A SYNOPSIS OF THE SCORPION FAUNA OF THE LOKY-MANAMBATO (DARAINA) REGION IN MADAGASCAR

Wilson R. Lourenço¹ & Steven M. Goodman²

¹ Muséum national d'Histoire naturelle, Département Systématique et Evolution, UMR7205, CP 053, 57 rue Cuvier, 75005 Paris, France – arachne@mnhn.fr

² Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA, and Vahatra, BP 3972, Antananarivo (101), Madagascar – sgoodman@fieldmuseum.org

Abstract: An overview is presented of the scorpion fauna of the Loky-Manambato (Daraina) region of northeastern Madagascar. Different scorpion taxa have been recently described from this area, belonging to four families, five genera and five species (with four microendemics). The preliminary results make the Loky-Manambato region one of the areas of the island with the highest level of diversity and endemism. Information is presented on the characters used to differentiate these species, including an identification key, and aspects of their ecology. Even given the remarkable level of habitat heterogeneity across the Loky-Manambato region, for the majority of locally occurring taxa there does not seem to be a close correlation between different aspects of soil composition and organic material relative to their distribution.

Key words: Scorpiones, diversity, endemism, Madagascar, Loky-Manambato.

Sinopsis de la fauna de escorpiones de la región de Loky-Manambato (Daraina), en Madagascar

Resumen: Se presenta una visión general de la fauna de escorpiones de la región Loky-Manambato (Daraina), en el noreste de Madagascar. Se han descrito recientemente de esta zona diferentes taxones de escorpiones, pertenecientes a cuatro familias, cinco géneros y cinco especies (cuatro microendémicas). Los resultados preliminares hacen de la región Loky-Manambato una de las zonas de la isla donde la fauna de escorpiones muestra un nivel de diversidad y endemismo más alto. Se presenta información sobre los caracteres utilizados para diferenciar estas especies, incluyendo una clave de identificación, y comentarios sobre aspectos de su ecología. Incluso teniendo en cuenta el notable nivel de la heterogeneidad del hábitat en la región Loky-Manambato, para la mayoría de los taxones locales no parece haber una correlación estrecha entre los diferentes aspectos de la composición del suelo y el material orgánico con respecto a su distribución. **Palabras clave:** Scorpiones, diversidad, endemismo, Madagascar, Loky-Manambato.

raiabras clave. Scorpiones, uversidad, endemismo, madagascar, Loky-manambato.

Un résumé de la faune de scorpions de la région Loky-Manambato (Daraina), à Madagascar

Résumé: Madagascar est parmi les régions du monde qui présentent une des plus grandes diversités biologiques. Pour comprendre cette diversité, les modèles biogéographiques présentés par différents groupes de scorpions ont été et continuent à être analysés. Malgré une certaine variabilité des modèles observés, certaines parties de l'île, notamment les régions sud, sud-est et nord, affichent un endémisme très élevé. Cependant, d'après une majorité des résultats obtenus jusqu'à présent, le nord de l'île apparaît comme un probable épicentre de diversité et endémisme.

Les études sur les scorpions malgaches ont débuté dès la première moitié du 19^{ème} siècle, et ont connu une certaine apogée entre 1890 et 1900. Malgré cela, c'est seulement depuis une quinzaine d'années que des inventaires méthodiques, suivis d'un nombre important de publications, ont été réalisés. La collecte de plusieurs centaines, voire de plusieurs milliers de scorpions depuis le début des années 1990 a permis un progrès considérable des connaissances sur cette faune de scorpions, avec une augmentation du nombre d'espèces connues de près de 500%.

La région de Loky-Manambato est un très bon exemple du progrès des connaissances des faunes régionales des scorpions à Madagascar. Les tous premiers spécimens de scorpions de cette région n'ont été collectés que depuis peu, et les résultats ont été publiés depuis 2002-2003. A présent, les premières synthèses montrent que cette région présente une richesse importante en espèces micro-endémiques. Parmi les nouvelles espèces décrites de la région de Loky-Manambato la plus remarquable est *Heteroscorpion magnus* Lourenço & Goodman, 2002. Cette espèce de près de 20 cm de long est le plus grand scorpion jamais trouvé à Madagascar, et un des plus grands trouvé dans le monde depuis un demi-siècle.

Six taxons distincts ont été décris depuis 2002 pour cette région malgache et appartiennent à quatre familles, cinq genres et six espèces. Bien que préliminaires, ces résultats attestent que la région de Loky-Manambato présente un des taux les plus élevés de diversité et d'endémisme à Madagascar, en ce qui concerne la faune des scorpions. Dans la présente synopse, des clés d'identification sont également proposée pour les six espèces.

Mots-clés: Scorpiones, diversité, endémisme, Madagascar, Loky-Manambato.

Introduction

Madagascar is one of the most biologically diverse regions on Earth for scorpions (Lourenço, 2003a,b, 2005) and certain areas of the island exhibit especially high diversity and microendemism. The southwestern and northern portions have been shown to be exceptionally species rich and in particular, the northern region has been considered a possible epicenter of scorpion diversity (Lourenço, 2003a, b, 2005).

Studies on Malagasy scorpions started in first half of the 19th-century, and knew a certain apogee between 1890 and 1900, when several taxa new to science were described. Since

1994, an important number of new taxa have been discovered and named for the Malagasy scorpion fauna. These different studies lead to a remarkable increase in taxonomic, biogeographic, and faunistic information on these animals. Continuing field inventories on Madagascar, which have included the collection of hundreds of scorpion specimens since the publication of a monograph providing a synopsis of the island's fauna (Lourenço, 1996), lead to considerable progress, and measures of species richness have increased by almost 500% since 1994. The region of Loky-Manambato is a perfect example of this growth in knowledge on regional scorpion faunas of Madagascar, as only a few years ago not a single specimen had been collected in this area, and now the fauna is known to be rich in microendemic species. The first papers on the scorpions of this zone were published by Lourenço & Goodman (2002) and Lourenço *et al.* (2003). Amongst the new species found in the Loky-Manambato region, the most remarkable is *Heteroscorpion magnus* Lourenço & Goodman, 2002, the largest species known from the island, or for that matter described in the world for over one-half century.

Methods

Scorpion specimens were collected during biological inventories conducted in the Loky-Manambato region by several different research teams. Considerable collections were made, which were sent to the first author for taxonomic identification. Three principal techniques were used: (i) leaf litter sampling and associated Winkler extractions, (ii) 15 l pitfall traps, and (iii) random searching under rocks, in dead wood, and in crevices along cliff faces and areas of exposed rock. All sampling was conducted in natural forest habitats and no information is available on the scorpion fauna occurring in the local anthropogenic pseudo-steppe areas.

For the different scorpion species known from the Loky-Manambato region, only summary diagnoses are proposed in this chapter. The full species descriptions, illustrations, and morphometric values are presented in the various cited papers describing these taxa. For definitions of different morphological characters, the reader is referred to Hjelle (1990); cheliceral dentition and trichobothrial patterns are defined after Vachon (1963, 1974, 1975). Illustrations presented herein are limited to the characters necessary for the identification of the different species. Some details are also presented on the ecology of the different scorpions of the region, including habitat notes associated with specimens.

At all of the different localities within the Loky-Manambato region inventoried for small mammals, reptiles, and amphibians, soil collections were made near the first bucket of the three different pit-fall lines installed at each site. Analyses of these samples for soil characteristics and carbon/nitrogen ratios (C/N) were conducted in the 'laboratoire de l'Ecole Supérieure des Sciences Agronomiques de l'Université d'Antananarivo'. See Rakotondravony (2006) for specific details on techniques and the results of these tests.

Scorpions known from the Loky-Manambato region

Family Buthidae C. L. Koch, 1837

Genus Grosphus Simon, 1880

Grosphus darainensis Lourenço, Goodman & Ramilijaona, 2004 (Fig. 1-5)

This species is only known from the male holotype, which was collected in the Province d'Antsiranana, Forêt de Bobankora, east side, 12 km E SE of Daraina, 13°12.7'S, 49°46.3'E, 100-350 m, X/2002-III/2003 (M. Raheriarisena & H. A. Rakotondravony).

DIAGNOSIS. Species related to the *Grosphus madagascariensis/G. hirtus* group. Medium size with a total length of 50

mm. Coloration yellowish to reddish yellow with some discrete dark zones on the body. Carapace yellowish with an inverted slightly dark triangular zone between median and lateral eyes. Chelicerae yellowish with dark variegated pigmentation. Carapace moderately granular; anterior margin almost straight, with a weak median concavity. Pectines: pectinal teeth count 18-17. Metasomal segments with 10-10-8-8-5 carinae. Segment I as long as wide. Dorsal carinae on segments II to IV with one small posterior spinoid granule. Telson with subaculear tooth absent. Cheliceral dentition with two distinct basal teeth present on the movable finger. Pedipalp-chela fingers with 12-13 oblique rows of granules. Trichobothriotaxy; orthobothriotaxy A- α (alpha).

GEOGRAPHICAL DISTRIBUTION. This species is only known from the 'Forêt de Bobankora', an isolated forest block in the south central portion of this region and just to the north of the Manambato River. It was collected within an elevational range between 100 and 350 m.

ECOLOGY. The specimen of *Grosphus darainensis* was found in a portion of the Loky-Manambato region with exceptional ecological heterogeneity associated with different parameters - elevation, aspect, soil type, and distance to the sea. Within this zone, in a distance of less than a few kilometers, there are pronounced shifts between forest formations typical of western dry deciduous forests and eastern humid forests. The remaining forests of Bobankora are extensively reduced in size and fragmented. The specific site where the holotype of *G. darainensis* was collected is composed of lowland dry deciduous forest that is relatively intact. The soils of the portion of the Bobankora Forest are dominated by calcareous elements, with a C/N ratio that indicates poorly decomposed organic material (Table I).

Grosphus goudoti Lourenço & Goodman, 2006 (Fig. 6-12) This species is known from the male holotype, which was collected in the Province d'Antsiranana, Forêt de Bobankora, Site 2, 11 km E of Daraina, 13°13.414'S, 49°45.586'E, 350-550 m, X/2002-III/2003 (M. Raheriarisena & H. A. Rakotondravony) and some supplementary material recently collected in Province d'Antsiranana, Ampondrobe, 41.1 km 175° Vohemar, 13°4292'S, 50°0610'E, 10 m, 29/XI - 1/XII/2004, littoral rainforest (B. L. Fisher)-11097: 17 males, 7 females (California Academy of Sciences, San Francisco).

DIAGNOSIS. Species related to the Grosphus madagascariensis/G. hirtus group. Medium to large size with a total length of 55 to 65 mm. General coloration reddish-brown to dark brown; carapace with one inverted black triangle stretching from the lateral eyes to the median eyes. Coloration reddishbrown to dark-brown. Chelicerae reddish-yellow with dark variegated pigmentation over the entire surface. Carapace covered with a thin but intense granulation; anterior margin almost straight. Pectines with 19 to 22 teeth in males, 17 to 19 in females; basal middle lamellae of female pectines dilated and with an semi-oval shape. Metasomal segments with 10-10-8-8-5 carinae. Segments I to V longer than wide. Dorsal carinae on segments II to IV without any posterior spinoid granules. Telson with a vestigial subaculear tooth. Cheliceral dentition with two distinct basal teeth present on the movable finger. Pedipalp-chela fingers with 11 to 12 oblique rows of granules. Trichobothriotaxy; orthobothriotaxy A- α (alpha). GEOGRAPHICAL DISTRIBUTION. Originally only known from the type locality: Province d'Antsiranana, Forêt de Boban-

Sites (n=number of specimens)	Sand %	Clay %	Lime %	C %	N %	C/N ^a	Species scorpions
Binara (n=4) 215-610 m	59.5	12.1	20.4	2.58	0.17	16.11	Titybuthus darainensis Microcharmus variegatus Heteroscorpion magnus
Binara (n=8) 720-950 m	57.8	10.0	25.5	2.39	0.17	14.92	Titybuthus darainensis Microcharmus variegatus
Bekaraoka (n=2) 140-150 m	18.7	12.4	67.2	3.31	0.25	13.41	Microcharmus variegatus Opisthacanthus darainensis
Ambilondambo (n=3) 400-540 m	63.4	6.9	22.8	3.18	0.20	16.39	Heteroscorpion magnus
Tsarahitsaka (n=3) 360-380 m	60.5	6.4	29.5	1.91	0.12	17.16	Heteroscorpion magnus
Bobankora (n=5) 130-210 m	29.8	15.5	51.5	1.93	0.12	17.22	Grosphus darainensis
Bobankora (n=3) 380-520 m	47.5	7.8	41.4	2.22	0.12	18.76	Grosphus goudoti
Antsahabe (n=6) 480-600 m	59.1	5.7	29.3	2.44	0.12	20.05	Microcharmus variegatus
Ampondrabe (n=2) 80-260 m	45.6	9.2	42.6	2.43	0.16	21.07	Microcharmus variegatus Opisthacanthus darainensis
Sahaka (n=3) 30-30 m	81.6	3.8	11.3	0.34	0.05	7.30	Microcharmus variegatus

Table I. Physical characteristics and aspects of carbon and nitrogen contents of soils coming from the Loky-Manambato region in zones scorpions were obtained.

^a We have adapted the system of C/N ratios of less than 8 as representative of soils with very low organic material reserves, those between 11 and 16 as having already decomposed organic material, and those greater than 16 as having non-decomposed organic material.

kora, Site 2, 11 km E of Daraina, 13°13.414'S, 49°45.586'E and now known from the littoral forest of Ampondrobe.

ECOLOGY. The type specimen was obtained in the Bobankora Forest to the east of Daraina (village). The lower portion of this massif, until 350 m, has dry deciduous forest, and the middle to upper section, 350 to 607 m, has a mixed deciduous and humid forest. The type series was obtained in the transitional forest between 350 and 550 m. The soils of this portion of the massif are composed of nearly equal portions of sand and lime, and with a C/N ratio that indicates poorly decomposed organic material (Table I). Interestingly, *G. darainensis* is known from this same massif, but in the zone from 100-350 m. *Grosphus goudoti* was obtained from a site with a notably different biotope. Here the forest rests on sand and is virtually at sea level. The sites of Bobankora and Ampondrobe are approximately 25 km from one another (Lourenço & Goodman, 2006a).

Genus Tityobuthus Pocock, 1893

Tityobuthus darainensis Lourenço & Goodman, 2002 (Fig. 13-20)

Tityobuthus darainensis was named based on a female specimen collected in the Province d'Antsiranana, Forêt de Binara, near the Analamazava River, 7.5 km southwest of Daraina, 13°15.3'S, 40°37.0'E, 325-600 m (S. M. Goodman) in a forest type dominated by eastern humid lowland elements and with some plants of dry deciduous forest. Subsequently, a male specimen was described (Lourenço, 2006), collected in the Forêt de Binara, Site d'Andohan'Analamazava, 3.8 km of Ankijabe, 13°15'40"S, 49°36'06"E. 850 m, X/2003 (M. Raheriarisena & H. A. Rakotondravony). This later locality is within a short distance of the original collection site.

DIAGNOSIS. Species of large size (with respect to the genus) with a total length of 27 mm for the male and 35 for the female. Coloration yellowish symmetrically marbled with dark reddish brown, giving an overall spotted appearance. Mesosoma yellowish, with four longitudinal brown stripes. Chelicerae yellowish, with dark spots on the anterior margin at the base of fingers. Carapace moderately to weakly granular; anterior margin with a moderately pronounced median concavity, forming a weak angle. Pectines: pectinal tooth count 17-18 in female, 16-16 in male; basal middle lamellae not dilated; fulcra present. Sternite V without any smooth or bright zone on posterior edge. Metasomal segments with 10-10-10-8-5 carinae. Telson smooth with a subaculear tooth strong and spinoid. Cheliceral dentition with basal teeth of movable fingers reduced and of same size. Pedipalp-patella with seven spinoid granules on internal face. Pedipalp-chela fingers with 8-9 oblique rows of granules. Trichobothriotaxy; orthobothriotaxy A- α (alpha).

GEOGRAPHICAL DISTRIBUTION. This species is only known from forested zones on the northern slopes of the Binara Massif, spanning the elevational range from 325-850 m.

ECOLOGY. The two sites this taxon is known from are on the slopes of the Binara Massif. The first site, near the Analamazava River (325-600 m), is an ecotonal zone between humid and dry deciduous formations, and the second site, Andohan'Analamazava (850 m), is at the headwaters of the Analamazava River and with distinctly more humid forest. Hence, this species has an elevational distribution that spans different vegetational communities. In both the zones on the massif where T. darainensis has been found, from 230-610 m and 720-950 m, there is little elevational variation in soil qualities, and they are predominantly sandy, with a moderate percentage of calcareous elements, and relatively little lateritic content. In both these zones, there is some soil litter and the soils have decomposed organic material (Table I). From a biogeographic perspective, the Binara Massif is in direct contact with the Sorata Ridge from the Tsaratanana complex, composed of the tallest mountain on the island, and this ridge may have been an important colonization source for the humid forest biota of this portion of the Loky-Manambato region.

Family Microcharmidae Lourenço, 1996

Genus Microcharmus Lourenço, 1995

Microcharmus variegatus Lourenço, Goodman & Fisher, 2006 (Fig. 21-23)

Although most species of Microcharmus can be considered as rare or at least difficult to collect (Lourenço et al., 2006), M. variegatus was described on the basis of a substantial number of specimens from the Loky-Manambato region, rendering this species, the most common in the genus with regards to available material. Known localities for M. variegatus include: Province d'Antsiranana, Forêt d'Analabe (Sahaka), 30 km 72° ENE Daraina, 30 m, 13°05'00"S, 49°54'5"E, littoral forest, sifted litter, leaf mold, rotten wood, 27-29/XI/2003 (B. L. Fisher *et al.*), one female holotype and various paratypes. Forêt d'Ampondrabe, 26.3 km 10° NNE Daraina, 175 m, 12°58'12"S, 49°42'00" E, tropical dry forest, sifted litter, leaf mold, rotten wood, 10/XII/2003 (B. L. Fisher et al.), one female paratype. Forêt de Bekaraoka, 6.8 km 60° ENE Daraina, 150 m, 13°10'00"S, 49°42'36"E, tropical dry forest, sifted litter, leaf mold rotten wood, 7/XII/2003 (B. L. Fisher et al.), one male, one female, three juvenile paratypes. Forêt de Binara, 7.5 km 230° SW Daraina, 375 m, 13°15'18"S, 49°37'00"E, semi-deciduous tropical forest, pitfall trap, 1/XII/2003 (B. L. Fisher et al.), two male paratypes. Forêt de Binara, 7.5 km 230° SW Daraina, 375 m, 13°15'18"S, 49°37'00"E, semi-deciduous tropical forest, sifted litter, leaf mold, rotten wood, 1/XII/2003 (B. L. Fisher et al.), one female paratype. Forêt de Binara, 9.4 km 235° SW Daraina, 1100 m, 13°15'48"S, 49°36'00"E, montane rainforest, sifted litter mold, rotten wood, 5/XII/2003 (B. L. Fisher), one male paratype. Forêt d'Antsahabe, 11.4 km 275° W, Daraina, 550 m, 13°13'7"S, 49°33'4"E, tropical dry forest, sifted litter, leaf mold, rotten wood, 12-14/XII/2003 (B. L. Fisher et al.), 1 male paratype.

DIAGNOSIS. Scorpions of average size when compared with most species of the genus Microcharmus, up to 12.9 mm total length in males and 17.8 mm in females. Coloration, yellowish to reddish-yellow with dark variegated spots over the body and appendages. Pedipalp femur and patella intensely marked with dark spots, except on the zones where trichobothria are inserted. Chelicerae yellowish with variegated spots on the lateral margins and base of the fingers. Carapace with moderate granulation; anterior margin with a weak concavity, almost straight. Sternum pentagonal. Pectinal tooth count 12-12 for males and 11-11 for females; basal middle lamellae of the pectines not dilated; fulcra absent. Sternites with semi-oval spiracles. Metasomal segments with 10-10-10-8-5 carinae. Telson with a very elongated pear-shaped structure, smooth with strong setation; aculeus short and weakly curved; subaculear tooth absent. Cheliceral dentition of fixed finger with two strong basal teeth; movable finger with two very weak but fused basal teeth. Pedipalp-patella with four to five spinoid granules; pedipalp-chela fingers with 6-7 linear rows of granules; extremity of fingers with one long and sharp denticle. Trichobothriotaxy; orthobothriotaxy A- α (alpha). GEOGRAPHIC DISTRIBUTION. This species has been recorded in the littoral forests of Analabe (Sahaka) at 30 m; in the dry

deciduous formations of the Forêt d'Ampondrabe and Forêt de Bekaraoka at elevations between 150-175 m, and in more slightly upland formation of Forêt d'Antsahabe at 550 m; and along the gradient in the Forêt de Binara from transitional semi-deciduous/humid formations at around 375 m to distinctly more montane conditions at 1100 m.

ECOLOGY. *Microcharmus variegatus* is only known from forested zones in the Loky-Manambato region. This includes several different localities and natural habitats in the zone, ranging from littoral forest at Sahaka near sea level, to lowland dry forest at Ampondrabe at 175 m, to the montane forest of Binara at 1100 m. Ecologically these different habitats are within relatively short distances from one another but have very different bioclimatic aspects associated with distance from the sea, topography, orography, and geology (See Lourenço *et al.* [2006] for further discussion about these points). The majority of specimens came from leaf litter samples, and not a single one was obtained from the vertebrate pitfall buckets. This presumably indicates that this taxon rarely ventures on the soil surface and is truly humicolous.

Associated with the broad ecological distribution of this species in the Loky-Manambato region, there is also no clear preference for specific soil types. Three different contrasting examples are presented here (Table I): in the Sahaka Forest it is found in zones with soils predominantly of a sandy nature and with very low reserves of organic material; in the Bekaraoka Forest at sites mostly with calcareous soils and already decomposed organic material; and in the Binara and Antsahabe Forests in largely sandy soils, but with a significant proportion of calcareous content, and with relatively well decomposed to poorly decomposed organic material.

Family Heteroscorpionidae Kraepelin, 1905

Genus Heteroscorpion Birula, 1903

Heteroscorpion magnus Lourenço & Goodman, 2002 (Fig. 24-25, 32-35)

Despite its very large size, with males reaching 185 mm in length, Heteroscorpion magnus had not been collected before recent inventory work in the Loky-Manambato region. Several specimens were obtained and the diagnoses of this species were based on a series of males and females (Lourenço & Goodman, 2002; Lourenço et al., 2003). Known specimens were obtained at: Province d'Antsiranana, Forêt de Binara, near Analamazava River, 7.5 km southwest of Daraina, 13°15.3'S, 40°37.0'E, 325-600 m (S. M. Goodman). The female holotype, three females, and two male-juveniles (all paratypes), were collected in eastern humid lowland forest, disturbed by cattle, with some elements of dry forest; these were found during the day under rocks. One female and two males (also paratypes) were collected in undisturbed eastern humid lowland forest with some elements of dry forest; these were found during the day under rocks along a riverbed. Forêt de Binara, Site Beamosy, à 2.5 km NNW du village d'Ankijabe, 13°14.3'S, 49°37.5'E, 215 m (MR 0154). One juvenile female. Forêt d'Ambilondambo, Site d'Andrafia, à 5 km N de Daraina, 13°09.853'S, 49°38.871'E, 300-550 m (MR 0343, 0346, 0347). Two juvenile males and one juvenile female. Forêt de Tsarahitsaka, à 7,7 km NW de Daraina, 13°08.929'S, 49°37.402'E, 250-450 m (MR 0367, 0368). Two males.

DIAGNOSIS. Scorpions of large size, with adult females reaching 145 mm and males 185 mm. Sexual dimorphism strongly marked, mainly by the allometric growth shown in males. Coloration reddish-brown. Carapace with some blackish nearby the eyes. Chelicerae reddish with some variegated dark spots that are masked by the dark coloration. Legs reddish-brown, with tarsi yellowish. Morphology. Anterior margin of carapace with a strongly pronounced concavity; two pairs of lateral eyes. Sternum pentagonal, higher than wider. Pectines: pectinal tooth count 8 to 14 in females and 11 to 15 in males; fulcra fused with median lamellae. Metasoma with all segments strongly flattened laterally. Carinae smooth on segment I, granular on segments II-V; granulation becomes spiniform on segments III-V; dorsal and ventral surfaces of segment V with a strong spinoid granulation. Telson weakly elongated with strongly marked spinoid granules; aculeus very short and strongly curved. Cheliceral dentition with two subdistal teeth and a basal tooth on movable finger. Pedipalppatella with a very strong apophysis on the internal aspect. Dentate margin on fingers with numerous granules randomly arranged on their basal 2/3, and forming two vestigial parallel series of granules on its distal portion. Movable fingers with a strong proximal apophysis. Trichobothriotaxy of type C; neobothiotaxic + (plethotaxic); patella with 14-19 ventral and 31-41 external trichobothria; chela with 12-15 ventral trichobothria. Hemispermatophore as in Figure 34.

GEOGRAPHICAL DISTRIBUTION. This species is known from three different sites in the Loky-Manambato region within the central and southern portion of the zone (Forêt de Binara, Forêt d'Ambilondambo, and Forêt de Tsarahitsaka) and across an elevational range of 215-600 m.

ECOLOGY. About two-thirds of the known specimens of Heteroscorpion magnus where obtained in the lower elevations and more deciduous portion of the Binara Forest, between 215 and 600 m. The vast majority of these animals where found in the narrow fissures between layers of splintered exposed standing rock, making it a lithophilic species (sensu Prendini, 2001). In many cases a thin layer of soil and other organic material had been deposited in these crevices, and virtually all, excluding two individuals, were solitary. With regards to habitat specifications, animals were found in relatively intact forest settings and in secondary forests that had been disturbed by tree extraction and cattle browsing. The other two sites this taxon is known from include Forêt d'Ambilondambo, between 300-550 m, which is composed of dry deciduous forest with some humid forest elements, and the Forêt de Tsarahitsaka, between 250-450 m, dominated by dense dry forest. In all of the sites this species occurs, the soils are composed of slightly more than one-half of sand, one-third to one-quarter lime, and with low clay content (Table I). Further, the C/N ratio of these soils is greater than 16, indicating poorly decomposed organic material.

Family Liochelidae Fet & Bechly 2001

Genus Opisthacanthus Peters, 1861

Subgenus Monodopisthacanthus Lourenço, 2001

Opisthacanthus darainensis Lourenço & Goodman, 2006 (Fig. 26-29, 36-44)

Opisthacanthus darainensis was described on the basis of a long series of specimens from the following localities: Antsiranana Province, Forêt de Bekaraoka, 6.8 km 60° ENE Daraina, 13°11'00"S, 49°42'36"E, 150 m, 7/XII/2003 (B. L. Fisher), general collecting, tropical dry forest. One male holotype, 18 males paratypes, 21 females paratypes; Antsiranana Province, Forêt d'Ampondrabe, 26.3 km 10° NNE Daraina, 12°58'12"S, 49°42'00"E, 175 m, 10/XII/2003 (B. L.

Fisher), tropical dry forest. Twenty males, 12 females paratypes; Antsiranana Province, Réserve Spéciale d'Analamerana, 28.4 km 99° Anivorano-Nord, 12°44.80'S, 49° 29.69'E, 60 m, 5-7/XII/2004 (B. L. Fisher), tropical dry forest. Twelve males, 10 females paratypes; Antsiranana Province, Réserve Spéciale d'Analamerana, 16.7 km 123° Anivorano-Nord, 12°48.3'S, 49°22.4'E, 225 m, 2-5/XII/2004 (B. L. Fisher), tropical dry forest. Ten males, 18 females paratypes.

DIAGNOSIS. Medium to small size scorpions: average total length in males is 39 mm and females 43 mm. Coloration reddish-brown to dark brown, with some blackish zones on the pedipalp carinae. Carapace reddish-brown with a paler zone on the posterior edge. Chelicerae reddish-brown; the whole surface with diffuse variegated dark spots. Carapace smooth with intense punctuation. Anterior margin with a strong concavity reaching as far as the level of the 2nd lateral eye; three pairs of large lateral eyes. Sternum pentagonal, wider than long. Genital operculum formed by two semi-oval plates in males, and one single large, almost oval-like shaped plate in females. Pectinal tooth count 5-7 teeth in males and females; mode 6 in males and females. Carinae weakly marked in metasomal segments I-IV; segment V slightly rounded with spinoids granules. Telson with a pear-like shape; smooth and covered with strong chetotaxy. Dentate margin of pedipalp-chela fingers forming two parallel series of granules. Chelicerae with teeth sharp. Trichobothriotaxy type C; orthobothriotaxic. Hemispermatophore as in Figure 44 with the distal lamina short and weakly enlarged.

GEOGRAPHICAL DISTRIBUTION. This species has been collected at two different sites within the Loky-Manamabato region, including Ampondrabe in the north and Bekaraoka in the central area, and across a narrow elevational range from 150-175 m. Further, it is known from the Réserve Spéciale d'Analamerana, a limestone area some 25 km to the north of the northern limit of the Loky-Manambato Region; the sedimentary zone of the Andrafiamena Mountains separates the Loky-Manambato and Analamerana regions (Lourenço & Goodman, 2006b).

ECOLOGY. *Opisthacanthus darainensis* has a restricted range in the Loky-Manambato region, where it is only known from dry deciduous formations including the Forêt de Bekaraoka and the Forêt d'Ampondrabe between 150 and 175 m. These two sites have soils with a considerable amount of calcareous material, which is the dominant component at Bekaraoka and with nearly equal portions of sand at Ampondrabe (Table I). The C/N ratio of the soils at Bekaraoka indicates already decomposed organic material and that of Ampondrabe as very poorly decomposed organic material.

Key to the scorpion species found in the Loky-Manambato Region

- 4. Pectinal tooth count 16-18; subaculear tooth strong (fig. 19, 20)......*Tityobuthus darainensis*

- Three lateral eyes; 3 ventral trichobothria on patella; pectinal tooth count 5-7 (fig. 31, 38)
 Opisthacanthus darainensis

Discussion

As mentioned in the introduction, considerable progress has been made in the past 17 years in documenting patterns of scorpion species diversity on Madagascar. On the basis of current information, several sites across the island in different biotopes are sufficiently well documented for the local scorpion fauna to start to make comparisons between levels of species richness and endemism. To date, the scorpion fauna of Madagascar is composed of four families, 11 genera and 81 species. On the basis of these comparisons several aspects can be noted.

The scorpion fauna of the Loky-Manambato region holds all four of the scorpion families known from Madagascar; the only other listed site with this level of family diversity is Montagne des Français. Among other well studied northern sites, the Loky-Manambato zone has a slightly lower measure of species richness than Ankarana and Montagne des Français. The Loky-Manambato fauna has the highest level of microendemism, just after Ankarana.

Now examining these comparisons in a broader geographical sense, species richness tends to be the highest in dry deciduous forests and spiny bush habitat, as compared to humid forest formations. Having in account that, the habitat diversity and surface area of the zone generally define as the southwestern region is notably greater than the other sites it is compared to, rendering the measures slightly asymmetric. The zone with the lowest level of microendemism is the spiny bush parcel of the PN d'Andohahela, which has four species, of which only one is a local endemic (Tityobuthus betschi). The other three taxa include Grosphus grandidieri, Opisthacanthus lucienneae, and Pseudouroplectes pidgeoni, which are known from other areas in southern and southwestern Madagascar. In a similar manner, the fauna from the southwestern region shows not pronounced level of microendemism, as compared to most of the other sites, and our impression is that there is a greater level of exchange and dispersal in this zone than in dry forest zones in the north. This is particularly true for Ankarana, an isolated limestone massif that has a scorpion fauna that is 100% endemic.

The distributions of scorpions across portions of the world are correlated with numerous ecological factors, including climate (relative humidity and temperature), substratum (hardness and composition), and predator prey relations (Warburg & Ben-Horin, 1978; Bradley & Brody, 1984; Bradley, 1986; Prendini, 2005). It has been suggested that 'the nature of the substratum' is probably the most important single factor that has and still determines the distribution of scorpions, which in turn is affected to a greater or lesser extent by vegetation, which is partly the result of prevailing climatic conditions (Lamoral, 1978, p. 305 in Prendini, 2005). On the basis of soil samples collected in the different surveyed sites within the Loky-Manambato region, we are able to address aspects of these possible correlated factors for the first time concerning the Malagasy scorpion fauna.

Comparisons of the physical aspects of soil composition, as well as carbon and nitrogen content, with regards to the distribution of different scorpion taxa demonstrate various patterns. The only site that had more than two local species of scorpion was the Binara Massif, with sampling in two zones spanning the elevational gamut from 230 to 950 m. Three species were collected in the first zone (*Titybuthus darainensis, Microcharmus variegatus,* and *Heteroscorpion magnus*), from 230 to 610 m, and in the second zone a single taxon (*T. darainensis*), from 720-950 m. The characteristics of the soils along this slope are notably homogenous with regards to composition (majority sand), organic material, and state of decomposition (Table I). Hence, the component that is variable within this system with regards to these factors is perhaps temperature associated with elevation.

Certain local endemic taxa occur at sites with very different soil types. Perhaps most notable in this regard is Microcharmus variegatus, a Microcharmidae, that tends to live in the upper level of the soil and associated litter (Lourenço et al., 2006). Hence, it is not surprising that virtually all of the specimens where obtained from leaf litter samples. This species was collected at five of the eight sites that showed considerable differences in soil types, from having a preponderance of calcareous soils (Bekaraoka), more than 50% of the soil composition of sand (Binara, Antsahabe, and Sahaka), to nearly equal percentages of these two elements (Ampondrabe). Further there was considerable variation in the organic content of the soil litter from being extremely low (Sahaka), to being well decomposed (Binara, Bekaraoka), to be poorly decomposed (Antsahabe, Ampondrabe). Hence, with regards to these different parameters of substratum type, this species seems to not be too specific. Heteroscorpion *magnus* also has considerable tolerance to sites with notably different soil composition and levels of organic material. In contrast to these two examples, Grosphus darainensis was recorded at a single site (Bobankora) where the substratum has a preponderance of calcareous elements and nondecomposed organic material.

The synopsis presented here attests to the importance of the Loky-Manambato region with regards to its notable species diversity and, more importantly, levels of microendemism. Six scorpion species have been reported and described from Loky-Manambato, and all but one are endemic to this specific zone.

To the north of the Loky-Manambato region are areas with exposed sedimentary rock and distinctly drier climates, although a few of these sites have habitats and biotic elements that are relictual of more mesic conditions in recent geological time. Just to the south of the Loky-Manambato region there is a band of humid forests known as the Northern Highlands that link the east and west coasts of Madagascar and pass across the mountainous regions of Marojejy, Anjanaharibe-Sud, Tsaratanana, and Manongarivo; these different connections serve an important role in the colonization and speciation history of northern Malagasy scorpions. For example, endemic species of Microcharmus species have been recorded on most of these massifs, and other sites to the north with drier habitats (Lourenço et al., 2006). Madagascar experienced notable vegetation shifts during the Quaternary that were associated with changes in climatic patterns (Burney, 1997; Burney et al., 2004); these vegetation changes were especially accentuated in montane regions. Given the geographic proximity of this transitional zone to the Northern Highlands, more southerly lowland humid forests, and northern and western dry deciduous forests, we assume that the forests of the Loky-Manambato Region have served as an important zone of biotic exchange during different periods of climatic vicissitudes. As a result, the zone has a remarkable regional mixture of what are considered eastern and western faunistic and floristic elements, including several endemic scorpion species (Lourenço & Goodman, 2002, 2006; Lourenço et al., 2003, 2004).

Acknowledgments

We are most grateful to Elise-Anne Leguin, Service des Collections, Muséum, Paris for the preparation of several photos used in this chapter.

References

- BRADLEY, R. 1986. The relationship between population density of paruroctonus utahensis (Scorpionida: Vaejovidae) and characteristics of its habitat. J. Arid. Environ., 6: 165-172.
- BRADLEY, R. & A. BRODY 1984. Relative abundance of three vaejovid scorpions across a habitat gradient. J. Arachnol., 11: 437-440.
- BURNEY, D. A. 1997. Theories and facts regarding Holocene environmental change before and after human colonization. In: Goodman, S. M. & B. D. Patterson (eds.), *Natural change and human impact in Madagascar*: 75-89. Smithsonian Institution Press, Washington, D. C.
- BURNEY, D. A., L. P. BURNEY, L. R. GODFREY, W. L. JUNGERS, S. M. GOODMAN, H. T. WRIGHT & A. J. T. JULL. 2004. A chronology for late Prehistoric Madagascar. J. Human Evol., 47: 25-63.
- HJELLE, J. T. 1990. Anatomy and morphology. Pp. 9-33, In: Polis, G. A. (ed.). *The biology of scorpions*. Stanford University Press, Stanford.
- LOURENÇO, W. R. 1996. *Scorpions*. In: *Faune de Madagascar*. Muséum national d'Histoire naturelle, Paris, 87.
- LOURENÇO, W. R. 2003a. The remarquable levels of diversity and endemicity in the scorpion fauna of Madagascar. Pp. 385-391, In: Legakis, A., S. Sfenthourakis, R. Polimeni & M. Thessalou-Legaki (eds.), *The new panorama of animal evolution*. Proc. 18th Int. Congr. Zoology, Athens 2000, Pensoft Publishers, Sofia, Moscow.
- LOURENÇO, W. R. 2003b. Scorpions. Pp. 575-579, In: Goodman, S. M. & J. P. Benstead (eds.), *The natural history of Madagascar*. The University of Chicago Press, Chicago.
- LOURENÇO, W. R. 2005. Diversity and endemism in Malagasy scorpions. *Biogeographica*, 80(1-4): 43-64.
- LOURENÇO, W. R. 2006. Scorpions de Loky-Manambato, Analamerana et Andavakoera. In: Goodman, S. M. & L. Wilmé (eds.), Inventaires de la faune et de la flore du nord de Mada-

gascar dans la région Loky-Manambato, Analamerana et Andavakoera. *Recherches pour le développement. Série Sciences Biologiques*, **23**: 57-66.

- LOURENÇO, W. R. & S. M. GOODMAN 2002. Scorpions from the Daraina region of northeastern Madagascar, with special reference to the family Heteroscorpionidae Kraepelin, 1905. *Rev. Ibér. Aracnol.*, **6**: 53-68.
- LOURENÇO, W. R. & S. M. GOODMAN 2006a. Further considerations regarding the status of *Grosphus madagascariensis* (Gervais) and *Grosphus hirtus* Kraepelin, and description of a new species (Scorpiones, Buthidae). *Rev. suisse Zool.*, **113**(2): 247-261.
- LOURENÇO, W. R. & S. M. GOODMAN 2006b. A reappraisal of the geographical distribution of the genus *Opisthacanthus* Peters, 1861 (Scorpiones: Liochelidae) in Madagascar, including the description of four new species. *Boletín de la Sociedad Entomológica Aragonesa*, **38**: 11-23.
- LOURENÇO, W. R., S. M. GOODMAN, M. RAHERIARISENA & O. RAMILIJAONA 2003. Description of the male of *Hetero-scorpion magnus* Lourenço & Goodman, 2002 (Scorpiones, Heteroscorpionidae). *Rev. Ibérica Aracnol.*, 8: 111-115.
- LOURENÇO, W. R., S. M. GOODMAN & O. RAMILIJAONA 2004. Three new species of *Grosphus* Simon from Madagascar (Scorpiones, Buthidae). *Rev. Ibér. Aracnol.*, 9: 225-234.
- LOURENÇO, W. R., S. M. GOODMAN & B. L. FISHER 2006. A reappraisal of the geographical distribution of the endemic family Microcharmidae Lourenço (Scorpiones) in Madagascar and description of eight new species and subspecies. *Proc. Calif. Acad. Sciences*, 4th ser., 57(26): 751-783.
- PRENDINI, L. 2001. Substratum specialization and speciation in southern African scorpions: the Effect Hypothesis revisited. Pp. 113-138, In: Fet, V. & P. A. Selden (eds.), *Scorpions* 2001. In Memoriam Gary A. Polis. British Arachnological Society, Burnham Beeches, UK.
- PRENDINI, L. 2005. Scorpion diversity and distribution in southern Africa: Pattern and process. Pp. 25-68, In: Huber, B. A., B. J. Sinclair & K.-H. Lampe (eds.), *African Biodiversity: Molecules, organisms, ecosystems*. Springer Verlag, New York.
- RAKOTONDRAVONY, H. R. 2006. Quelques caractéristiques physicochimiques des sols de la région Loky-Manambato, de la Réserve Spéciale d'Analamerana et de la Forêt Classée d'Andavakoera. In: Goodman, S. M. & L. Wilmé (eds.), Inventaires de la faune et de la flore du nord de Madagascar dans la région Loky-Manambato, Analamerana et Andavakoera. Recherches pour le développement, Série Sciences Biologiques, 23: 37-55.
- VACHON, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les Scorpions. *Bull. Mus. Nat. Hist. nat.*, Paris, 2è série, 35:161-166.
- 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. *Bull. Mus. Nat. Hist. Nat.*, Paris, 3è série, n° 140, Zool. 104: 857-958.
- VACHON, M. 1975. Sur l'utilisation de la trichobothriotaxie du bras des pédipalpes des Scorpions (Arachnides) dans le classement des genres de la famille des Buthidae Simon. C. R. Acad. Sciences, Paris, série D, 281: 1597-1599.
- WARBURG, M. R. & A. BEN-HORIN 1978. Temperature and humidity effects on scorpion distribution in northern Israel. *Symp. Zool. Soc. London*, 42: 161-169.



▲ Fig. 1-2. Grosphus darainensis, male holotype. Dorsal and ventral aspects. Fig. 13-14. Tityobuthus darainensis, male. Dorsal and ventral aspects.

▶ Fig. 3-5. *Grosphus darainensis*, male holotype 3. Disposition of granulations on the dentate margins of the pedipalp-chela movable finger. 4. Metasomal segments IV-V and telson, lateral aspect. 5. Chelicera, dorsal aspect. Fig. 6-12. *Grosphus goudoti*, male holotype. 6. Metasomal segments III-V and telson, lateral aspect. 7. Chelicera, dorsal aspect. 8-12. Trichobothrial pattern. 8. Femur, dorsal aspect. 9-10. Chela, dorso-external and ventral aspects. 11-12. Patella, dorsal and external aspects.





▲ Fig. 15-20. *Tityobuthus darainensis*, male. 15. Disposition of granulations on the dentate margins of the pedipalp-chela movable finger. 16. Patella, dorsal aspect. 17. Femur, dorsal aspect. 18. Chelicera, dorsal aspect. 19-20. Metasomal segment V and telson, lateral aspect (male and female). Fig. 21-23. *Microcharmus variegatus*, female. 21. Disposition of granulations on the dentate margins of the pedipalp-chela movable finger. 22. Sternum, genital operculum and pectines. 23. Metasomal segment V and telson, lateral aspect.

▶ Fig. 24-25. *Heteroscorpion magnus*, male. Dorsal and ventral aspects.

▶ Fig. 26-29. Opisthacanthus darainensis, dorsal and ventral aspects. 26-27. Male. 28-29. Female.















Fig. 30-31. Lateral eyes. 30. Two pairs, *Heteroscorpion*. 31. Three pairs, *Opisthacanthus*. Fig. 32-35. *Heteroscorpion magnus*, male. 32-33. Patella, dorsal and ventral aspects, showing trichobothria. 34. Hemispermatophore, external aspect. 35. Chelicera, dorsal aspect. Fig. 36-44. *Opisthacanthus darainensis*, male holotype and female paratype. 36. Chelicera, dorsal aspect (male). 37-38. Patella, dorsal and ventral aspects, showing trichobothria (male). 39-40. Metasomal segment V and telson, lateral aspect (male & female). 41-42. Sternum and genital operculum (male & female). 43. Disposition of granulations on the dentate margins of the pedipalp-chela movable finger (male). 44. Hemispermatophore, external aspect.