>M. sp. B</i> Ivohibe 900 m	18.4	18.1	12.8	12.6	12.7	6.7	12.9	5.6	7.5	-			
11. <i>M. sp. B</i> Ste. Luce 20 m	19.2	19.1	13.4	13.2	13.2	0.6	13.3	7.4	8.0	6.5	-		
12. <i>M. sp. A</i> Marojejy 610 m	20.3	21.7	13.9	13.7	13.7	13.6	13.6	13.6	14.5	12.7	13.4	-	
13. <i>M. sp. A</i> Manongarivo 400 m	19.9	18.9	13.3	13.1	13.0	14.0	12.7	13.4	13.8	13.3	13.7	13.7	-
14. <i>M. camillae</i> Borneo	18.9	18.5	12.9	12.6	12.9	14.0	13.6	12.2	12.3	12.7	13.8	14.0	12.9

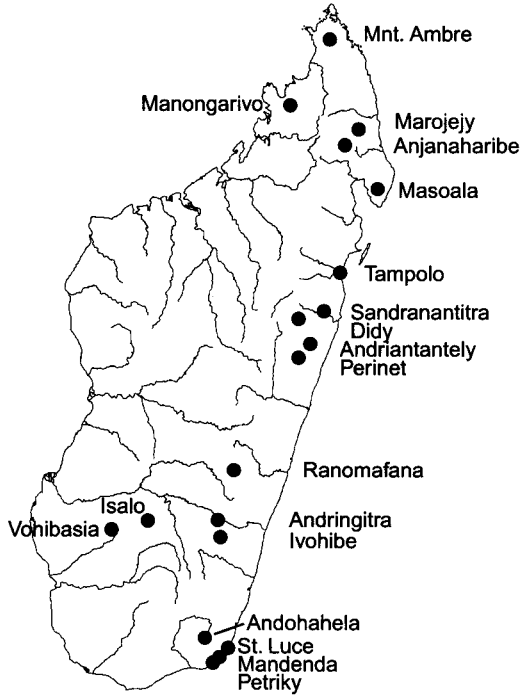


Fig. 1. The 19 collection localities of the 69 species of *Strumigenys* and *Pyramica*.

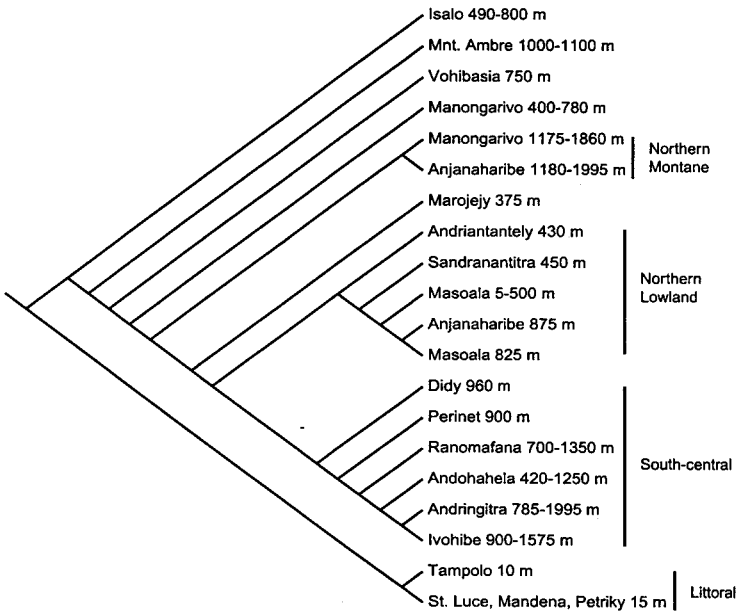


Fig. 2. Relationship among 20 sites in Madagascar based on a PAE of 69 species of dacetonines endemic to Madagascar. This is single most parsimonious tree (length 138, consistency index 0.50).

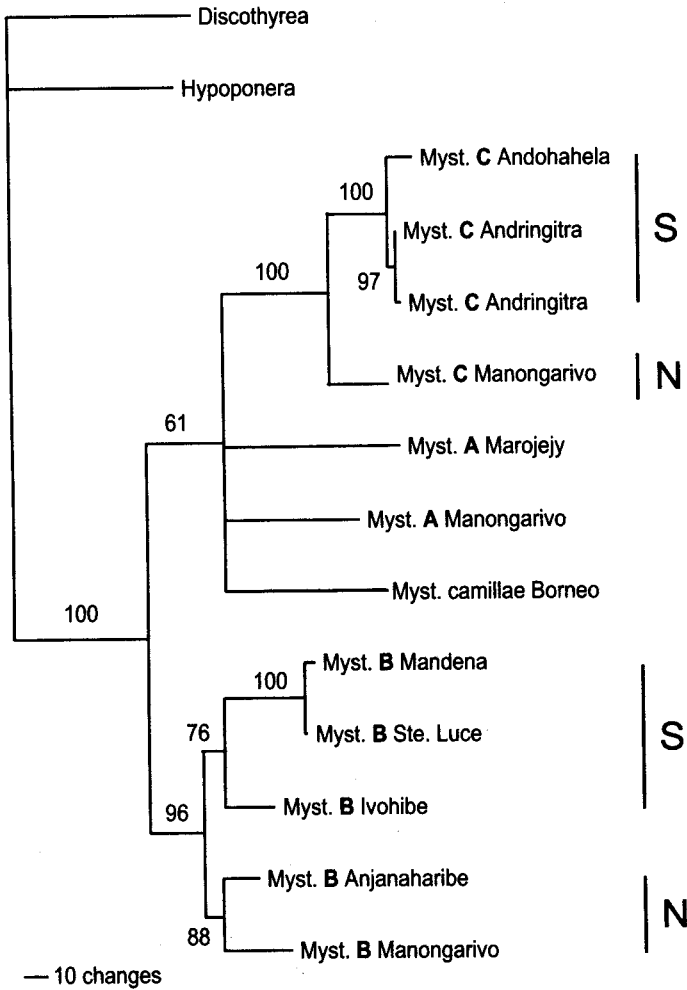


Fig. 3. Relationship among *Mystrium camillae* from Borneo and three species (A, B, C) endemic to Madagascar and among populations of each set, based on an unweighted parsimony analysis of a 790 bp fragment of the mtCOI gene (199 parsimony-informative characters). This is the strict consensus tree of the 3 best trees (consistency index 0.65, retention index 0.626), resulting from 1000 BS replicates. The number above the internal branches are bootstrap values. Outgroup taxa are *Discothyrea* and *Hypoponera*.