The Geographic Pattern of Distribution of the Genus *Rhopalurus* Thorell, 1876 in the Guayana-Amazon Region (Scorpiones: Buthidae)

Wilson R. Lourenço

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(Scorpiones: Buthidae)

Wilson R. Lourenço

Muséum national d’Histoire naturelle, Département de Systématique et Évolution, Section Arthropodes (Arachnologie), CP 053, 57 rue Cuvier 75005 Paris, France. E-mail: arachne@mnhn.fr

Summary

A new discussion is proposed on the geographic patterns of distribution presented by the species of the genus *Rhopalurus* Thorell, inhabiting the savannah formations of the northern South America. Two lineages of *Rhopalurus* species are defined for this region, each one containing forms with very weak morphological differences, a consequence of only a minor process of differentiation. The observed pattern of distribution and differentiation is suggested to be directly associated with more or less recent palaeoclimatic vicissitudes, which took place in tropical South America during Pleistocene. Two new subspecies are also described, representing new records of *Rhopalurus* for Brazil and French Guiana.

Introduction

In South America, the genus *Rhopalurus* is typical for open vegetation formations. Its core area of distribution is composed by the “Cerrados” and “Caatingas” formations of central and northeastern regions of Brazil. One species is also known from a single enclave in a savannah formation inside oriental Amazonia, and ‘a priori’ three other species are known from the savannahs of the Guayanian region (*sensu* Mori, 1991). Finally, two species are distributed in Venezuela and Colombia, respectively, in the Llanos of Orinoco and Llanos of the Magdalena (Lourenço, 1986; Lourenço & Sastre, 1988; Teruel & Roncallo, 2008). In recent contributions, the composition and the validity of the geographic and ecological patterns of several species have been discussed and questioned (Teruel, 2006; Teruel & Roncallo, 2008; Teruel & Tietz, 2008). For this reason, I decided to re-open the discussion, in particular in relation to the species distributed in the northern South American savannah formation, with also the presentation of two new elements.

Biogeographic Model Presented by the Genus *Rhopalurus*

The biogeographic pattern presented by the genus *Rhopalurus* constitutes a good example of a group showing a discontinuous distribution. This kind of pattern can be observed in two different cases, among scorpions exclusively adapted to savannahs or to rainforests. These examples have an important relationship with species endemic to present islands of savannah in Amazonian and Guayanian enclaves, but also to those isolated in forest islands inside open vegetation formations (Caatingas, Cerrados, and Campos). The endemic populations isolated inside savannah islands provide good evidence in support of the hypothesis of past connections between the savannahs of central Brazil and the savannah enclaves in Amazon and Guayanian regions. When forest cover was reduced, open vegetation formations probably coalesced during past dry periods (Fig. 1; Ab’Saber, 1977; Van der Hammen, 1983).

Good examples to support this suggestion have been based on scorpion patterns of distribution. *Rhopalurus* most certainly exhibited a continuous distribution during Pleistocene dry periods and the present disrupted distribution is a possible consequence of the reestablishment of rainforest over the regions which previously served as corridors (Lourenço, 1986, 2001). Good evidence for this presumed palearctic distribution was provided with the discovery and description of a new species, *Rhopalurus amazonicus* Lourenço, 1986, endemic to a savannah enclave in the region of Alter do Chão (State of Pará, Brazil), totally isolated within oriental Amazon forest (Pires & Prance, 1985). A careful analysis of *R. amazonicus* placed it in a closed position to *Rhopalurus acromelas* Lutz et Mello, 1922 distributed in central Brazil, but with a range of distribution nearby the area of transition between Cerrados and Amazon forest.

Since my revision of the genus (Lourenço, 1982) and my reanalysis of its distribution (Lourenço, 1986), very few new species have been described for South
Figure 1: Presumed dispersal tracks of *Rhopalurus* spp., between 18,000 and 13,000 years BP. A and B illustrate possible corridors between North-South and East-West savannah formations which coalesced during past dry periods (base map after Ab’Saber, 1977).
The taxonomic status of the species distributed in the northern South American savannah formations, always proved to be difficult to define. This is due to the fact that these savannahs are composed of several isolated fragments which probably coalesced during past dry periods (Fig. 1). The most recent of these events can be dated as only 18,000 to 13,000 years BP (Ab’Saber, 1977). This very recent isolation led to a minor process of speciation and differentiation, and as a consequence the populations now found in several isolate fragments of savannahs show very little morphological differences.

In face of the observed patterns of distribution and differentiation, it becomes rather difficult to be sure about the true taxonomic status of these isolate populations. Consequently, one question can be addressed: are these populations true species, subspecies, or only local morphs belonging to large, polymorphic populations?

Patterns of Polymorphism Exhibited by Amazonian Scorpions

Most of the well studied populations of Amazonian scorpions belong to monomorphic species. Analysis of different biogeographic patterns revealed two examples of a peculiar type of polymorphism. *Tityus gasci* Lourenço, 1981 shows a distribution which ranges from French Guiana to Peru and Ecuador, including an important region of the forests of the Amazon and Guayana. Analysis of the variability of body pigmentation and the morphometrics of the chela and metasomal segments allows to recognize a gradual geographic cline along a transect from French Guiana to Ecuador. Pigmentation gradually intensifies, and the length of the chela and metasomal segments decreases from French Guiana to Ecuador. This suggests that *T. gasci* is a cinal polymorphic species (Lourenço, 1991a, 2001).

*Tityus silvestris* Pocock, 1897 exhibits a wide distribution over the Amazon and Guayana forests. An analysis similar to that for *T. gasci* has been based on specimens from a number of sites. Pigmentation did not vary over the entire range. Morphometric values, however, showed considerable variation. This variation showed little geographical correlation (Lourenço, 1988). The same phenomenon, first encountered by botanists, is termed “ochlospecies” (White, 1962). According to Prance (1982), “ochlospecies” are common in many large genera of plants containing over 100 species. The genus *Tityus* has almost 190 (Lourenço, 2006). According to Prance (1982) during some of the dry periods, which took place during palaeoclimatic episodes, the forest cover was reduced to small patches and became fragmented into isolated allopatric populations. Such isolated populations of ecologically adaptable species, which was the case with some opportunistic species of Buthidae, rapidly recolonized the forest that became reestablished after wet episodes. Consequently, previously isolated populations became contiguous. Temporary reproductive isolation did not produce genetic incompatibility. This is apparently the case both for woody plants and for scorpions. Only minor morphological differences evolved, and when species reunited, geographical variation was no longer well-correlated. Prance (1982) suggested that this type of variation is attributable to recent Pleistocene climate changes, and not to actual, completed speciation. The number of generations in both woody plants and scorpions since the last dry period (from 13,000 years BP to the present) is much less than in other groups of organisms, such as butterflies (Turner, 1971). Only a limited amount of speciation therefore probably occurred. Most valid species in all probability originated long before the recent Pleistocene palaeoclimatic episodes.

It is possible to suggest that a similar process took place for species dwelling exclusively in savannahs, naturally in inversed epochs to those from forests. It is quite possible that final answers to these questions can only be obtained with the help of a more sophisticated approach such as those of the molecular (DNA) analysis. Since we do not yet possess these answers, I decided to address in this note some new insights and considerations on the northern South American savannah species of *Rhopalurus*.

*Rhopalurus laticauda* Thorell, 1876

This species type of the genus and the genus itself were described simultaneously by Thorell (1876) based on specimens labelled “America meridionalis, Columbia”. During my revision of the genus (Lourenço, 1982), I examined two females labeled ’types’ (NMG-N°170). In Colombia and Venezuela, the elements that better match the original types of the species are those from the Llanos formation or Orinoquian region. In this point, Teruel & Roncallo (2008) seem to agree with my opinion. The species was precisely diagnosed and illustrated in my revision (Lourenço, 1982), and again by Teruel & Roncallo (2008), as well as by González-Sponga (1978, 1984, 1996). González-Sponga (1984, 1996) suggested that *R. laticauda* is one of the most common species in Venezuela, and clearly showed that this species or any other species of *Rhopalurus* are...
Euscorpius — 2008, No. 73

Table 1: Morphometric values in mm of the studied species of Rhopalurus. A = R. laticauda (male/female); B = R. crassicauda (male/female); C = R. crassicauda paruensis ssp. n. (male holotype); D = R. pintoi kourouensis ssp. n. (male holotype).

* without telson. For values on R. pintoi refer to Teruel & Tietz (2008).

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<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
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<td>44.1/44.8</td>
<td>41.2</td>
<td>80.7</td>
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<td>- length</td>
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<td>5.2/4.6</td>
<td>6.2</td>
<td>11.0</td>
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<tr>
<td>- anterior width</td>
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<td>3.5/3.4</td>
<td>4.0</td>
<td>6.9</td>
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<tr>
<td>- posterior width</td>
<td>6.6/7.6</td>
<td>5.9/5.5</td>
<td>6.9</td>
<td>11.4</td>
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<tr>
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<td>4.0/3.5</td>
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<td>7.8</td>
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<tr>
<td>- length</td>
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<td>5.7</td>
<td>10.9</td>
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<td>5.0/3.0</td>
<td>5.7</td>
<td>10.8</td>
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<tr>
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<tr>
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<td>5.9/5.0</td>
<td>6.4</td>
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absent from the southern regions of the state of Bolivar which borders the state of Roraima in Brasil (Gonzalez-Sponga, 1978). This point will show its importance in relation to the status of R. crassicauda distributed in the savannahs of central/South Guiana and Roraima. The argument of gaps in the inventory work does not hold in this case since the state of Bolivar was intensely prospected by Gonzalez-Sponga and collaborators.

**Rhopalurus crassicauda** Caporiacco, 1947

Species described from the savannahs of Rupumuni (Rupununi) in Guiana (Caporiacco, 1947, 1948). For my revision of the genus (Lourenço, 1982), I examined the type material of Caporiacco, composed of two males and one female indicated as types and collected by Beccari, XI/1931. In my revision work, I misidentified both *R. crassicauda* and *R. pintoi*, mainly because of the impossibility to examine the type specimen of this last species (which is lost), but also because of my misinterpretation of some characters proposed by Mello-Leitão (1932) for *R. pintoi*. I will discuss further on this matter in the section dedicated to *R. pintoi*. In my fauna of Brazil (Lourenço, 2002), however, I revalidated *R. crassicauda* and proposed a clear diagnosis which is reproduced here.

“Scorpions of small to medium size, 40 to 45 mm in total length. General coloration basically yellowish to reddish-yellow. Metasomal segments I to III yellowish; IV and V reddish-yellow. Granulation and carinae moderate to strong. Pectines: pectinal tooth count 20 to 25. Metasomal segments with 10-10-10-8-5 carinae, crenulate. Telson, smooth with a short and curved aculeus. Subaculear tooth very small and not spinoid. Movable fingers with 8/9 oblique rows of granules. This species is most closely related to *Rhopalurus laticauda*, which is known from the Llanos of Venezuela and Colombia. Geographical distribution: State of Roraima in Brazil and Guyana.”

Although I clearly associate *R. crassicauda* with *R. laticauda*, I still prefer to reject their possible synonymy. In contradiction to the opinion of Teruel & Tietz (2008), the two populations are distinct geographically, and the presence of *R. crassicauda* in Venezuela (southern Bolivar State), was never demonstrated (Gonzalez-Sponga, 1978). In the remarks done by Teruel & Tietz (2008), these authors affirmed that the female specimens
studied by me in my revision (Lourenço, 1982) were in fact juveniles. This observation is incorrect, mainly because these females gave birth in captivity, and some of the juveniles are also listed under the material studied. If a true contact between the populations of *R. laticauda* and *R. crassicauda* can finally be established in Venezuela, then the subspecific status may be applied to these taxa.

*Rhopalurus caribensis* Teruel et Roncallo, 2008

The *Rhopalurus* population recently described by Teruel and Roncallo as *R. caribensis* is distributed in the Llanos of the Magdalena (Sarmiento, 1984), in the region of La Guajira in Colombia. In my paper about the fauna of the region of Santa Marta (Lourenço, 1991b), I call the attention about some differences between the *Rhopalurus* of this region and those of the central Llanos without taking any decision about the definition of a new species. Teruel & Roncallo (2008) defined these differences with more details and decided for the description of a new species. Here again, we are faced by the same dilemma; do we have two different species or only two different subspecies or morphs of a single species? Even if these two populations truly have an allopatric distribution, their now isolated territories most probably coalesced during past dry periods (Ab’Saber, 1977). For the moment, I will accept this new taxon as valid; however, I am almost convinced that some minor zones of contact may prove to exist between the two populations. In this case, as for *R. crassicauda*, the status of subspecies may be better applied. Most certainly, only the use of molecular techniques will led us out of this impasse. I will present in this note two more cases of possible new subspecies, representing once again such “biogeographic puzzles”.

*Rhopalurus pintoi* Mello-Leitão, 1932

In my revision of the genus *Rhopalurus* (Lourenço, 1982), I assumed that the species *Rhopalurus pintoi* Mello-Leitão, 1932, described from the State of Roraima
(Brazil), and *Rhopalurus crassicauda* Caporiacco, 1947 described from the British Guiana (now Guyana) could be synonyms. In fact, I made a mistake, mainly because I based my observations only on specimens of *R. crassicauda*. This misidentification was caused by a few precise reasons. The type of *R. pintoi* originally deposited in the collection of Prof. Cezar Pinto has been lost and the description of Mello-Leitão (1932) is poor. In their recent publication, Teruel & Tietz (2008), correctly revalidate this species, and insisted about its very easy identification based on its unique blackish coloration. In his description, Mello-Leitão (1932) refers to a blackish-brown species, and compared it to *Rhopalurus borellii* Pocock, 1902 (a junior synonym of *R. agamemnon* (C. L. Koch, 1839)). “A presente especie é notavel pelo colorido uniforme, quasi negro, aproximando-se mais de *R. Borelli* Poc.” In fact, *R. agamemnon* is not a blackish species at all, but rather reddish-brown. Moreover, Mello-Leitão refers to a male specimen with 55 mm in total length, which in fact should correspond to a juvenile female. The examination of the specimens of *R. crassicauda*, which can also be reddish-brown over the carapace and tergites and, with a size reaching 50 to 55 mm in total length conducted me to the misidentification. It is also important to recall that *R. pintoi* is not uniformly blackish, but rather dark, with reddish-brown sternites and reddish-yellow legs (see Figs. 2–3). In all cases, its dark coloration has nothing to see with the true blackish coloration of some rain forest species such as *Tityus asthenes* Pocock, 1893 or *Brotheas granulatus* Simon, 1877. Nevertheless, *R. pintoi* is a valid species.

**Rhopalurus piceus** Lourenço et Pinto da Rocha, 1997

*Rhopalurus piceus* was also described from the State of Roraima (Lourenço & Pinto da Rocha, 1997). In my fauna of Brazil (2002), I suggested that this species could eventually be associated with *R. pintoi*; however, on account of the impossibility of knowing, at that date, the real status of *R. pintoi*, I decided to regard this last species as a *nomen nudum* and to retain *R. piceus* as valid species. At present, on light of the results published by Teruel & Tietz (2008), but also thanks to non published information provided by Alessandro Giupponi from the Museu Nacional in Rio de Janeiro, the status of *R. pintoi* is clear. Teruel & Tietz (2008), considered also *R. piceus* as a junior synonym of *R. pintoi*. This decision may prove to be correct, however, a few doubts subsist yet. The pattern of coloration of *R. piceus* shows some differences, with a more intense blackish pigmentation over the pedipalps and legs, and the body and appendages have a weaker setation. Naturally, these differences are probably only due to intraspecific variation, but a more extensive study of the fragmented biome of Roraima and savannas of the Rio Branco-Rupununi could bring more evidence to a possible exclusion of these two elements. Finally, in their remarks Teruel & Tietz (2008) erroneously suggested that the holotype and paratype of *R. piceus*, sexed as males would in fact be females. This observation is fallacious, because the holotype illustrated in figures 17–18 of Lourenço & Pinto da Rocha (1997), and also one paratype are probably pre-adults, but without any question males. One should recall that Teruel & Tietz (2008) did not examine the type material of *R. piceus*.

**Two New Subspecies from Guayana Savannahs**

In this section I will present two new elements, which I was able to study, from two other zones of savannahs within the Guayana floristic region (Fig. 4). One was collected in the “campos” of Paru in northeastern Pará South of the Serra do Tumucumaque, with the adjacent Sipaliwini Savannah in Suriname (Eiten, 1978; Murça Pires & Prance, 1985). This form, which I will define as a subspecies, can be considered as a sibling of *R. crassicauda*.

The second element was collected in the Coastal savannahs of the Guayanas (Sarmiento, 1984), more precisely in the region of Kourou in French Guyana. Once again I will define this form as a subspecies and as a possible sibling of *R. pintoi*. In both cases, these savannah areas of the Guayana region most certainly coalesced with those of Rio Branco-Rupununi area in past dry epochs. The definition of subspecies normally requires the demonstration of contact zones between the more or less isolated subpopulations. This could be the case here, however, at the present stage of our knowledge we do not have significant information about the scorpion population of the savannah of Suriname. More complete studies about the fauna of Suriname will probably bring the answer to these questions.

With description of these two subspecies, the nominal subspecies are automatically established as well: *Rhopalurus crassicauda crassicauda* Caporiacco, 1947, from Rupununi in Guyana (the type locality) and Roraima (Brazil); and *Rhopalurus pintoi pintoi* Mello-Leitão, 1932, from Roraima (type locality) and Rupununi in Guyana.

**Methods**

Illustrations and measurements were produced using a Wild M5 stereo-microscope with a drawing tube and an ocular micrometer. Measurements follow Stahnke (1970) and are given in mm. Trichobothrial notations...
follow Vachon (1974) and morphological terminology mostly follows Vachon (1952) and Hjelle (1990).

*Rhopalurus crassicauda paruensis* ssp. n.
(Figs. 5–9)


Etymology: The subspecific name makes reference to the Campos of Paru in state of Pará.

Diagnosis: Small scorpion in relation to the species of the genus, with 41.2 mm in total length. Very pale coloration, yellowish to pale yellow. Pectinal tooth count 25–25; fixed and movable fingers of pedipalps with 7–8 rows of granules.
Figures 5–9: *Rhopalurus crassicauda paruensis* ssp. *n.*, male holotype. 5–7. Chela, dorso-external, ventral and internal aspects, showing trichobothria. 8–9. Tarsi of leg IV, lateral and ventral aspects, showing setation.
LOURENÇO: Rhopalurus in the Guayana-Amazon

Relationships: This subspecies is clearly related to R. crassicauda. It is distinguished, however, by a much paler general coloration with the absence of a solid blackish stripe on the ventral aspect of metasomal segments.

Description based on male holotype. Measurements in Table 1.


Ecology: The type specimen of R. crassicauda paruensis ssp. n. was collected in the “Campo firme” formation. A gradient of Cerrados also defined as “dry campo”. This gradient can present trees and shrubs forming a sparse to open cover (Eiten, 1978). The scorpion was collected under the bark of a tree (Bowdichia sp.), about 1.5 m from the ground.

Rhopalurus pintoi kourouensis ssp. n.

(Figs. 10–17)


Etymology: The subspecific name makes reference to Kourou region in French Guiana.

Diagnosis: Large scorpion in relation to the species of the genus, with 89.7 mm in total length. Very dark coloration, uniformly blackish. Pectinal tooth count 24–25; fixed and movable fingers of pedipalps with 9–10 rows of granules.

Relationships: This subspecies is clearly related to R. pintoi. It is distinguished, however, by a darker general coloration almost entirely blackish and a smaller number of pectinal teeth, 24–25. Teruel & Tietz (2008) indicate 27 to 30 for the male of R. pintoi with a mean of 28.33.

Description based on male holotype. Measurements in Table 1.


Morphology. Carapace strongly granular; anterior margin with a median concavity. Anterior median and posterior median carinae strong. All furrows moderately deep. Median ocular tubercle distinctly anterior to the center of the carapace. Eyes separated by more than one ocular diameter. Three pairs of lateral eyes. Sternum triangular. Mesosoma: tergites strongly granular. Median carina strong in all tergites. Tergite VII pentacarinate. Venter: genital operculum divided longitudinally forming two semi-triangular plates. Pectines: pectinal tooth count 24–25. Sternites smooth with elongate spiracles; VII with four carinae and some lateral granulations. Metasoma: segments I and II with 10 carinae; III and IV with 8 carinae; V with 5 carinae; inframedian carinae complete on II. Telson weakly granular, with a long and strongly curved aculeus. Dorsal surface smooth; ventral surface granular; subacicular tooth absent. Cheliceral dentition characteristic of the family Buthidae; ventral aspect of both fingers and manus with dense, long setae (Vachon, 1963). Pedipalps: femur pentacarinate; patella with 7 carinae; chela with 9 carinae; internal face of patella with spinoid granules; all faces moderately to weakly granular. A very intense chetotaxy can be observed in all segments. Fixed and movable fingers with 9-10 oblique rows of granules. Internal and external accessory granules strongly marked. Trichobothriotaxy:
Figures 10–13: *Rhopalurus pintoi kourouensis* ssp. n. 10. Chela, dorso-external aspect, showing trichobothria and very intense setation. 11. Chela, idem, represented without setation. 12–13. Patella and femur, dorsal aspect. Again an important setation can be observed.

Ecology: The type specimen of the new subspecies was collected in the Coastal savannahs of the Guianas near Kourou (Sarmiento, 1984), in a zone where some forested spots (taches forestières) could be observed. In the case of *R. pintoi*, Teruel & Tietz (2008) stated that the specimens they studied were collected “inside a small relict patch of primary forest enclave inside surrounding hilly grasslands…” It is important to notice that inside the Cerrados or Savannah formations of South America several vegetation gradients can be observed. According to Eiten (1978), “within the Cerrado province a small percentage of the uplands (terrain not effected by water accumulation in valleys) is covered with mesophytic forest. These are small scattered areas of more fertile latosol…” Also in a few places, “upland mesophytic forest may intergrade to Cerradão, the arboreal forest or woodland form of Cerrado.” Consequently, one should not associate the *R. pintoi* or *R. pintoi kourouensis* ssp. n. to real forest formations.

**Discussion**

The present analysis of the species of *Rhopalurus* distributed in the savannahs of northern South American clearly shows the existence of two distinct lineages. One represented by *R. laticauda* with three associated forms (species or subspecies?), and the other represented by *R. pintoi*, with possibly two associated forms.

In both cases, the forms within each of the two lineages present only very weak morphological differences, demonstrating a recent and only minor process of differentiation. This pattern of both distribution and differentiation is directly associated with more or less recent palaeoclimatic vicissitudes which took place in Tropical South America during the Pleistocene, the most recent dated only of 18.000–13.000 years BP (Ab’Saber, 1977; Van der Hammen, 1983). During dry periods most of the South American savannahs and/or open vegetation formations coalesced to form continuous areas of distribution of species exclusively adapted to these formations (Fig. 1) such as those belonging to the genus *Rhopalurus*. During wets periods, such as the present one, these same savannah formations know a process of fragmentation with a subsequent isolation of small populations.

The consequences on the process of speciation during the subsequent wet/dry/wet periods is difficult to measure, but probably was rather weak on groups such as scorpions with long term reproduction process and a low number of generations when compared to other zoological groups such as insects (Prance, 1985; Lourenço, 2001). It is therefore rather difficult to assign a precise status to the forms within the two well established lineages. Are we in face of species, subspecies or only morphs of a large polymorphic species? If, at least for some of these forms, their specific condition could be demonstrated in association with a clear allopatric distribution of the populations, than the condition of superspecies *sensu* Mayr (1931) could be applied to each of the two lineages. The species within each lineage would be represented by allopatric, parapatric our weakly sympatric groups, really or potentially intersterile in nature (Bernardi, 1980). Each of these species could then be defined as a “prospecies” in the sense of Birula (1910).

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**References**


