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ORIGINS AND AFFINITIES OF THE SCORPION FAUNA OF MADAGASCAR

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ABSTRACT.- Since the appearence of the classical publications of POCOCK (1894) and KRAEPELIN (1905), the biogeography of the scorpions of Madagascar has been a complex puzzle: a very long period of separation between the great island and Africa was postulated by POCOCK (1894). Subsequent contributions (*e.g.*, FAGE, 1929; MILLOT, 1948; PAULIEN, 1961; LEGENDRE, 1972), have increased considerably our knowledge of the scorpion fauna of Madagascar. However, many interpretations as to the origins and especially of the affinities of this fauna, have been impaired by lack of precise knowledge of the phylogeny of Madagascan scorpions. Affinities with African scorpions have been accepted by most authors for quite some time (VACHON, 1979). The apparent demonstration of affinities with the Indo-Malayan and Australian regions (FAGE, 1929; MILLOT, 1948; LEGENDRE, 1972), proved, however, to be the consequence of misinterpretation when a typical Gondwanian lineage was finally established by LOURENÇO (1983, 1985). This Gondwanian lineage was detected by the study of all the genera of Ischnuridae distributed between Australia and Cocos Island near the Central American Pacific coast, suggesting that the present representatives of the Madagascar scorpion fauna are derived from protoelements of both the families Buthidae and Ischnuridae which were already present in Gondwanaland, previous to fragmentation and continental drift. Finally, recent study of new elements from Madagascar (LOURENÇO, 1995, 1996a,b,c) reinforces the likelihood of affinities with Africa, and of new affinities with Sri Lanka and India.

KEY-WORDS.- Scorpion, Madagascar, Archaic, Affinities, Continental drift, Biogeography

RESUME.-Depuis la publication des travaux classiques de POCOCK (1894) et KRAEPELIN (1905), la biogéographie des Scorpions de Madagascar semble correspondre à un véritable puzzle: une très longue période de séparation et d'isolement entre la grande île et l'Afrique a été postulée par POCOCK (1894). Des contributions subséquentes (*e.g.*, FAGE, 1929; MILLOT, 1948; PAULIAN, 1961; LEGENDRE, 1972), ont considérablement augmenté les connaissances sur la faune des Scorpions malgaches. Néanmoins, plusieurs explications et/ou interprétations visant à élucider les origines et en particulier les affinités de cette faune, ont été biaisées par un manque de connaissance précise concernant la phylogénie des Scorpions malgaches. Des affinités avec la faune africaine ont été acceptées depuis fort longtemps par la plupart des auteurs (VACHON, 1979). L'apparente démonstration d'affinités avec les faunes des régions Indo-Malaise et Australienne (FAGE, 1929; MILLOT, 1948; LEGENDRE, 1972), se sont avérées être le résultat des mauvaises identifications, en particulier depuis qu'une lignée typiquement Gondwanienne a été établie par LOURENÇO (1983, 1985). Cette lignée Gondwanienne a pu être établie à partir de l'étude de tous les genres de la famille des Ischnuridae, répartis depuis l'Australie jusqu'à l'île de Cocos proche des côtes pacifiques de l'Amérique Centrale. Cette étude suggère que les représentants actuels de la faune scorpionique malgache dérivent des protoéléments des familles Buthidae et Ischnuridae, lesquels étaient déjà présents dans la Gondwanie avant la fragmentation et la dérive des masses continentales. Finalement, l'étude récente de plusieurs nouveaux éléments de la faune malgache (LOURENÇO, 1995, sous-presse), vient renforcer la véracité des affinités avec la faune africaine et démontre l'existence de nouvelles affinités avec le Sri Lanka et l'Inde.

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MOTS-CLES.- Scorpion, Madagascar, Archaique, Affinités, dérive continentale, Biogéographie

INTRODUCTION

Contributions to the knowledge of the scorpion fauna of Madagascar began with descriptions of species by GERVAIS (1844) POCOCK (1890, 1894), KRAEPELIN (1896, 1901) etc. FAGE (1929) produced the first monographic study of the group which was a comprehensive work for the period in which it was produced.

The peculiarities of the fauna of Madagascar have attracted the attention of several authors who have attempted to reach biogeographical conclusions regarding their origins and affinities. However, since the classical publications of POCOCK (1894) and KRAEPELIN (1905), the biogeography of the scorpions of Madagascar has proved to be a complex puzzle. As long as 1894, POCOCK suggested that Madagascar had been isolated from Africa for a very long period of time.

Subsequent contributors (FAGE, 1929; MILLOT, 1948; PAULIEN, 1961; LEGENDRE, 1972; VACHON, 1979), proposed interpretations of the origins and especially of the affinities of Madagascar's fauna which have been biased by two major factors: (i) lack of precise knowledge regarding the phylogeny of Madagascan scorpions in relation to those of Africa and the Orient; and (ii) overestimation of the extent of contemporary knowledge of Madagascar's fauna. FAGE (1929) stated: « since scorpion species are of large size and have been collected in all the regions of the island, it is possible to estimate that we know all the populations of the island as well as their relative density and distribution ». MILLOT (1948) followed this up by claiming: « Scorpions are the best known Arachnida of Madagascar. Because of their large size they can easily be observed and collected. Therefore, most of the species of the great island are certainly identified at present ».

Even though between 1929 and 1969 only two new species were recorded and described from Madagascar (FAGE, 1946; VACHON, 1969), the scorpion fauna of the island is not really well known. In fact, as with most zoological groups, when more species are described and the group appears to be well known, further smaller species begin to be recorded and described, and the average body size of the group is reduced (FENCHEL, 1993; BLACKBURN & GASTON, 1994). The recent discovery and description of several new taxa in Madagascar (LOURENÇO, 1995, 1996a,b,c) refer, in most cases, to microscorpions whose existance had not previously been suspected (see Table I below). The discovery of small species depends upon the use of sophisticated methods of collecting which were not available at the time when FAGE and MILLOT published their work (*e.g.* detection with Ultra-Violet light).

In this paper my aim is to present a clear view of the origins and affinities of the scorpions of Madagascar by (i) modifying previously incorrect data on phylogeny, and

(ii) supporting new evidence by the introduction of new elements which reinforce the likehood of affinities with Africa, and of new affinities with Sri Lanka and India.

Table I. Comparative composition of the present scorpion fauna of Madagascar and that of three different periods.

FAGE 1929

FAMILY BUTHIDAE

Grosphus Simon, 1880

Gr. madagascariensis (Gervais, 1844)

Gr. hirtus Kraepelin, 1901

Gr. flavopiceus Kraepelin, 1901

Gr. bistriatus Kraepelin, 1901

Gr. limbatus Pocock, 1889

Gr. limbatus annulata Fage, 1929

Gr. grandidieri Kraepelin, 1901

Odonturus Karsch, 1879

O. baroni (Pocock, 1890)

Uroplectes Peters, 1861

U. fischeri nigrocarinatus Kraepelin, 1913

FAMILY SCORPIONIDAE

Heteroscorpion Birula, 1903

H. opisthacanthoides (Kraepelin, 1895)

Opisthacanthus Peters, 1861

O. madagascariensis Kraepelin, 1894

Total: 2 families, 6 genera, 10 species

2 subspecies

MILLOT 1948

FAMILY BUTHIDAE

Gr. bistriatus

Gr. flavopiceus

Gr. hirtus

Gr. limbatus

Gr. limbatus annulata

O.baroni

U.fischeri nigrocarinatus

Babycurus Karsch, 1886

Babycurus gracilis Fage, 1946

Isometrus Hemprich & Ehrenberg, 1829

Isometrus maculatus (DeGeer) **- Alien**

FAMILY SCORPIONIDAE

H.opisthacanthoides

O.madagascariensis

Doubtful species (*)

Babycurus centrurimorphus Karsch, 1886

Isometrus madagassus Roewer, 1943

Total: 2 families, 7 genera, 10 species,

2 subspecies

(*) *Grosphus madagascarienis* is not mentioned by Millot.

VACHON 1969/79

FAMILY BUTHIDAE

Gr. madagascariensis

Gr. hirtus

Gr. grandidieri

Gr. flavopiceus

Gr. limbatus

Gr. limbatus annulata

Gr. bistriatus

Gr. griveaudi Vachon, 1969

Tityobuthus baroni

Tityobuthus gracilis

FAMILY SCORPIONIDAE

H.opisthacanthoides

O.madagascariensis

Doubtful species (*)

B.centrurimorphes

U.fischeri nigrocarinatus

Total: 2 families, 4 genera and 12 species

(*) *I.madagassus* is not mentionned by Vachon

THIS STUDY

FAMILY BUTHIDAE

Gr. madagascariensis

Gr. hirtus

Gr. grandidieri

Gr. flavopiceus

Gr. limbatus

Gr. annulata

Gr. bistriatus

Neogrosphus Lourenço, 1995

Neogrosphus griveaudi (Vachon)

Isometrus maculatus - **Alien** (*)

T. baroni

T.gracilis

Tityobuthus guillaumeti Lourenço, 1995

Tityobuthus pococki Lourenço, 1995

Tityobuthus lucileae Lourenço, 1996

Microcharmus Lourenço, 1995

Microcharmus cloudsleythompsoni Lourenço, 1995

Microcharmus hauseri Lourenço, 1996

Pseudouroplectes Lourenço, 1995

Pseudouroplectes betschi Lourenço, 1995

FAMILY ISCHNURIDAE (**)

H. opisthacanthoides

O. madagascariensis

Opisthacanthus punctulatus Pocock, 1896

Paleocheloctonus Lourenço, 1996

Paleocheloctonus pauliani Lourenço, 1996

Total: 2 families, 9 genera, 19 species

(*) *Isometrus madagassus* is a synonym of *I.maculatus*

(**) The genera of Scorpionidae were separated into two families Scorpionidae and Ischnuridae by LOURENÇO (1985).

I. POSSIBLES ORIGINS OF THE SCORPION FAUNA OF MADAGASCAR

As proposed in a recent paper (LOURENÇO, 1996d), a useful and didactic approach can be based on UDVARDY'S (1981) division of biogeography into three spatio-temporal entities. In correlation with UDVARDY'S model, three major biogeographical events may tentatively be used to explain the distribution patterns currently observed. In the present paper, which provides an explanation of possible origins of the fauna of Madagascar, I shall limit myself to the first of the three scales: the phylogenetic or palaeobiogeographical scale. The other two scales are treated in a another paper (LOURENÇO, 1996d).

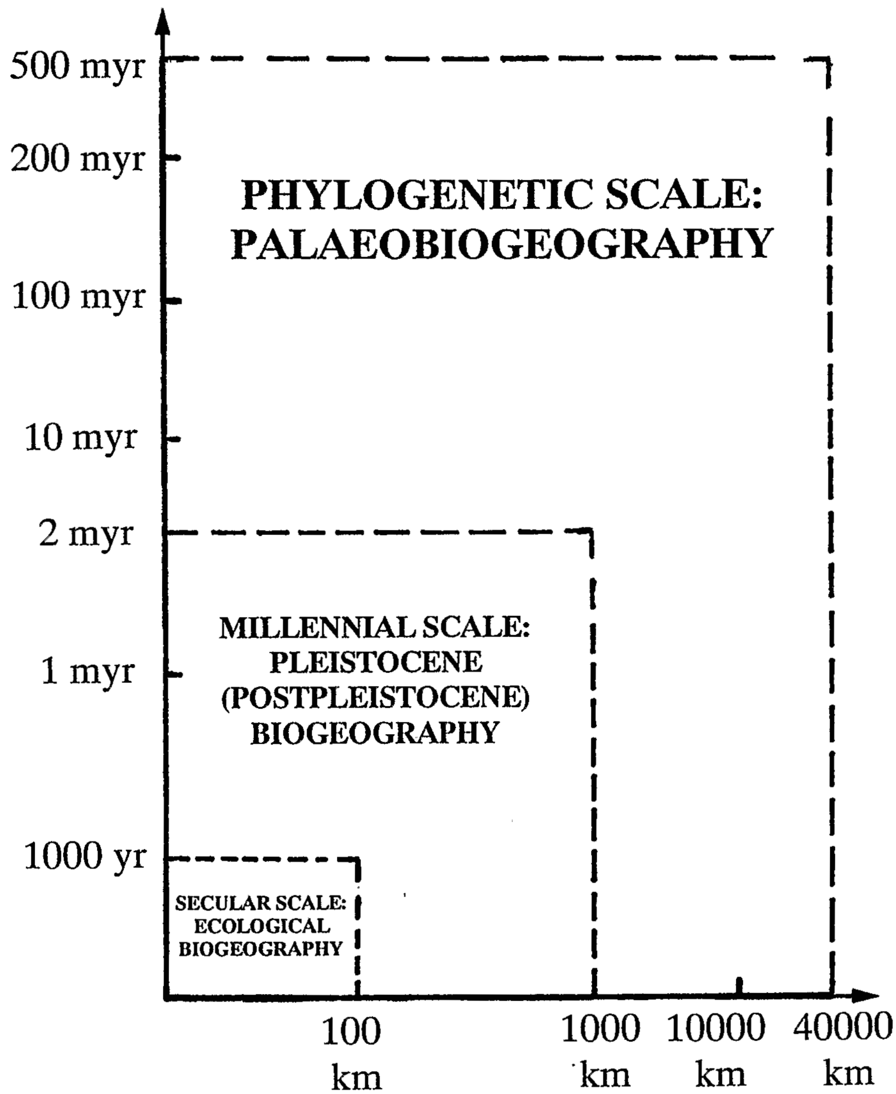

Fig. 1. Division of biogeography into the three spatio-temporal scales of Udvardy (modified after Udvardy, 1981).

The phylogenetic scale encompasses the evolutionary time of all biota and is limited in space only by the size of the earth (UDVARDY, 1981). On this scale only historical factors can be assumed since, for almost all ecological conditions, data are largely or totally unknown. At this level the evolutionary process of biogeography is, to a considerable extent, a tributary of continental drift and plate tectonics. In relation to Madagascar the following biogeographical assumptions can be proposed: (i) the two major lineages of scorpions present today, *i.e.* the families Buthidae and Ischnuridae, are derived from pulmonate (Neoscorpionina) elements that originated in Laurasia and Gondwanaland during Pangean times; (ii) protobuthids were the dominant fauna during Pangean times, and the present distribution of Buthidae on all continental lands of the world is the result of a vicariant process resulting from the fragmentation of Laurasia and Gondwanaland; (iii) the protoischnurids certainly evolved in Gondwanaland during Pangean times, and the present distribution of the Ischnuridae clearly suggests a typical Gondwanian lineage (LOURENÇO, 1985); (iv) a precise analysis of the present scorpion fauna of Madagascar reveals several primitive lineages which show only patchy distributions in other continental lands such as Africa and India; and (v) the presence of these primitive lineages suggests a long period of isolation between Madagascar and other land masses, following the fragmentation of Gondwanaland and continental drift.

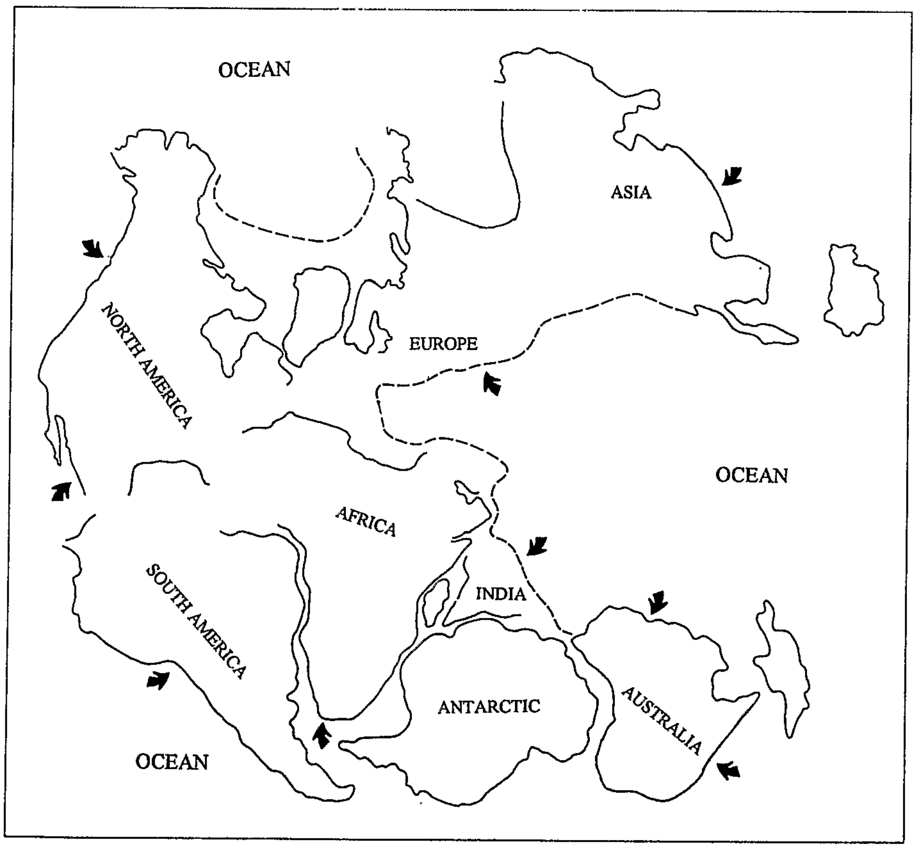

Fig. 2. Position of Pangea about 200 my B.P., and hypothetical ways of coastal colonisation by aquatic scorpions.

II. PRESENT AFFINITIES OF THE SCORPION FAUNA OF MADAGASCAR

A. African affinities

Affinities with African scorpions have been accepted by most authors for some time (FAGE, 1929; MILLOT, 1948; VACHON, 1979), and the present configuration of the fauna seems to indicate significant affinities with Africa. The following examples will be discussed. (i) *Grosphus,* the Madagascan genus most rich in species, and *Neogrosphus*, a genus which probably evolved more recently from *Grosphus*, and which clearly show affinities with the African genera *Odonturus* and, in particular, with *Uroplectes*. These three genera share very remarkable sexual dimorphism of the pectines (FAGE, 1929). (ii) The recently discovered and described genus *Pseudouroplectes* also shows affinities with the genus *Uroplectes*. However, the morphology of the new genus suggests a more primitive lineage when compared, with both *Uroplectes* and *Grosphus*. These two genera evidently evolved later. *Pseudouroplectes* corresponds with primitive lineages, still present in Madagascar, which have vanished in other regions of the world. (iii) The genus *Tityobuthus* was poorly defined phylogeneticly until recently. The discovery of three new species, however, improves our knowledge of this group. Many affinities with the Gondwanian genus *Ananteris*, present today in west Africa and in South America are indicated. *Ananteris* seems to have had its centre of origin in the west part of Gondwanaland. This corresponds today with the South American continent. These two genera present several primitive characteristics *e.g.*, small size and the absence of fulcra in the pectines ([1]). (iv) The genus *Opisthacanthus* is the most typical Gondwanian lineage observed today. Its present distribution ranges from Madagascar through Africa to South America with one population in the Island of Hispaniola in the Caribbean and another in the Island of Cocos in the Pacific. The centre of origin of this genus is probably in South Africa (LOURENÇO, 1985). Previous statements concerning the presence of *Opisthacanthus* in the Indo-Malayan and Australian regions (FAGE, 1929; MILLOT, 1948; LEGENDRE, 1972) have proved to be the consequence of misinterpretation. As stated by FAGE (1929) and by MILLOT (1948), the species of *Opisthacanthus* in Madagascar are closely allied to *Opisthacanthus davydovi* Birula, of the Aru Islands, Indonesia. Subsequent studies, including one of the type specimen of *O.davydovi* by LOURENÇO (1983) have revealed that this species belongs in fact to the genus *Liocheles* ([2]), a common genus in the Indo-Malayan and Australian regions. This genus, however, is absent from Madagascar and Africa. *Opisthacanthus* also presents some affinities with the genera *Cheloctonus* from Africa and *Chiromachetes* from India.

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[1] The absence of fulcra is observed in at least one species of *Tityobuthus*

[2] Presumably Fage nor Millot never examined Birula's type. Moreover, these authors seem totally to ignore the genus *Liocheles* (previously *Hormurus*) in their studies.

Affinities with the latter, however, have, to be established better. (v) The recent discovery of the genus *Paleocheloctonus* in the southwest region of Madagascar (LOURENÇO, 1996c), clearly reinforces the claim for affinities with African scorpions. This genus is closely associated with the South African genus *Cheloctonus*. It represents, however, a more primitive lineage, which probably survived in Madagascar after the separation with Africa.

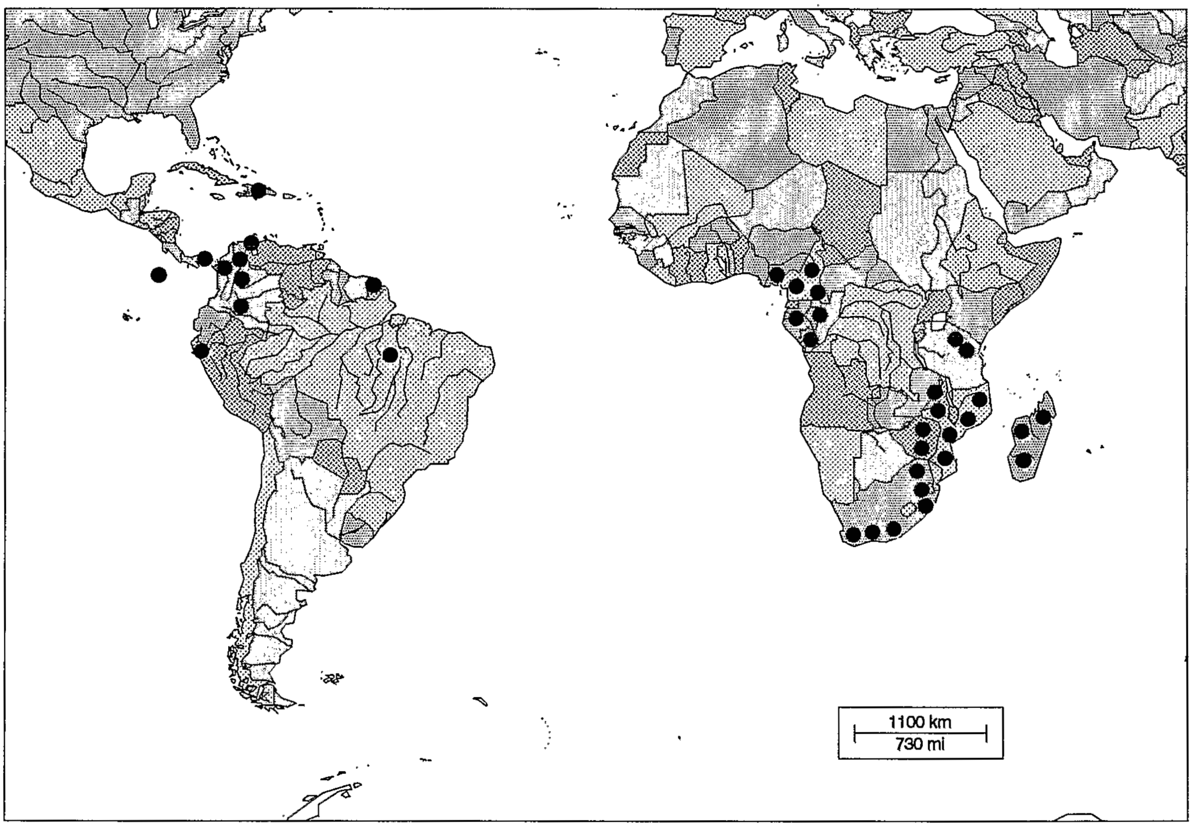


Fig. 3. Gondwanian distribution (black circles) of scorpions of the genus *Opisthacanthus*.

B. Oriental affinities

With the discovery of the new genus *Microcharmus* in the North-east region of Madagascar, clear affinity is established with the genus *Charmus* of India and Sri Lanka. Both *Microcharmus* and *Charmus* represent primitive lineages whose characteristics show that they are among the very first modern buthid scorpions. No other evidence is at present available to indicate affinities between Madagascar and the Indo-Malayan region, and no evidence is available to suggest affinities between Madagascar and the Australian region.

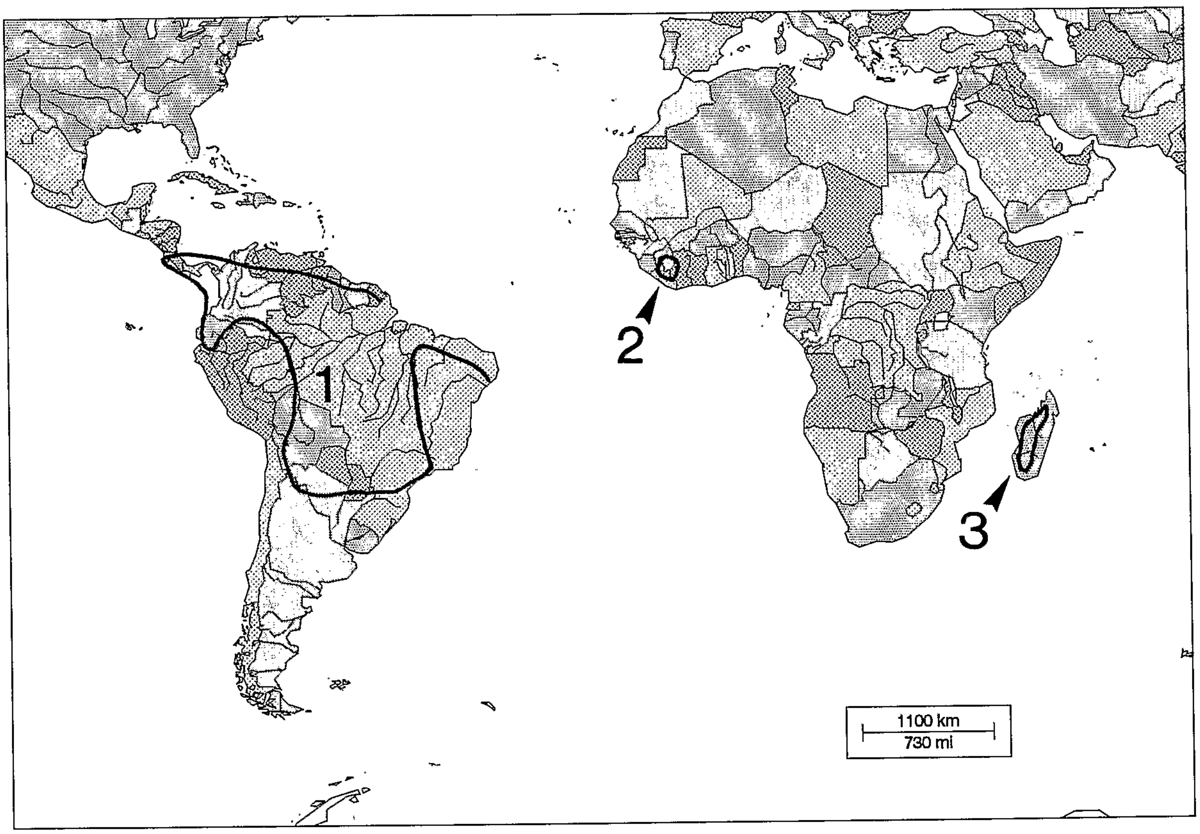


Fig. 4. Distribution of the genus *Ananteris* in tropical America (1) and Africa (2), and of the related species of *Tityobuthus* in Madagascar (3).

C. Particular cases

The phylogenetic and biogeographical position of some of the scorpions of Madagascar and the islands of the Indian Ocean are a complex puzzle. (i) The genus *Heteroscorpion* is monotypic and endemic to the north of Madagascar; some affinities can be suggested between it and the South African genus *Hadogenes*. However, many common characteristics can only be due to convergence. The genus *Heteroscorpion* certainly represents a very old lineage, much older than *Hadogenes*. (ii) The genus *Chiromachus*, another monotypic genus, is only known from the Seychelles and Mauritius. Its absence from Madagascar is difficult to explain. Some affinities can be seen between this genus and the genus *Chiromachetes* of India.

In conclusion, the main event which determined the original biogeographical pattern of the scorpion fauna of Madagascar, on the palaeogeographic scale, was the fragmentation of Gondwanaland and subsequent continental drift. Difficulties in explaining the patchy distribution of the genera *Heteroscorpion* and *Chiromachus* point not only to the great geological age of most groups, but also to the relict biogeographical patterns which they exhibit today.

Fig. 5. Distribution of *Charmus* in India and Sri Lanka (black circles) and of *Microcharmus* in Madagascar (black circle with star).

III. SIGNIFICANT GAPS IN THE SCORPION FAUNA OF MADAGASCAR

As pointed out by PAULIAN (1952), the fauna of Madagascar has not only to be seen in connection with its remarkable originality, but also in respect to the gaps it presents. If two of the major lineages represented in Africa and in the Indo-Malayan region, *i.e.* the families Buthidae and Ischnuridae, are also present in Madagascar, others are not. Two major gaps can be observed in Madagascar: (i) the family Scorpionidae which is present in Africa and in the Indo-Malayan region, and (ii) the family Chaerilidae which occurs in the Indo-Malayan region.

As long ago as 1894, POCOCK stated that the apparent absence from Madagascar of large African genera of Scorpionidae was significant, and he concluded that this indicated that this family had made its way to Central and South Africa when the separation of Madagascar and Africa had been concluded. In fact, the Scorpionidae represent a more recent lineage than do either the Buthidae or the Ischnuridae. They probably evolved in some part of what is today North Africa, and later colonised the South and East (via the Middle East), displacing the Ischnuridae to the South. This is implied by the biogeographical patterns observed today. By the time they had colonised most of Africa, the separation of Madagascar had already taken place so they were unable to reach it (see also HEWITT, 1923).

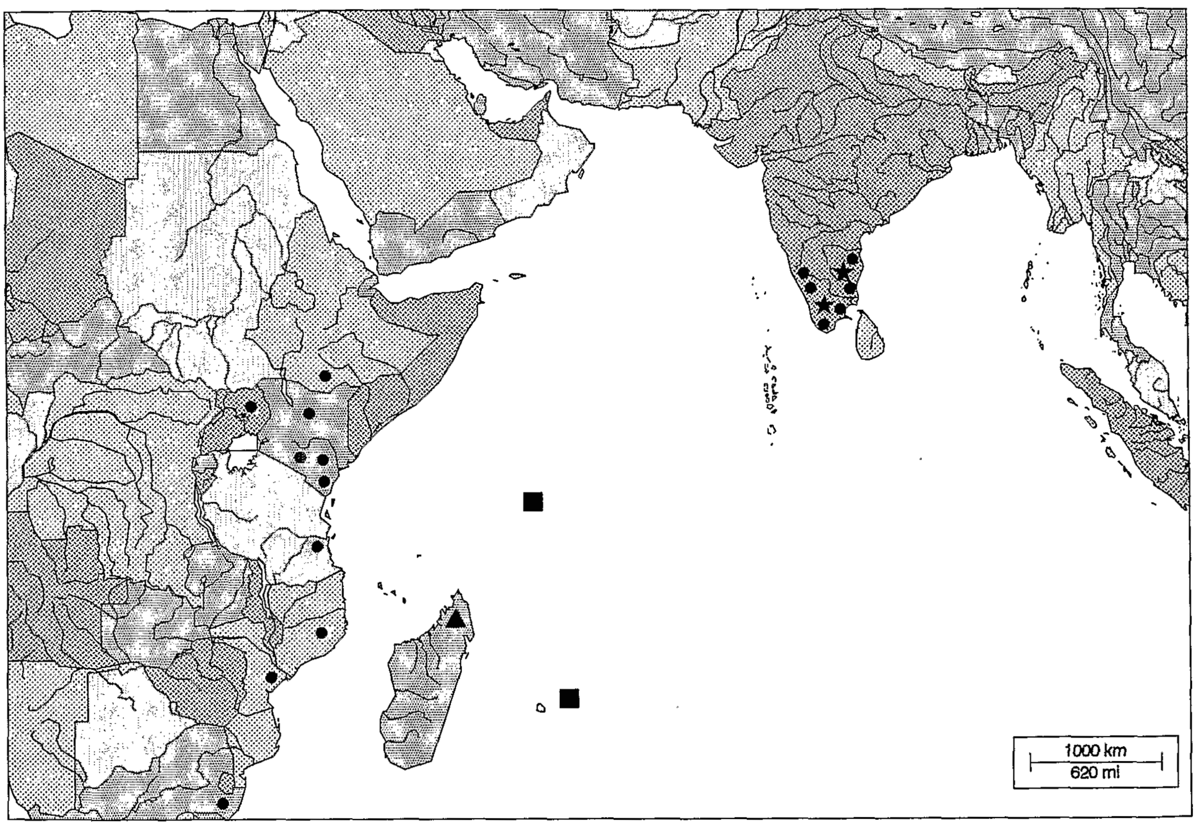


Fig. 6. Distribution of the genera *Heteroscorpion* (black triangle), *Chiromachus* (black squares), *Chiromachetes* (black stars) and *Iomachus* (black circles), in Madagascar, Seychelles, India and Africa.

With regard to the family Chaerilidae, LAMORAL (1980) proposed a possible explanation of its present pattern of distribution. According to this author, the protoelements of the Chaeriloids evolved in Laurasia, and the restriction of the Chaerilidae to the Oriental faunal region suggests that they are a relict of an eastern

Laurasian element that moved in after the conjunction with India. For this reason it seems logical to assume that the family Chaerilidae doen not exist in Madagascar.

IV. DIVERSITY AND ENDEMISM OF THE SCORPION FAUNA OF MADAGASCAR

Subsequent to the biogeographical approach developed in the previous sections, it may be useful consider the diversity and endemicity of the scorpion fauna of Madagascar. When compared with other well studied regions of the world (Table II) which have approximately the same surface area or are smaller, Madagascar appears to possess a poor scorpion fauna. The total number of native species (19) is remarkably low when compared with Baja California (61), or with countries having a much smaller surface area, such as Ecuador (36). The number of families is also low; but other regions such as Imeri in Brazilian/Venezuelan Amazonia, or Imataca in Guayana, which are likewise typical centres of endemicity, also contain only a small number of families. The total number of genera in Madagascar, however, seems significantly greater (8) when compared with that of Ecuador (8), or even of Baja California (11). Moreover, the inventory of species in Baja California and Ecuador is more complete than it is in Madagascar. Therefore, it seems probable that many new species and possibly new genera will be discovered. and described from Madagascar in the future. In recent additions to the scorpion fauna of Madagascar (LOURENÇO, 1995, 1996a,b,c,d,), 7 species have been described or revalidated and 4 new genera were described. This suggests that one of the particularities of the scorpion fauna of Madagascar is the presence of many generical lineages which apparently are not very rich in species.

As far as endemicity is concerned, the picture is quite different. Madagascar appears to be a region of the world which possesses one of the highest (if not the highest) level of endemic species of scorpions (and of other taxa also; see PAULIAN, 1952). Of the 19 native species of scorpions ([3]) all are endemic to Madagascar. Seven genera out of 8 are also endemic to Madagascar which corresponds to 87.5%.

CONCLUSIONS

In conclusion, although this study is only preliminary, the following characteristics of the scorpion fauna of Madagascar can be suggested:

1. The majority of taxa found in Madagascar correspond with primitive or archaic lineages which no longer exist in most other regions of the world.

2. Most genera appear to be poor in species. However, it is reasonable to expect the future discovery of several new species in some genera of micro-scorpions such as *Tityobuthus*, *Microcharmus* and *Pseudouroplectes*.

[3] *Isometrus maculatus* an imported species, only occasionaly found in some coastal areas is not included here.

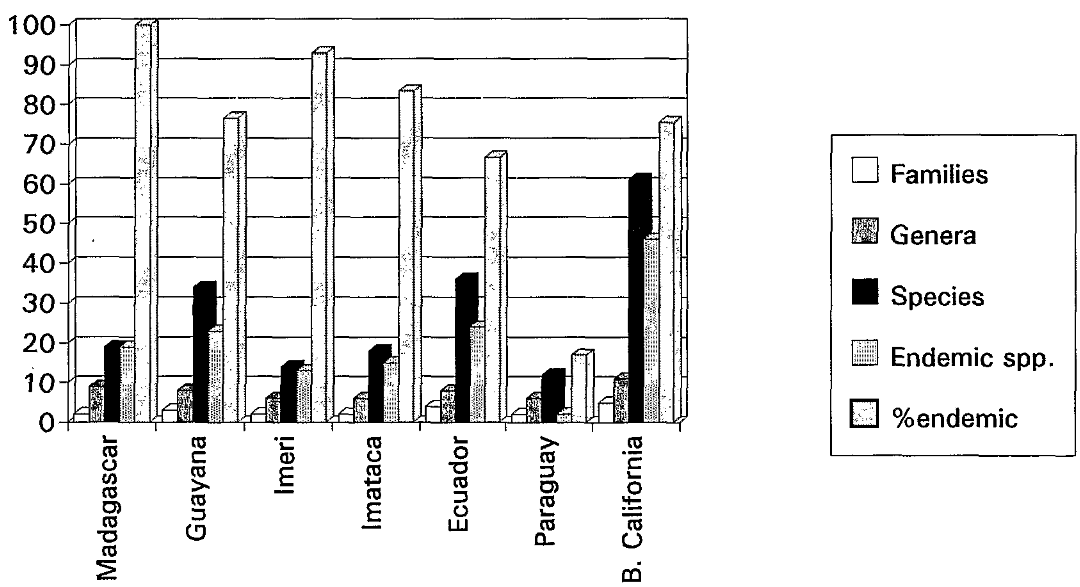
3. The number of recorded species is apparently of little importance, however, and the faunistic inventories which have been carried out so far are largely incomplete.

4. The total number of genera is significant, even when compared with other well-studied regions of the world.

5. The most remarkable characteristic of the scorpion fauna of Madagascar is the impressive level of endemicity, both in species and in genera. This supports the hypothesis of the very early isolation of the island from other land masses.

Table II and Graph I. Comparative values of diversity and endemism observed in the Madagascan scorpion community and in several other well-studied regions of the world.

	Families	Genera	Species	Endemic spp.	%endemic
Madagascar	2	9	19	19	100.0
Guayana	3	8	34	23	76.5
Imeri	2	6	14	13	93.0
Imataca	2	6	18	15	83.3
Ecuador	4	8	36	24	66.7
Paraguay	2	6	12	2	17.0
B. California	5	11	61	46	75.4



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