

Description of a new species of *Heteroscorpion* Birula, 1903 (Scorpiones, Heteroscorpionidae) from the Montagne des Français in extreme northern Madagascar

WILSON R. LOURENÇO¹ & STEVEN M. GOODMAN²

¹Département de Systématique et Evolution, USM 0602, Section Arthropodes (Arachnologie), Muséum national d'Histoire naturelle, CP 053, 61 rue Buffon 75005 Paris, France. E-mail: arachne@mnhn.fr

²Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA, and WWF, BP 738, Antananarivo (101), Madagascar. E-mail: sgoodman@fieldmuseum.org

Abstract

The endemic Malagasy genus *Heteroscorpion* Birula, 1903, of the family Heteroscorpionidae was monotypic for a century with *H. opisthacanthoides* (Kraepelin, 1896). Extensive field surveys conducted over the last 15 years in the different bioclimatic regions of Madagascar have resulted in the collection of numerous scorpions, including specimens belonging to the genus *Heteroscorpion*. These collections led to the description of three new species, *H. goodmani* Lourenço, 1996, *H. magnus* Lourenço & Goodman, 2002, and *H. raselimanana* Lourenço & Goodman, 2004. In this paper another species new to science is described from the extreme north of the island and is presumed to be locally endemic. With this taxon, the number of species in the genus *Heteroscorpion* is now five, and its distribution covers numerous zones of the island, including humid and dry forests. Aspects of the geographic distribution and ecology of the different species are also commented upon.

Key words: Madagascar, scorpion, *Heteroscorpion*, new species, geographic distribution, ecology

Introduction

At the end of the 19th-century and the beginning of the 20th-century, the Malagasy scorpion fauna was composed of two families: the Buthidae C. L. Koch, 1837 and the Scorpionidae Latreille, 1802. This latter family was represented by the subfamily Ischnurinae Simon, 1879, with two genera: *Opisthacanthus* Peters, 1861 and *Heteroscorpion* Birula, 1903. The genus *Heteroscorpion* remained monotypic for the next century, represented by *H. opisthacanthoides* (Kraepelin 1896), known from the northwest portion of the island, until

Lourenço (1996) described a second species, *H. goodmani* from the Réserve Naturelle Intégrale d'Andohahela (now classified as a Parc National). In that same publication, Lourenço (1996) raised the taxonomic rank of the subfamily Heteroscorpioninae Kraepelin, 1905 to a family, a move that was subsequently supported by Prendini (2000) based on a cladistic analysis with all characters weighted equally. Subsequent faunal inventories in previously unexplored or poorly known areas of the island led to a series of new descriptions, but in most cases these refer to scorpions of the families Buthidae and Microcharmidae Lourenço, 1996, although there are exceptions, such as the description of *Palaeocheloctonus pauliani* Lourenço, 1996, new genus and species of Liochelidae (Fet & Bechly 2001) from the southwest.

A remarkable discovery concerning the genus *Heteroscorpion* took place near Daraina in the northeast, where the remaining natural habitat cover is composed of transitional dry and humid forests. Here a distinct population of *Heteroscorpion* was found in a humid forest block, and described as *H. magnus* by Lourenço and Goodman (2002). The most noteworthy aspect of this species is its overall size, with adult females reaching 144 mm and adult males 187 mm in total length (Lourenço *et al.* 2003), making it the largest scorpion known from the island. Subsequently, *H. raselimanana* Lourenço & Goodman was described from the region of Midongy-Sud in the southeastern portion of the eastern humid forest. With the description of that species, the geographical range of the genus *Heteroscorpion* included a considerable variety of different forest habitats in the northwest and several different areas of the eastern half of the island.

The new species of *Heteroscorpion* described herein is from the dry forests of Montagne des Français in the extreme north. This is the first *Heteroscorpion* occurring exclusively in this forest formation. Aspects of the geographic distribution and ecology of all the species of this genus are discussed.

Material and 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), Hjelle (1990), Sissom (1990) and partly Prendini (2000).

Taxonomic treatment

Family Heteroscorpionidae Kraepelin, 1905

The phylogenetic position and taxonomic rank of *Heteroscorpion* have been the subject of

discussions amongst scorpion systematists in recent years (Prendini 2000; Soleglad & Fet 2003; Soleglad *et al.* 2005). In a recent publication, Prendini and Wheeler (2005) re-established Heteroscorpionidae as a family, following Lourenço (1996) and Prendini (2000), after it was downgraded to a subfamily of Urodacidae Pocock, 1893 by Soleglad & Fet (2003) and a subfamily of Hemiscorpiidae Pocock, 1893 by Soleglad *et al.* (2005). The classification of Prendini and Wheeler (2005) is adopted here.

Genus *Heteroscorpion* Birula, 1903

Diagnosis. Scorpions of large size, with female adults reaching 60 to 145 mm and male adults 100 to 187 mm. Sexual dimorphism strongly marked, mainly by the allometric growth shown in males. Two pairs of lateral eyes. Metasomal segments I to IV very flattened laterally with single ventral median carina. Telson weakly elongated in both sexes. Dentate margin on fingers with numerous granules arranged on their basal two-thirds, and forming two parallel series of granules on its distal portion; a few stronger accessory granules may be present. Trichobothriotaxy of type C, neobothriotaxic majorante (+), plethotaxic in one species (*H. magnus*) on the patella and chela (chela + fixed finger). Hemispermatophore (see figures 4–5 in Lourenço & Goodman 2002). Venom glands presumed to be simple.

Geographic distribution: both the family and genus are endemic to Madagascar.

Heteroscorpion kraepelini sp. n. (Figs. 1–7)

Type material. Holotype: 1 male, Madagascar, Province d’Antsiranana, Montagne des Français, tropical dry forest, I/III/2000 (F. Glaw & M. Vences leg.).

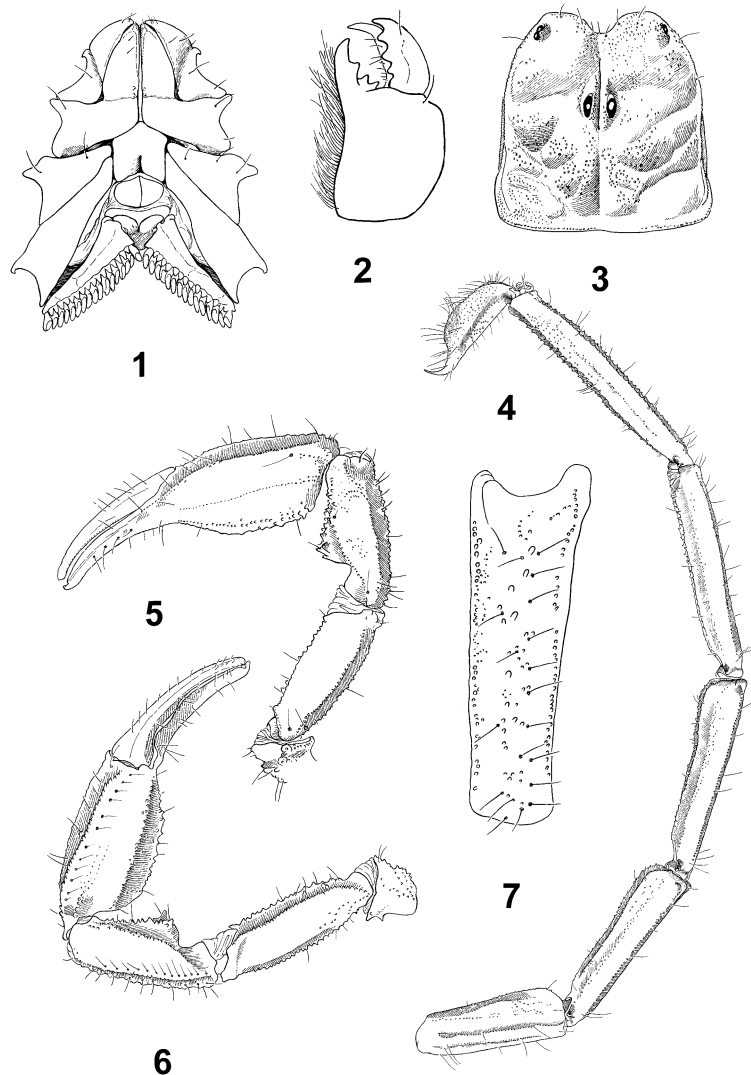
Depository: Holotype in the Muséum national d’Histoire naturelle, Paris. No paratype.

Etymology: The specific name is a patronym in honor of Karl Kraepelin from Hamburg, Germany, who described the first species of *Heteroscorpion* and proposed the family-group name Heteroscorpionidae.

Diagnosis. Scorpion of moderate size, with adult male reaching 100 mm in total length. Coloration, basically brownish to reddish-brown, including the legs, although the tip of pedipalp fingers and chelicera are paler than the body and approaching reddish-yellow. Body and pedipalps covered with a moderate setation. Trichobothriotaxy of type C, neobothriotaxic majorante (+); patella with 20 external trichobothria, and 13/15 ventral trichobothria; chela (chela + fixed finger) with 11/12 ventral trichobothria. Hemispermatophore not observed.

Relationships: *Heteroscorpion kraepelini* can be distinguished from other species in the genus *Heteroscorpion*, and in particular from *H. opisthacanthoides* and *H. goodmani* by the following characters: (i) a paler reddish-brown to reddish-yellow coloration over

the body and appendages, with the legs, the tip of pedipalp finger and chelicera paler than the body; (ii) a smaller overall adult size, with distinct morphometric values (see Table 1); and (iii) a distinct trichobothrial pattern; patella with 13–15 ventral and 20 external trichobothria; chela with 11–12 ventral trichobothria (see also comparative table after the description). Internal trichobothria of both femur and patella very much displaced to the internal surface.



FIGURES 1–7. *Heteroscorpion kraepelini* **sp. n.**, male holotype. 1. Venter, showing coxapophysis, sternum, genital operculum and pectines. 2. Chelicera, dorsal aspect. 3. Carapace. 4. Metasomal segments I to V and telson, lateral aspect. 5–6. Pedipalp in dorsal and ventral aspects, showing trichobothrial pattern. 7. Patella, external aspect, showing trichobothria.

Description. Based on male holotype. Measurements in Table 1.

Coloration. Body basically brownish to reddish-brown. Prosoma: carapace reddish-

brown, with some blackish coloration near the eyes. Mesosoma: tergites reddish-brown; sternites III to VI reddish with conspicuous yellow spots; sternite VII darker than the others. Coxapophysis and sternum reddish-yellow; genital operculum and pectines pale yellow. Metasoma: all segments reddish to reddish-brown; dorsal and ventral carinae darker; vesicle reddish-brown; aculeus yellowish at the base and dark reddish at the tip. Chelicerae reddish-yellow with variegated dark spots; fingers reddish-brown with reddish-yellow teeth. Pedipalps: femur, patella, and chela reddish-brown with the tip of the fingers reddish yellow. Legs reddish-yellow with tarsi yellowish.

Morphology. Carapace (Fig. 3) with a rough tegument and moderate to strong granules; anterior margin with a strongly pronounced concavity; carinae practically absent; posterior furrows strongly pronounced; median ocular tubercle anterior to the center of the carapace; two pairs of moderate to small lateral eyes; the first lateral eye almost twice the size of the second eye. Sternum (Fig. 1) pentagonal, slightly wider than long. Mesosoma: tergites almost acarinate with only a very weak median carina and some weak granulations; tergite VII with a more intense granulation. Venter (Fig. 1): genital operculum formed by two semi-oval plates; genital papillae not protruded, therefore not observable. Pectines: pectinal tooth count 15–17; fulcra conspicuous. Sternites almost smooth with some minute granulations on the lateral edges; presence of two longitudinal parallel furrows on III to VI; spiracles linear and conspicuous; and sternite VII with two vestigial carinae. Metasoma (Fig. 4) with all segments flattened laterally; dorsal carinae with minute spinoid granules on segments I and II; spinoid granulation becomes more strongly marked on segments IV to V; ventromedian and ventrolateral carinae vestigial on segments I to III, spiniform on IV and intensely spinoid on V; ventral surface of segment V with a strong spinoid granulation; all intercarinal surfaces sparsely granular to smooth. Telson weakly elongated with strongly marked spinoid granules on ventral and lateral surfaces; aculeus proportionally very short and strongly curved; and a notable covering of setae on ventral and lateral faces. Cheliceral dentition (Fig. 2) characteristic of the Scorpionoidea (Vachon 1963); movable finger with one subdistal and one median tooth almost of the same size and a basal tooth reduced. Pedipalps (Figs. 5, 6) with moderate granulation; femur with dorsal external, dorsal internal, ventral external and ventral internal carinae, all complete; patella with dorsal internal, dorsal, dorsal lateral, external, ventral lateral and ventral internal carinae complete, and a very strong double apophysis on the internal aspect; chela with dorsal axial, dorsal accessory, median, dorsal external, ventral external and ventral internal carinae; weak to moderate; dentate margin on fingers with numerous granules not forming discrete rows on their basal two-thirds, and forming two vestigial parallel series of granules distally; presence of a few stronger accessory granules. Trichobothriotaxy of type C; neobothriotaxic (Vachon 1974); patella with 13/14 ventral and 20 external trichobothria; chela with 11/12 ventral trichobothria. Body and pedipalps covered with a moderate setation. Legs: tarsi of legs III and IV with three prolateral and three retrolateral spines.

TABLE 1. Comparative morphometric values (in mm) of the species of *Heteroscorpion*.

	<i>H. opisthacanthoides</i>		<i>H. goodmani</i>		<i>H. magnus</i>		<i>H. raselimanana</i>	<i>H. kraepelini</i> sp. n.
	M	F	M	F	M	F	F	M
Total length	142.0	110.0	115.0	63.0	187.2	144.0	73.1	101.7
Carapace								
- length	14.1	14.0	10.2	11.4	15.6	19.4	10.4	10.3
- anterior width	8.6	8.9	6.2	7.0	9.8	11.6	6.3	6.1
- posterior width	14.2	14.1	9.3	10.0	16.2	19.6	10.1	10.4
Metasomal segment I:								
- length	15.6	7.0	10.0	5.4	21.1	10.7	5.5	9.8
- width	3.8	4.2	2.3	3.1	3.1	4.2	2.9	2.9
Metasomal segment V:								
- length	23.3	12.3	17.2	10.2	29.1	16.2	9.6	15.2
- width	2.3	2.6	1.8	2.4	1.8	2.8	2.1	1.7
- depth	3.2	3.2	2.4	2.6	3.3	3.4	2.4	2.2
Vesicle:								
- width	4.0	3.4	2.8	3.0	3.1	3.3	2.5	2.4
- depth	5.2	3.6	3.1	3.0	3.9	4.2	2.6	2.3
Pedipalp:								
-Femur length	12.4	12.1	10.9	10.7	16.9	18.4	10.1	11.2
- Femur width	4.5	4.8	3.4	3.6	5.7	7.1	3.6	3.8
- Patella length	13.8	13.2	10.3	10.7	15.2	18.1	10.2	10.8
- Patella width	6.3	6.6	4.5	4.7	7.1	9.7	4.8	4.9
- Tibia length	27.4	25.6	20.9	21.5	33.8	39.1	19.8	21.4
- Tibia width	9.5	9.0	6.0	7.5	8.4	11.4	5.8	6.3
- Tibia depth	7.2	6.9	5.0	5.3	6.4	8.2	4.8	4.5
Movable finger:								
- length	15.2	14.2	11.8	11.9	18.2	19.2	10.5	10.3

Geographic distribution. Only known from the type locality.

The following characters can distinguish the four species of the genus *Heteroscorpion*:

	Color	Adult total length	Trichobothrial pattern
<i>H. opisthacanthoides</i>	brownish	110–42 mm	Patella with 10–11 ventral and 17–19 external. Chela with 8–9 ventral.
<i>H. goodmani</i>	blackish	60–115 mm	Patella with 8–9 ventral and 17 external. Chela with 9 ventral.
<i>H. magnus</i>	blackish	145–187 mm	Patella with 14–19 ventral and 31–40 external. Chela with 12–15 ventra
<i>H. raselimanana</i>	blackish	70 mm	Patella with 8 ventral and 16 external. Chela with 6 ventral.
<i>H. kraepelini</i> sp. n.	Reddish- brown	100 mm	Patella with 13/15 ventral and 20 external. Chela with 11/12 ventral.

Ecology and distribution of the described species of *Heteroscorpion*

1. *Heteroscorpion opisthacanthoides* is only documented in the forests of Nosy Komba and Lokobe on Nosy Be, to the northwest of Ambanja. It is certainly a lowland species, as the maximum elevation of either these two islands does not exceed 500 m.a.s.l. The ocean depth separating these islands from mainland Madagascar is shallow (Service Géographique de Madagascar 1958) and during the Quaternary these two islands were connected to one another and to mainland Madagascar.

Nosy Be and Nosy Komba, together with the mainland area surrounding Ambanja, form a distinct phytogeographic region referred by Perrier de la Bâthie (1921, 1936) as the Sambirano Region. In a more modern definition of this region, Humbert (1965) included the Sambirano River valley, up to an elevation of 800 m at the foothills of the Tsaratanana and Manongarivo Massifs, a portion of the northwestern coast between Baie d'Ambaro and Baie d'Ampasindava, Nosy Be, and Nosy Komba. The region holds variable habitats ranging from dry deciduous to humid forests, containing many endemic plants. The local dry season is four to five months long, and the total annual rainfall exceeds 2100 mm (Legris & Blasco 1965; Donque 1975). For a detailed description of the Sambirano Region see Gautier and Goodman (2003).

The mainland forests of the Manongarivo region, as well as the Ampasandava Peninsula, have been the subjects of biological inventories and the scorpions collected at

these sites do not include material of *H. opisthacanthoides* (Lourenço 2002). Whether this species is truly endemic to the offshore islands of the Ambanja region will necessitate further inventory work on the lowland mainland region. Additional scorpion species are endemic to the Manongarivo Massif, such as *Microcharmum cloudsleythompsoni* and *Neoprotobuthus intermedius* (Microcharmidae), but to date unknown from Nosy Be and Nosy Komba (Lourenço 2002).

2. *Heteroscorpion goodmani* is found in the lowland humid forests of Parcel I of the Réserve Naturelle Intégrale d'Andohahela (now classified as a Parc National), in the extreme southeast. This zone receives > 1500 mm of rain, and a dry season of approximately two months per year (Donque 1975; Goodman 1999). *Heteroscorpion goodmani* has been observed at night climbing up and resting on vertical tree trunks in lowland forest (Lourenço & Goodman 1999). The elevational range within the Andohahela forest is 400–440 m.a.s.l. (Lourenço & Goodman 1999). The region immediately west of the Andohahela Massif is characterized by a dramatic reduction in annual precipitation, which is marked by a narrow ecotone to spiny bush. For a detailed description of this region see Goodman (1999).

3. *Heteroscorpion magnus* has been recorded in two different forest blocks near Daraina in the extreme northeastern portion of the island. This is a region of dramatic ecotones between different forest types over distances of a few kilometers, linked to bioclimatic parameters (Cornet 1972), complex geological formations (Besairie 1964), and considerable orographical variation. The closest weather station to Daraina is at Vohémar, 40 km to the southeast, which receives < 1500 mm of annual rain and experiences a pronounced dry season for about seven months (Donque 1975). This species known elevational range is from 325–600 m.a.s.l.

4. *Heteroscorpion raselimanana* has been collected in lowland humid forest formations of Mt. Ambatobe, to the north of Midongy-Sud. This is a zone of extensive forested areas, but with little remaining at lower elevations. The holotype was found during the day under a large rock and within a few meters of the source of a small and permanent stream (Lourenço & Goodman 2004). Another individual of the genus *Heteroscorpion*, presumably *H. raselimanana*, was observed climbing the trunk of a small tree within the same forest block during the early night hours (Lourenço & Goodman 2004). The closest weather station to the holotype collection site is at Midongy-Sud, 9.5 km to the south, which receives about 1800 mm of annual rain and the dry season approaches six months per year (Donque 1975). This species known elevational range is at 650 m.a.s.l.

5. *Heteroscorpion kraepelini* is only known from the holotype obtained in the dry limestone region of Montagne des Français, close to the provincial capital of Antsiranana. No specific collection details are associated with the specimen. However, much of this mountain range is sparsely vegetated with dry deciduous forest along steep cliff faces and a distinct flora dominated by several locally endemic plants on the upper slopes of the

massif. The zone receives little rainfall and permanent water sources are very limited. To the south of the Montagne des Français is a largely continuous zone of exposed limestone passing through the region of Analamerana to the Andriafiamena Mountains. The region of Analamerana was the subject of biological inventories in 2003, at two different sites. Specimens of *Grosphus* Simon, 1880, *Tityobuthus* Pocock, 1893 and *Microcharmus* Lourenço, 1995 (presently under study) were obtained at the site, but *Heteroscorpion* was not found. To the south of the Andriafiamena Mountains the geology shifts to igneous and metamorphic rock, and this is the region of Daraina and within the range of *H. magnus*. The closest weather station to Montagne des Français is at Antsiranana, which has annual precipitation of less than 1,000 mm and a very pronounced dry season of seven to eight months (Donque 1975).

Key to the species of *Heteroscorpion*

1. Coloration brownish or reddish-brown to reddish-yellow 2
- (1). Coloration blackish 3
2. Adults ranging from 110 to 142 mm in total length; patella with 10–11 ventral and 17–19 external trichobothria; chela with 8–9 trichobothria *H. opisthacanthoides*
- (2). Adults ranging from 60 to 100 mm in total length; patella with 13–15 ventral and 20 external trichobothria; chela with 11–12 trichobothria *H. kraepelini* **sp. n.**
3. Adults ranging from 145 to 187 mm in total length; patella with 14–19 ventral and 31–40 external trichobothria; chela with 12–15 ventral trichobothria *H. magnus*
- (3). Adults ranging from 60 to 120 mm in total length; patella with 8–9 ventral and 16–17 external trichobothria; chela with 6–9 ventral trichobothria 4
4. Chela with 6 ventral trichobothria; carinae and granulations on the body and pedipalps strongly developed *H. raselimanana*
- (4). Chela with 9 ventral trichobothria; carinae and granulations on the body and pedipalps moderately developed *H. goodmani*

Acknowledgements

We are very grateful to Michèle Bertoncini, Département de Systématique et Evolution, Muséum national d'Histoire naturelle, Paris, for drawing the illustrations.

References

- Besairie, H. (1964) *Carte Géologique de Madagascar*, au 1:1,000,000e, trois feuilles en couleur. Antananarivo: Service Géologique.
- Cornet, A. (1974) *Essai de cartographie bioclimatique à Madagascar*. Carte à 1/200.000 et notice no. 55. Paris: ORSTOM, 28 pp.

- Donque, G. (1975) *Contribution géographique à l'étude du climat de Madagascar*. Tananarive: Nouvelle Imprimerie des Arts Graphiques, 478 pp.
- Fet, V. & Bechly, G. (2001) Case 3120a. Liochelidae, fam. Nov. (Scorpiones): proposed introduction as a substitute name for Ischnuridae Simon, 1879, as an alternative to the suggested emendment of Ischnurinae Fraser, 1957 (Insecta, Odonata) to Ischnurainae in order to remove homonymy. *Bulletin of the Zoological Nomenclature*, 58 (4), 280–281.
- Gautier, L. & Goodman, S.M. (2003) Introduction to the flora of Madagascar. In: Goodman, S.M. & Benstead, J.P. (Eds.). *The natural history of Madagascar*. Chicago: The University of Chicago Press, pp. 229–250.
- Goodman, S.M. (1999) Editor. A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, new series, 94, 297 pp.
- Hjelle, J.T. (1990) Anatomy and morphology. In: Polis, G.A. (Ed.). *The biology of scorpions*. Stanford University Press, Stanford, pp. 9–63.
- Humbert, H. (1965) Description des types de végétation. In: Humbert, H. & Cours-Darne, G. (Eds.). Notice de la carte de Madagascar. Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry, hors série, 6, pp. 46–78.
- Legris, P. & Blasco, F. (1965) Carton des bioclimats. In: Humbert, H. & Cours-Darne, G. (Eds.). Notice de la carte de Madagascar. Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry, pp. 31–45.
- Lourenço, W.R. (1996) *Scorpions*. Faune de Madagascar. Muséum national d'Histoire naturelle, Paris, 102 pp.
- Lourenço, W.R. (2002) Scorpions of the Réserve Spéciale de Manongarivo, Madagascar. In: Gautier, L. & Goodman, S.M. (Eds.). Inventaire Floristique et Faunistique de la Réserve Spéciale de Manongarivo (NW Madagascar). *Boisieria*, pp. 329–337.
- Lourenço, W.R. & Goodman, S.M. (1999) Taxonomic and ecological observations on the scorpions collected in the Réserve Naturelle Intégrale d'Andohahela, Madagascar. In: Goodman, S.M. (Ed.). A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, new series, 94, pp. 149–153.
- Lourenço, W.R. & Goodman, S.M. (2002) Scorpions from the Daraina region of northeastern Madagascar, with special reference to the family Heteroscorpionidae Kraepelin, 1905. *Revista Ibérica de Aracnología*, 6, 53–68.
- Lourenço W.R. & Goodman, S.M. (2004) Description of a new species of *Heteroscorpion* Birula (Scorpiones, Heteroscorpionidae) from the eastern lowland humid forest of south-eastern Madagascar. *Revista Ibérica de Aracnología*, 9, 319–323.
- Lourenço, W.R., Goodman, S.M., Raheriarisena, M. & Ramilijaona, O. (2003) Description of the male of *Heteroscorpion magnus* Lourenço & Goodman, 2002 (Scorpiones, Heteroscorpionidae). *Revista Ibérica de Aracnología*, 8, 111–115.
- Perrier de la Bâthie, H. (1921) La végétation malgache. *Annales de l'institut botanico-géologique colonial de Marseille*, sér., 3, 9, 1–268.
- Perrier de la Bâthie, H. (1936) *Biogéographie des plantes à Madagascar*. Paris: Société d'Éditions Géographiques, Maritimes et Coloniales, 156 pp.
- Prendini, L. (2000) Phylogeny and classification of the superfamily Scorpionoidea Latreille 1802 (Chelicerata, Scorpiones): An exemplar approach. *Cladistics*, 16, 1–78.
- Prendini, L. & Wheeler, W.C. (2005) Scorpion higher phylogeny and classification, taxonomic anarchy, and standards for peer review in online publishing. *Cladistics*, 21, 446–494.
- Service Géographique de Madagascar (1958). Nossi-Bé, feuille RS—33, Carte de Madagascar au 100.000^E. Tananarive: Service Géographique de Madagascar.
- Sissom, W.D. (1990) Systematics, biogeography and paleontology. In: Polis, G.A. (Ed.). *The Biology of Scorpions*. Stanford University Press, Stanford, pp. 64–160.

- Soleglad, M.E. & Fet, F. (2003) High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11, 5–175.
- Soleglad, M.E., Fet, V. & Kovařík, F. (2005) The systematic position of the scorpion genera *Heteroscorpion* Birula, 1903 and *Urodacus* Peters, 1861 (Scorpiones: Scorpionoidea). *Euscorpius*, 20, 1–38.
- Stahnke, H.L. (1970) Scorpion nomenclature and mensuration. *Entomological News*, 81, 297–316.
- Vachon, M. (1952) Etudes sur les Scorpions. Institut Pasteur d'Algérie, 482 p. Alger.
- Vachon, M. (1963) De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 2e sér. 35(2), 161–166.
- Vachon, M. (1974) Etude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle*, Paris 3e sér., n° 140, Zool. 104, 857–958.

