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MADAGASCAR'S BIOGEOGRAPHICALLY MOST INFORMATIVE LAND-SNAIL TAXA

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ABSTRACT.- Madagascar's known native land-snail fauna is currently classified into 540 species (97% endemic) in 68 genera (29% endemic) in 25 families (0% endemic). Recent survey work throughout the island may as much as double this number of species and should provide, for the first time, adequate material and distributional data for robust cladistic and biogeographic analyses. Preliminary analysis of existing cladograms and range maps suggests areas of endemism with recurrent patterns of vicariance. Which of the many Madagascan taxa will yield the most biogeographic information per unit of effort? Based on the criteria of species number, monophyly, vagility, character accessibility, and Gondwanan areas of endemism, the best candidates are (a) acavoids (giant, k-selected, « bird's-egg snails »), (b) *Boucardicus* (minute, top-shaped shells with flamboyant apertures), (c) charopids (minute, discoid shells with complex microsculptures), and (d) streptaxids (small-to-medium-sized, white-shelled, high-spired carnivores).

KEY-WORDS.- Land-snail, Madagascar, Informative, Biogeography

RESUME.- La faune connue à l'heure actuelle des escargots terrestres de Madagascar peut être classée dans 540 espèces (97% endémiques), 68 genres (29% endémiques) et 25 familles (0% endémiques). Un récent travail d'inventaire réalisé dans l'ensemble de l'île pourra amener à doubler le nombre d'espèces et devra fournir pour la première fois un matériel et des données adéquates sur la distribution des espèces permettant des analyses cladistiques et biogéographiques robustes. Une analyse préliminaire des cladogrames et des cartes de distribution suggère des aires d'endémisme vicariantes. Quelles taxa donneront le plus d'information biogéographique par unité d'effort ? Basé sur des critères tels le nombre estimé des espèces, la monophylie, la capacité de dispersion, l'accessibilité des caractères, et les aires d'endémisme gondwanien, les meilleurs candidats sont (a) Acavoidea (stratèges-K géants, « escargots à oeufs d'oiseaux »), (b) *Boucardicus* (à coquilles minuscules avec des ouvertures flamboyantes, (c) Charopidae (minuscules, coquilles discoïdales avec microstructures complexes), et (d) Streptaxidae (carnivores à coquilles blanches petites ou moyennes, très pointues).

MOTS-CLES.- Escargots terrestres, Madagascar, Indicateur, Biogéographie

INTRODUCTION

Madagascar's history of separation from Africa about 170 Myr, separation from India about 80 Myr (STOREY, 1995), and internal vicariance events due to volcanism and periodic climatic changes (BURNEY, 1987, this volume; RAXWORTHY & NUSSBAUM,

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1995, in press; RAXWORTHY, this volume), makes it an ideal subject for vicariance-biogeographic studies (GRISWOLD, 1991; LUCKOW, *in litt.*). The basic requirements for vicariance biogeography are (a) at least two monophyletic clades for which there are (b) accurate range maps defining discrete, shared areas of endemism and (c) robust phylogenetic hypotheses (KLUGE, 1988; GRISWOLD, 1991; EMBERTON, 1994a).

Land snails are particularly well suited for vicariance biogeography due to their Paleozoic origins and great evolutionary and faunal stabilities (SOLEM, 1979, 1981; EMBERTON, 1994a). The purposes of this paper, therefore, are (a) to summarize the current, published state of knowledge concerning the species numbers and world distributions of Madagascar's land-snail genera; (b) to assess the potential of Madagascan land snails for intra-island vicariance biogeography, using available cladograms and range maps; (c) to report on recent, extensive surveys that, when sorted and analyzed, should provide sufficient material to begin to take advantage of this potential; and (d) to determine which major taxa of Madagascan land snails should be targeted first in order to obtain the maximum biogeographic information per unit of effort.

MATERIAL AND METHODS

The most recent summary of Madagascar's land-snail genera (EMBERTON, 1995a), prepared in 1992, listed them in systematic order and reported for each genus its general range of shell sizes in Madagascar, its world distribution, its number of described and unsynonymized Madagascan species, and the percentage of those species believed to be endemic to Madagascar. For this paper, we have updated that 1992 summary to incorporate the additional 162 new species (an increase of 43%) and two new genera that have since been described, and the numerous new generic combinations that have since been proposed (FISCHER-PIETTE *et al.*, 1993, 1994; EMBERTON, 1994b).

To assess the potential value of land snails for vicariance biogeography within Madagascar, we used published phylogenetic hypotheses and range maps. Three cladograms have been published so far concerning Madagascan land snails. The first analyzed 19 species of acavids (giant, k-selected, « bird's-egg snails »: EMBERTON & ARIJAONA, in press), using published anatomical data, from which five informative characters were hypothesized (EMBERTON, 1990). The second treated 18 species of acavids (five species shared with the first study), based on 71 informative allozyme characters (EMBERTON, 1995b). The third cladogram analyzed nine taxa (genetically cohesive, operational taxonomic units) of *Tropidophora* (large, split-sole, operculate snails: EMBERTON & ARIJAONA, in press), using distributions of 117 allozyme alleles (EMBERTON, 1995c). Range maps for acavids were sketched approximately by EMBERTON (1990) from then available published data, but these were superceded by the much more accurate dot maps of FISCHER-PIETTE *et al.* (1994: cartes 5-19). FISCHER-PIETTE *et al.* (1993: cartes 6-15) also published dot maps for *Tropidophora* species, but the complex, confused systematics of that genus (EMBERTON, 1995c) render their maps of dubious value, so we used only the collecting localities of cladistically analyzed taxa (EMBERTON, 1995c: fig. 1, table I).

For acavids we used the allozyme cladogram (EMBERTON, 1995b: fig. 1) and modified it slightly by incorporating the synonomies of *Clavator johnsoni* under *C. eximius* and *Ampelita subfunebris* under *A. xystera* (FISCHER-PIETTE *et al.*, 1994), and by adding *Leucotaenius* and enhancing resolution among genera based on the anatomy

cladogram (EMBERTON, 1990: fig. 2). Onto this modified cladogram we then wrote the approximate geographic range (S, N, SE, etc.) of each species. For *Tropidophora* we followed the same process, using the allozyme cladogram (EMBERTON, 1995c: fig. 2 left) without modification, and writing on it the geographic region where each taxon was collected. The results were visually compared to assess the possible existence of areas of endemism that fall into coherent cladistic patterns suggesting vicariance. No more formal or rigorous analysis was attempted because of the preliminary natures of both the cladograms and the range maps.

Most Madagascan land snails are minute (<5mm) and inconspicuous, and virtually all are both patchily distributed and low in density (EMBERTON, 1995a, this paper, unpublished). Adequate collection of a station, therefore, requires both numerous person-hours of on-site search time and sieving and sorting of leaf-litter/soil samples (EMBERTON *et al.*, in review). Geographic ranges of individual species can be extremely narrow (EMBERTON, in press, in review), and morphological differences among regional races of widespread species can be drastic (EMBERTON, 1995c, unpublished), so it is important to collect as many and as varied stations as possible. Therefore we evaluated our recent surveys using the criteria of (a) average person-hours per station, (b) average volume of leaf-litter/soil processed per station, (c) number of stations, (d) geographical range and distribution of stations.

Major taxa of Madagascan land snails were initially screened for biogeographic information content based on described species: those with fewer than 15 were eliminated. The remaining taxa were then ranked for each of seven criteria: (1) predicted total number of species on Madagascar (rank 1 for >100, rank 2 for <100); (2) monophyly (1 well supported, 2 uncertain); accessibility of phylogenetic characters in their (3) shells (1 many, 2 few, 3 virtually none), (4) genital anatomies (1 many known, 2 unknown, 3 known and few or none), and (5) allozymes (1 frozen tissues archived and proven informative, 2 archived but untested, 3 no frozen tissues); (6) relative vagilities (1 low or suspected low, 2 moderate or unknown); and (7) presence in Gondwanan areas of endemism (1 for three or more areas, 2 for two or fewer areas). Summed ranks were then used to rank each taxon from most (lowest sum) to least (highest sum) expediently informative for biogeography.

RESULTS

Table I summarizes current published knowledge of Madagascar's land-snail genera. It is important to emphasize that this summary is certain to undergo major modifications as existing and future collections are processed (see below), and as corrections are made to the self-admittedly tenuous taxonomic hypotheses of the late FISCHER-PIETTE. With these caveats, there are 68 genera of land snails currently known on the island, comprising 540 species. Endemism levels in Madagascar (including nearby volcanic islands) are extremely high: 29% of genera, 97% of species.

Of the non-endemic genera, 17 (36%) also inhabit Africa only, nine (20%) also inhabit one or more eastern regions (Indian-Ocean non-volcanic islands, India, Southeast Asia, Pacific Islands) only, five (11%) are also in both Africa and in one or more eastern regions, one (2%) each is also known only in South America and only in Australia/New Zealand, and ten (22%) have world-wide distributions. These percentages will probably undergo major adjustment as the systematics become better understood. Thus, the listed

number of world-wide genera occurring in Madagascar is probably inflated by introduced species erroneously described as new and/or by species in native genera convergent on and mistaken for world-wide or Laurasian genera (most likely in such genera as « *Assiminea*, » *Pupisoma*, *Gastrocopta*, *Ceciloides*, *Lamellaxis*, *Opeas*, *Succinea*). Furthermore, the listed number of Asian-Madagascan genera is probably lower than reality, due to geographically biassed taxonomy. For example, closer scrutiny may determine that the Madagascan *Boucardicus* is a synonym of the Indian-Asian *Alycaeus*, and that the Madagascan *Kalidos* is synonymous with an Indian ariophantid (EMBERTON, unpublished). Thus Madagascan snails, in addition to their dominant African ties (BRUGGEN, 1981, 1982), have very strong India-Asia connections paralleling, for example, Madagascan plants (SCHATZ, this volume).

Figure 1 gives a consensus cladogram for 17 acavids and a cladogram for nine *Tropidophora*, along with the approximate known geographical range of each species. Possible areas of endemism include « north » (six lineages), « south » or « southwest » (four or five lineages), « southeast » (two lineages), and « east-central » (two). Two possible vicariance area-cladistic relationships are conspicuous in the recurrent patterns [N(SW(SE)] and (E-cent, N).

Collections were made, 1992-1995, during three expeditions designed to include all eleven bioclimatic regimes of KOECHLIN *et al.* (1974), emphasising undercollected areas of predicted high diversity, such as rainforests, humid deciduous forests, and limestone areas (EMBERTON, 1994b: fig. 1). The survey consisted of altitudinal transects in many unprotected areas (*e.g.* EMBERTON, in press), as well as in 21 Reserves and Parks: Ambatovaky, Analamera, Andasibe, Andohahela, Andranomena, Andringitra, Anjanaharibe Sud, Ankarafantsika, Ankarana, Bemaraha, Betampona, Cap Sainte Marie, Lokobe, Manombo, Marojezy, Masoala, Montagne D'Ambre, Namoroka, Nosy Mangabe, Ranomafana, and Tsaratanana. In total, 1,026 stations were collected, devoting an average of 12.9 person-hours per station, and processing an average litter/soil sample of 1.34 liters per station. These collections may as much as double the number of land-snail species known from Madagascar (EMBERTON, 1995a); for example, of 64 species of *Boucardicus* and « *Trachycystis* » collected in the southeastern half of Madagascar, 47 (73%) are new (EMBERTON, in press). The collections, when sorted and analyzed, are expected to provide the first solid base for phylogenetic and biogeographic analyses of Madagascan land snails.

Table II evaluates the eight major taxa most promising for biogeographic studies. Based on seven criteria, the Acavoidea ranked highest (sum of ranks = 9). Three taxa tied for second (sum of ranks = 11): *Boucardicus* (Cyclophoridae: minute, top-shaped shells with flamboyant apertures), Charopidae (minute, discoid shells with complex microsculptures), and Streptaxidae (small-to-medium-sized, white-shelled, high-spired carnivores). Of the third- and fourth-ranked taxa (sums of ranks = 14 and 15), three were simple-shelled members of the Helicarionidae (*Kalidos*, *Sitala*, *Microcystis*), and one was the systematically complex and enigmatic pomatiasid *Tropidophora* (EMBERTON, 1995c).

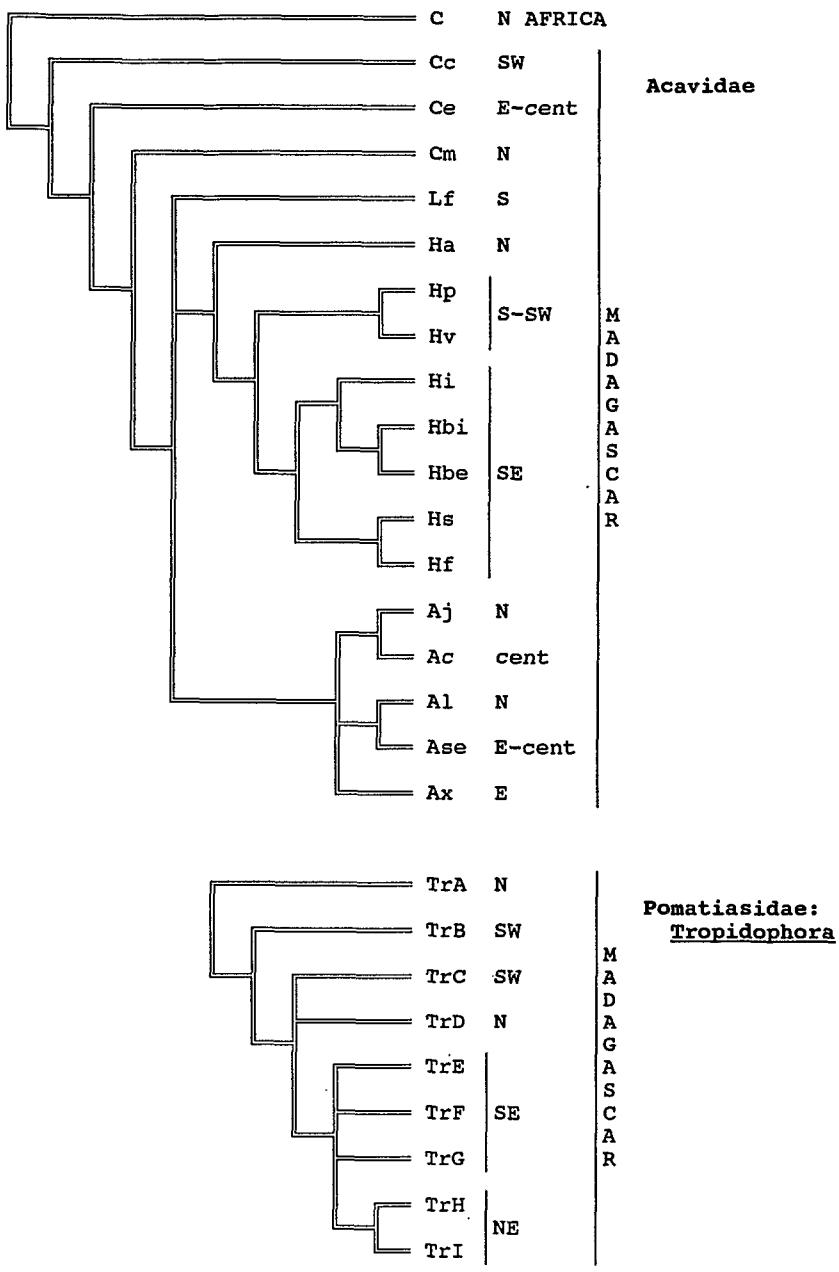

Fig. 1. Non-robust cladograms and approximate geographic distributions of 17 of Madagascar's approximately 100 species of acavids (top) and nine of Madagascar's estimated 60 taxa of *Tropidophora* (bottom). Ac = *Ampelita cedaryi*, Aj = *A. julii*, Al = *A. lamarei*, Ase = *A. sepulchralis*, Ax = *A. xystera* (+ *A. subfunebris*), Cc = *Clavator clavator*, Ce = *C. eximius* (+ *C. johnsoni*), Cm = *C. moreleti*, Ha = *Helicophanta amphibulima*, Hbe = *H. betsileoensis*, Hbi = *H. bicingulata*, Hf = *H. farafanga*, Hi = *H. ibaraoensis*, Hp = *H. petiti*, Hs = *H. souverbiana*, Hv = *H. vesicalis*, Lf = *Leucotaenius favanii*, TrA to TrI = *Tropidophora* taxon A to taxon I. Data from EMBERTON (1990, 1995b, 1995c) and FISCHER-PIETTE *et al.* (1994).

DISCUSSION AND CONCLUSIONS

The recent, posthumous publication of FISCHER-PIETTE's two-volume monograph summarizing some 25 years of work on the Madagascan land-snail fauna (FISCHER-PIETTE *et al.*, 1993, 1994) provides a valuable base from which to begin taking advantage of this fauna's potential as biogeographic indicators. Although FISCHER-PIETTE was a self-acknowledged splitter, working primarily on limited shell material sent to him in Paris (EMBERTON, 1995a, 1995c), many of his judgements will surely stand the test of time, and he and his colleagues made it easy to build on their work by providing dot maps, dispositions of types, and complete synonymies of all their recognized taxa.

Preliminary analysis of existing cladograms and range maps indicates that land snails will prove valuable for biogeographic analysis within Madagascar. Among suggested areas of endemism, for example, « north » is consistent with RAXWORTHY and NUSSBAUM'S (in press) recent correction of Humbert's biogeographic domains. Recurrent patterns of geographic areas in the cladograms suggest historical vicariance events that are documented in the living snail fauna. More complete and robust cladistic and biogeographic analyses are needed to realize this potential.

Extensive survey work needs to be done to find the vast numbers of undiscovered species that remain and to provide sufficient material to delimit true species, define and refine distributional maps, and perform phylogenetic analyses. For the latter, shells are often inadequate or misleading, so collecting and archiving anatomical and biochemical material are essential (EMBERTON, 1995a). Because of the low densities and patchy distributions of living land snails in Madagascar, and because of the small geographic ranges of many species, surveying is best done in large teams of collectors that sample as many and as varied stations as possible, searching for minute-sized snails and slugs, and only picking up large specimens as they are encountered incidentally; collection, sieving, and sorting of leaf-litter/soil samples are also essential to ascertain the total fauna (EMBERTON *et al.*, in review). The authors' recent three expeditions, which sampled 1,026 stations throughout the island, averaging 13 person-hours and 1.3 liters of litter/soil per station, are a step in the right direction. These collections, when sorted and analyzed, may as much as double the current 540 species known from the island, and should provide an initial base for phylogenetic and biogeographic studies.

Based on previous, preliminary studies and on limited current knowledge and material, the Madagascan land-snail taxon predicted to yield the greatest degree of biogeographic information per unit of effort is the superfamily Acavoidea. The Madagascan representatives of this clade are also of interest to evolutionary theory because of their remarkable morphological and ecological radiations on the island (EMBERTON, 1990, 1994b, 1994c, 1995d). Because these snails are very large and conspicuous, they have been collected relatively extensively, so their geographic ranges can probably be fairly accurately defined.

Also large and frequently collected are the operculate, pomatiasid snails *Tropidophora*. This genus is one of Madagascar's most magnificent endemic land-snail radiations and is of great interest to evolutionary biology because of its cryptic, genetically extremely divergent, polytypic, and polymorphic taxa (EMBERTON, 1995c). Unfortunately, however, these same properties make them too complex systematically to be of expedient value to biogeography.

Three other taxa that are promising for biogeography -*Boucardicus*, Charopidae, and Streptaxidae- are all small to minute in size, but have sufficiently complex shell morphologies to be tractable for efficient phylogenetic analysis. The former two have also proven useful as indicators of forest-floor-invertebrate patterns of biodiversity and endemism (EMBERTON, in press; EMBERTON & PEARCE, 1995).

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Table I. Genera of terrestrial molluscs known from Madagascar as of February 1996. All are in the phylum Mollusca and class Gastropoda. Higher classification follows ABBOTT and BOSS (1989) for subclasses Prosobranchia and Gymnomorpha and NORDSIECK (1986) for subclass Pulmonata: order Stylommatophora. Shell size refers to the maximum dimensions of the shell(s) of Madagascan species, and is classified as minute (< 2 mm), small (2-5 mm), medium (6-15 mm), large (16-30 mm), huge (31-40 mm), or giant (> 40 mm). Endemic genera are those known only from Madagascar and nearby volcanic islands; distributions elsewhere are approximate. # Spp = number of species described and unsynonymized from Madagascar as of February 1996; % Endm = percent of those species that are endemic. Species introduced since human colonization are not included. Also not included are the semiterrestrial Neritidae and Truncatellidae. The Veronicellidae are shell-less slugs for which some data are lacking. Data are from FISCHER-PIETTE *et al.* (1993, 1994), EMBERTON (1990, 1994b), BRUGGEN (1981), TILLIER (1979), WENZ (1938-1944), ZILCH (1959-1960), and specimens in the Paris Museum.

Genus & Higher Classific	Shell Size	Distribution Elsewhere	# Spp	% Endm
Subclass PROSOBRANCHIA				
Order ARCHAEOGASTROPODA				
Superfamily HYDROCENOIDEA				
Hydrocenidae				
Georissa	minute	S&E Asia,Pac	6	100%
Order MESOGASTROPODA				
Superfamily CYCLOPHOROIDEA				
Cyclophoridae				
Acroptychia	large	endemic	10	100%
Anosycolus	medium	endemic	2	100%
Boucardicus	sm-med	endemic	33	100%
Chondrocyclus	medium	Afr	2	100%
Cyathopoma	minute	IndOc	10	90%
Cyclotus	small	S&E Asia,IndOc	4	100%
Hainesia	large	endemic	4	100%
Diplommatinidae				
Diplommatina	minute	S&E Asia,Pac	1	100%
Malarinia	minute	endemic	2	100%
Pupinidae				
Madecataulus	medium	endemic	6	100%
Superfamily LITTORINOIDEA				
Pomatiasidae				
Cyclotopsis	medium	IndOc	4	100%
Tropidophora	lg-giant	Afr	95	99%
Superfamily RISSOIDEA				
Assimineidae				
'Assiminea'	minute	World	5	100%
Omphalotropis	small	Pac	3	100%
Subclass GYMNOMORPHA				
Order SOLEOLIFERA				
Veronicellidae				
Desmocaulis	-	-	1	100%
Drepanocaulis	-	-	2	100%
Imerinia	-	-	11	100%
Laevicaulis	-	-	3	33%
Sarasinula	-	-	1	100%
Semperula	-	-	1	100%
Subclass PULMONATA: Order STYLOMMATOPHORA				
Suborder ORTHURETHRA				
Superfamily PUPILLOIDEA				
Valloniidae				
Pupisoma	minute	World	2	50%
Pupillidae				
Pupoides	small	World	1	0%
Superfamily CHONDRINOIDEA				
Chondrinidae				
Gastrocopta	minute	World	1	100%
Vertiginidae				
Nesopupa	minute	Afr,S&E Asia,Pac	4	100%
Truncatellina	minute	World	1	100%
Orculidae				
Fauxulus	medium	Afr	2	100%

Superfamily BULIMINOIDEA				
Buliminidae (Enidae)				
Cerastua	large	Afr	1	0%
Conulinus	medium	Afr,Ind	1	100%
Rachis	medium	Afr, Ind	4	75%
Suborder SIGMURETHRA				
Infraorder ACHATINIDA				
Superfamily ACHATINOIDEA				
Ferrussaciidae				
Cecilioides	small	World	1	100%
Subulinidae				
Curvella	medium	Afr,Ind,S Asia	2	100%
Homorus	large	Afr	1	0%
Lamellaxis	medium	World	1	0%
Opeas	sm-med	World	1	100%
Pseudoglessula	medium	Afr	1	100%
'Subulina'	med-lg	SAmer	2	50%
Achatinidae				
Achatina	giant	Afr	1	0%
Superfamily STREPTAXOIDEA				
Streptaxidae: Streptaxinae				
Edentulina	med-lg	Afr	14	100%
Gulella	sm-med	Afr	12	100%
Pseudelma	medium	endemic	1	100%
Streptaxidae: Enneinae				
Gonospira	medium	endemic	5	100%
Streptostele	med-lg	Afr	1	100%
Superfamily ACAVOIDEA				
Acavidae				
Ampelita	hg-giant	endemic	69	100%
Clavator	giant	endemic	11	100%
Helicophanta	giant	endemic	15	100%
Leucotaenius	hg-giant	endemic	7	100%
Superfamily RHYTIDOIDEA				
Rhytididae				
'Rhytida'	giant	AustNZ	1	100%
Superfamily PUNCTOIDEA				
Charopidae				
'Pilula'	medium	endemic	2	100%
'Trachycystis'	sm-med	endemic	16	100%
Infraorder ELASMOGNATHA				
Superfamily SUCCINEOIDEA				
Succineidae				
Succinea	medium	World	1	0%
Quickia	medium	Afr	1	0%
Infraorder HELICIDA				
Superfamily HELICARIONOIDEA				
Euconulidae				
Euconulus	minute	World	2	100%
Helicarionidae: Helicarioninae				
Caldwellia	medium	endemic	1	100%
Bathia	large	endemic	1	100%
Helicarionidae: Sesarinae				
Kaliella	min-sm	S&E Asia,Pac	2	50%
Helicarionidae: Ereptinae				
Ctenophila	medium	endemic	2	100%
Helicarionidae: incertae sedis				
Gaillardia	sm-med	endemic	2	100%
Helicarionidae: Microcystinae				
Microcystis	sm-med	Pac	15	100%
Helicarionidae: Ariophantinae				
Kalidos	lg-giant	endemic	72	100%
Malagarion	medium	endemic	5	100%
Helicarionidae: Macrochlamydinae				
Macrochlamys	large	S&E Asia	1	100%
Sitala	sm-med	Ind,IndOc, Afr	33	91%
Urocyclidae				
Chlamydarion	sm-med	Afr	5	100%
Elisolimax	medium	Afr	2	100%
Granularion	medium	Afr	4	100%
Trochonanina	sm-med	Afr	2	50%
Superfamily VITRINOIDEA				
Vitrinidae				
'Vitrina'	medium	World	2	100%

Table II. Eight taxa of Madagascan land snails most promising for biogeographic analysis. The next-to-last column summarizes probable world distribution; all other columns refer strictly to Madagascan species. * allozymes known to be informative phylogenetically. Biog. Rank = level of biogeographic information per unit of effort (high to low = 1 to 4), as calculated from data in the table (see text).

Taxon	Named Spp.	Total Spp.	Mono-phyly	Shell Chars.	Genital Chars.	Froz. Tiss.	Vagi-lity	Areas of Endemism	Biog. Rank
Boucardicus	33	120?	yes?	yes	?	no	low?	Madg., India+S.E.Asia (Alycaeus)	2
Tropidophora	95	60?	?	no	no	yes*	mod.	Madg., Africa	4
Streptaxidae	33	150?	?	yes	?	no	low?	Madg., Afr., India+S.E.Asia, S.Amer.	2
Acavoidea	102	90?	yes	few	yes	yes*	low	Madg., S.W.Afr., India (+S.E.Asia?), E.Austr., S.Amer.	1
Charopidae	18	80?	yes	yes	?	no	low	E.Madg., Afr., E.Austr., (S.Amer.?)	2
Microcystis	15	100?	?	no	?	no	?	Madg., Pac.Islands, (other?)	4
Kalidos	72	75?	?	no	?	yes	low?	Madg., (India+S.E.Asia?, other?)	3
Sitala	33	175?	no?	no	?	no	?	Madg., Afr., India+S.E.Asia	3