C. R. Biologies xxx (2015) xxx–xxx

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Biodiversity/Biodiversité

More about the geographical pattern of distribution of the genus *Pseudouroplectes* Lourenço, 1995 (Scorpiones: Buthidae) from Madagascar

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ARTICLE INFO

Article history:
Received 13 October 2015
Accepted after revision 9 November 2015
Available online xxx

Keywords:
Scorpion
Pseudouroplectes
Madagascar
Bemaraha
Tsingy
New species
Neogrosphus rule
Biogeography

Mots clés :
Scorpion
Pseudouroplectes
Madagascar
Bemaraha
Tsingy
Nouvelle espèce
Règle *Neogrosphus*
Biogéographie

ABSTRACT

The genus *Pseudouroplectes* Lourenço, 1995 (Buthidae) remains among the less speciose Malagasy genera and all the known species are extremely rare. A new species is described from the dry forests in the Tsingy formations of the National Park Bemaraha, extending the distribution of the genus further north. Once again, the single holotype specimen was obtained by extraction with the use of Berlese system. With the description of the new species, the distributional pattern of this genus is confirmed for dry forest formations from the south to the middle of the island; however, for the first time the group's distribution overlaps that of another micro-scorpion genus, *Microcharmus* Lourenço, 1995. The distribution patterns of the humicolous micro-scorpions endemic to Madagascar are considered to further explore the "*Neogrosphus* rule" as a possible explanation of global species distribution patterns in changing environments.

RÉSUMÉ

Le genre *Pseudouroplectes* Lourenço, 1995 (Buthidae) est, parmi les genres malgaches, l'un des plus pauvres par le nombre d'espèces, et toutes les espèces connues sont extrêmement rares. Une nouvelle espèce est décrite des forêts sèches rencontrées entre les formations de *Tsingy* du Parc national du Bemaraha, étendant ainsi la distribution du groupe vers le nord. L'holotype a une fois de plus été récolté par la méthode Berlese. Avec la description de la nouvelle espèce, la distribution du genre *Pseudouroplectes* remonte jusqu'au centre ouest de l'île, mais surtout, et cela pour la première fois, elle se superpose avec celle de *Microcharmus* Lourenço, 1995, un autre genre de micro-scorpions. Les modèles de distribution des micro-scorpions humicoles endémiques de Madagascar sont considérés afin de mieux définir la « règle *Neogrosphus* » qui explique globalement les modèles de distribution des espèces dans des milieux changeants.

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http://dx.doi.org/10.1016/j.crvi.2015.11.001
1631-0691/

1. Introduction

As outlined in previous publications [1,2], the genus *Pseudouroplectes*, which is composed of soil-dwelling species, is extremely rare. In Madagascar, the other group of micro-scorpions, also composed of soil species, is represented by members of the endemic family Microcharmidae [3]. This group can be suggested to be better represented than *Pseudouroplectes*, and was better studied until now [3]. The first known species, *Pseudouroplectes betschi* Lourenço, 1995, was originally described based on two females collected with the use of extraction systems, in the dry southwestern spiny bush formation at Andramanoetse Be, Plateau Mahafaly [4]. Subsequently, a second species, *Pseudouroplectes pidgeoni* Lourenço & Goodman, 1999 was collected in the extreme southeastern dry forests of the "Parc national d'Andohahela" (parcel 2) [5]. This scorpion was collected in a soil litter sample from the spiny bush parcel of the reserve, within a few kilometers of the ecotone between dry and wet forest formations. Only several years later, additional material was obtained of the genus *Pseudouroplectes*. This led to the description of a third species, *Pseudouroplectes maculatus* Lourenço & Goodman, 2006 [1]. Subsequently, material collected in the dry forests of Ifaty in the Province of Toliara, revealed one more new species, *Pseudouroplectes lalyae* Lourenço & Ythier, 2010 [2] (Fig. 1).

Recent investigation on some non identified material, collected by the late J.-M. Betsch in Madagascar, and now deposited in the Museum in Paris, led to the location of one more specimen of *Pseudouroplectes*. The material was again collected in dry forests in a Tsingy formation of the P. N. Bemaraha. After detailed examination of the specimen we concluded for yet a new species. The number of species in the genus *Pseudouroplectes* is now raised to five.

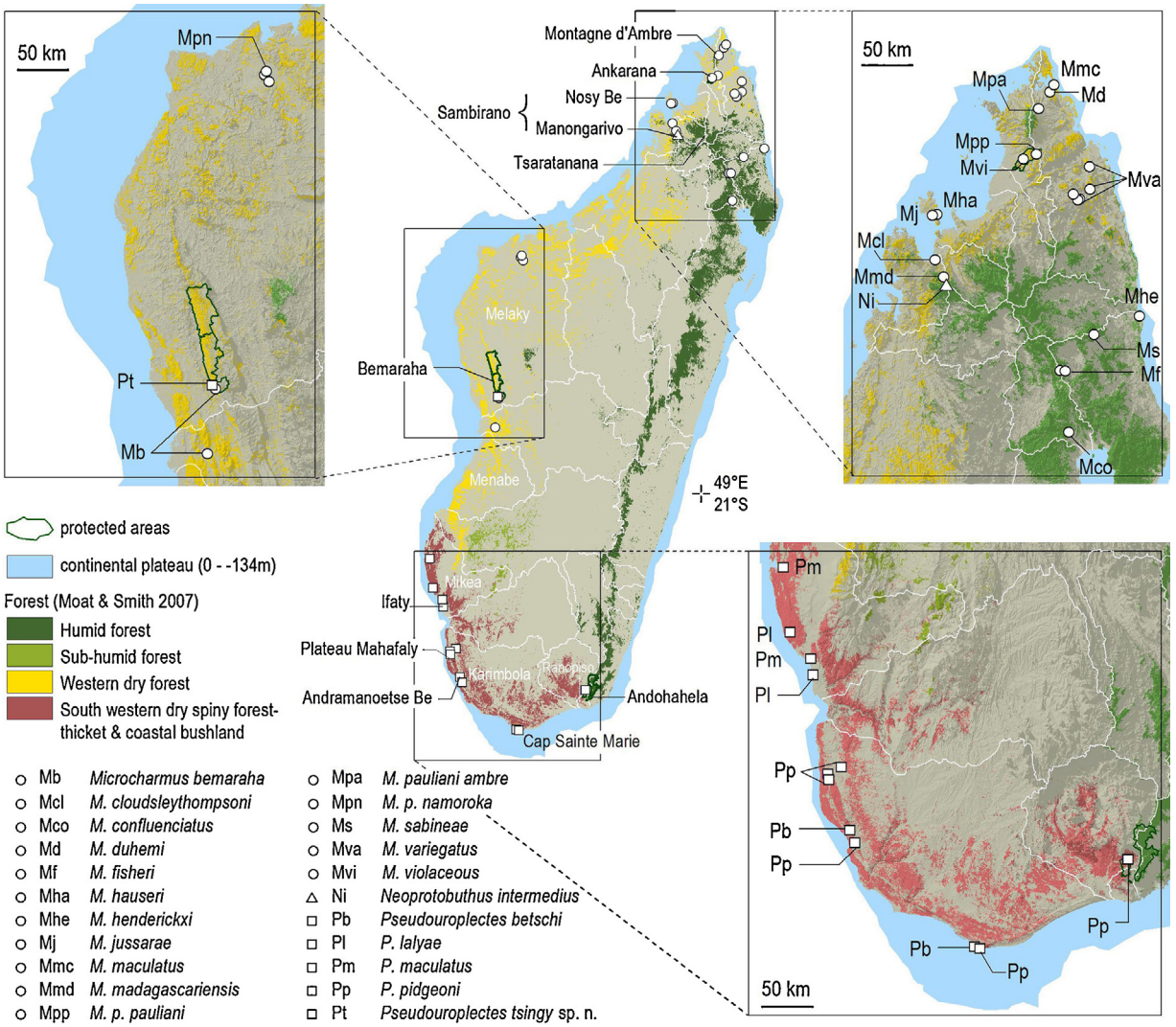

Fig. 1. Collection localities of the humicolous micro-scorpions in the genera *Microcharmus*, *Neoprotobuthus*, and *Pseudouroplectes*, and forest types.

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2. Distributional pattern presented by the genus *Pseudouroplectes*

The distributional pattern of the genus *Pseudouroplectes* was already discussed in detail in the two previous publications dealing with this group [1,2]. In these publications, detailed lists of known localities for members of this genus are proposed. All the species of this genus, with the exception of the new species described here, are restricted to the extreme southern dry forest formations. *Pseudouroplectes betschi* and *P. pidgeoni* apparently present a parapatric or even a small sympatric zone of distribution in the southern portion of the island. A similar situation is observed between *P. maculatus* and *P. lalyae*, with the two species presenting, at least, a small zone of sympatry. This very restrict distribution could eventually be attributed to incomplete sampling collections, but a large portion of the southwestern region of the island was extensively prospected by several teams. Consequently, a more plausible explanation has been explored in the recent past of the genus' evolution in respect to its modern distribution, but also considering the other species of humicolous micro-scorpions of the islands, more specifically the species in the endemic family Microcharmidae. The new species described here extends the distribution area of the genus into western Madagascar, and for the first time the distribution area of the genus *Pseudouroplectes* overlaps that of another micro-scorpion genus, *Microcharmus* Lourenço, 1995.

3. Methods

Illustrations and measurements were made with the aid of a Wild M5 stereo-microscope with a drawing tube (camera lucida) and an ocular micrometer. Measurements follow Stahnke [6] and are given in mm. Trichobothrial notations follow Vachon [7] while morphological terminology mostly follows Hjelle [8].

4. Taxonomic treatment

Family Buthidae C.L. Koch, 1837
Genus ***Pseudouroplectes*** Lourenço, 1995
Pseudouroplectes tsingy sp. n. (Figs. 2–3)

Type-material, female holotype. Madagascar, Melaky Region, ex-Province Mahajanga, P. N. Bemaraha, dry forest in Tsingy, XI/1972 (J.-M. Betsch), extraction by Berlese.

Etymology: the specific name is a noun in apposition to the generic name and refers to the formation in which the new species was collected.

Diagnosis: small scorpions, when compared with the average size of most species of micro-buthid genera, and measuring 18.96 mm in total length (see morphometric values after the description). General coloration yellow marbled with light reddish-brown confluent spots over tergites; pedipalps, legs and metasomal carinae without spots. Carinae and granulations moderately to strongly marked; dorsal carinae on metasomal segments I to IV with conspicuous posterior spinoid granules. Metasomal segment I wider than long. Chela fingers with only 6–7 rows of granules. Pectines with 15–14 teeth and without fulcra. Trichobothriotaxy A-α (alpha), orthobothriotaxic.

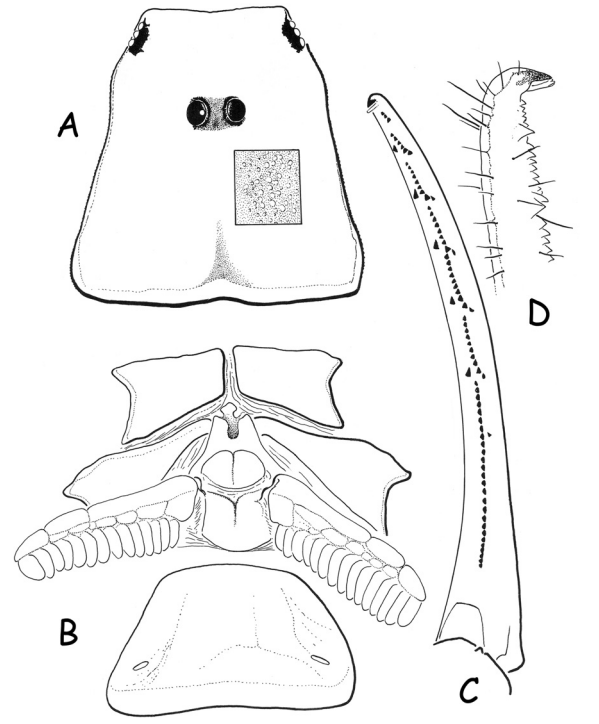

Fig. 2. *Pseudouroplectes tsingy* sp. n. Female holotype. A. Carapace, dorsal aspect; the square zone shows the granulation pattern. B. Ventral aspect, showing coxapophysis, sternum, genital operculum, pectines and sternite III with spiracles. C. Disposition of granulations on the dentate margins of the pedipalp chela movable finger, dorsal aspect. D. Extremity of the finger, in detail, lateral aspect.

Relationships: the new species can be readily distinguished from all the other species of the genus *Pseudouroplectes* and in particular from *P. betschi* by a number of features:

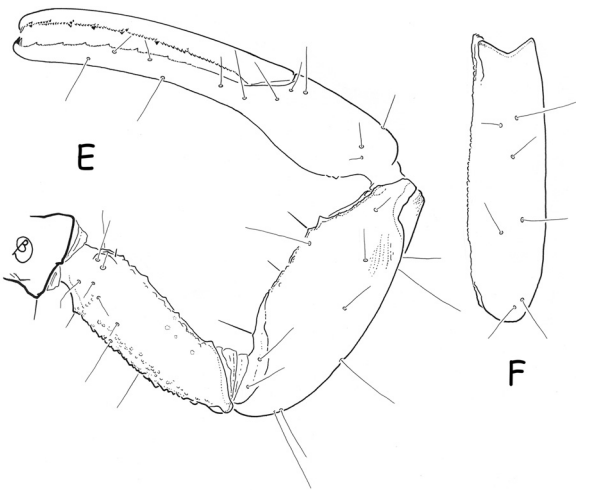

Fig. 3. Trichobothrial pattern of the pedipalp. A. Chela, patella nd femur PAR E. Chela, patella and femur. B. Patella, external aspect PAR F. Patella, external aspect.

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- a general pale yellow coloration, but with pale confluent spots on tergites;
- carapace and tergites with a intense granulation;
- metasomal segment I wider than long;
- chela fingers with 6–7 rows of granules;
- dorsal carinae on metasomal segments I to IV with conspicuous posterior spinoid granules.

Description based on female holotype. Coloration yellow; only tergites are marbled with light reddish-brown confluent spots. Carapace yellow to slightly reddish-yellow; eyes blackish. Pedipalps and legs pale yellow without spots; rows of granules on chela fingers reddish. Metasomal segments yellow with carinae slightly reddish; telson yellow with aculeus reddish. Venter yellow; pectines and genital operculum pale yellow. Chelicerae yellow with finger's teeth reddish.

Morphology. Carapace with a moderately to strongly marked granulation; anterior margin almost straight. Carinae weak; furrows inconspicuous. Median ocular tubercle distinctly on the anterior third of the carapace; median eyes separated by less than one ocular diameter. Three pairs of lateral eyes. Sternum subpentagonal. Mesosoma: tergites moderately to strongly granular. Median carina moderate in all tergites. Tergite VII pentacarinate. Venter: genital operculum divided longitudinally, each plate having a more or less subtriangular shape. Pectines large: pectinal tooth count 15–14 in female holotype; basal middle lamellae of the pectines not dilated; fulcra absent. Sternites smooth with very short semi-slit-like spiracles; VII with minute granulations and two vestigial carinae. Metasoma: segments I to III with 10 carinae, moderately crenulate; IV with 8 carinae, crenulate; ventral carinae reduced or vestigial on segments I to IV; dorsal carinae with strongly marked posterior spinoid granules; intercarinal spaces weakly granular. Segment V rounded with vestigial carinae. Telson with a very elongated "pear-like" shape, smooth and with a strong setation; aculeus short, weakly curved; subaculear tooth absent. Cheliceral dentition characteristic of the family Buthidae [9]; fixed finger with two moderate basal teeth; movable finger with two very weak and almost fused basal teeth; ventral aspect of both finger and manus with dense, long setae. Pedipalps: femur pentacarinate; patella with vestigial carinae; internal face of patella with 4–5 spinoid granules; chela with vestigial carinae; all faces moderately granular. Fixed and movable fingers with 6–7 almost linear rows of granules; two accessory granules present at the base of each row; extremity of fixed and movable fingers with one long and sharp denticle. Trichobothriotaxy, A-α (alpha) orthobothriotaxic [7,10]. Legs: tarsus with very numerous fine median setae ventrally. Pedal spurs reduced; tibial spurs absent.

Morphometric values (in mm) of female holotype. Total length (including telson), 18.96. Carapace: length, 2.40; anterior width, 1.40; posterior width, 2.54. Mesosoma length, 6.07. Metasomal segments. I: length, 1.14; width, 1.20. II: length, 1.34; width, 1.14. III: length, 1.47; width, 1.07. IV: length, 1.80; width, 1.00. V: length, 2.47; width, 0.97; depth, 0.93. Telson: length, 2.27. Vesicle: width, 0.67; depth, 0.67. Pedipalp: femur length, 1.77, width, 0.74; patella length, 2.47, width, 0.94; chela length, 3.50, width, 0.67, depth, 0.74; movable finger length, 2.34.

5. Key to the known species of *Pseudouroplectes*

1. Pale scorpions, yellowish to reddish-yellow, with or without spots_____2

(1). Dark scorpions with confluent blackish spots over the body and appendages.....*P. maculatus*

2. Coloration yellowish without any spots; pectinal tooth count 18–20.....*P. betschi*

(2). Coloration yellowish with light reddish-brown confluent spots or two to four longitudinal reddish-brown stripes over the tergites; pectinal tooth count 14–16.....3

3. Coloration yellow with light reddish-brown confluent spots over the tergites; granulations strongly marked on carapace and tergites.....*P. tsingy* sp. n.

(3) Two to four longitudinal reddish-brown stripes over the tergites; granulations moderately to strongly marked on carapace and tergites.....4

4. Two longitudinal brownish stripes over the tergites; carapace, pedipalps and metasomal segments without spots.....*P. pidgeoni*

(4). Four longitudinal brownish stripes over the tergites; carapace, pedipalps and metasomal segments strongly spotted.....*P. lalyae*

6. Biogeography of the Madagascar humiculous microscorpions: Current distribution

The Microcharmidae family has its modern area of distribution centered in northern Madagascar and is currently represented by 16 taxa, including 14 species with only two species occurring in the west (Fig. 1). With the exception of *M. pauliani* occurring from the humid forest of Montagne d'Ambre and in the dry and subhumid forests of Ankarana in the north, and in the dry forest in the northwest, with three localized subspecies, the other 13 species show small areas of distribution (Fig. 1) [11]. In northern Madagascar, the *Microcharmus* species are encountered in every type of vegetation, including the humid forest of the northeast and Montagne d'Ambre, the dry forest in the north and northwest, and also in the almost subarid types of vegetation encountered near the northern tip of the island (Fig. 1). As exemplified in niche conservatism [12,13], sister species inhabit environments that bear some similarities. Hence, the ancestor clade of the current *Microcharmus* spp. lived in all types of habitat.

Neoprotobuthus is only know from the type species *N. intermedius*, documented by two specimens collected at an altitude of 1240 m a.s.l. in the Sambirano region in March 1999 [14].

Pseudouroplectes tsingy sp. n. has been collected in the dry forest of the Bemaraha protected area. The species previously described in the genus have been collected in the subarid region along the southern coast of the island, including in the driest environment on the Mahafaly plateau and in the Mikea Forest where mean annual

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rainfall is below 500 mm (Fig. 1) [15,16]. The genus *Pseudouroplectes*' known distribution was circumscribed in the driest centers of endemism of Ranopiso, Karimbola and Mikea. The new species expands the range of the genera to the Melaky center of endemism, but without encompassing the Menabe [17,18]. The four species previously described have a large range, as in the case of *P. pidgeoni*, or medium ranges with few records in the Karimbola center of endemism (*P. betschi*) or limited ranges as in the case of *P. maculatus* and *P. lalyae* both endemic to the Mikea center of endemism, sensu Wilmé et al. [18]. *P. pidgeoni* has been collected in the dry spiny forest-thicket of the southeast, at only some 12 km from the humid forest where it has not been recorded (Fig. 1) [5].

7. Some explanations on the humicolous micro-scorpion distribution

Since the Cretaceous and until the Eocene (56.0–33.9 million years ago), Madagascar was positioned on the high-pressure desert belt and was mainly arid, from north to south. Wells [19] proposed that the oldest biome is the one encountered in the driest part of the island, in southern Madagascar and near the extreme northern tip of the island. The known species of humicolous scorpions in the Microcharmidae family or the genus *Pseudouroplectes* have an extremely old history going back at least to the Miocene (23.03–5.333 million years ago). They have retained a basal behavior in living in the upper humid soil surface, in the humus where moisture is retained. In order to explore and better understand the current distribution of these species, we will limit our biogeographical considerations to the last million years circumscribed within the Plio-Quaternary (5.333 million years ago); this also allows the comparison with *Neogrosphus* spp. [20].

8. "Neogrosphus rule"

It has been shown that northern Madagascar has experienced rapid changes over the past million years, with new geographic barriers explaining allopatric speciation in some groups (e.g., *Neogrosphus* [20]). As other primitive micro-scorpions, the Microcharmidae and *Pseudouroplectes* spp. are humicolous micro-scorpions, mostly limiting their "open air excursion" for foraging and reproduction [21–23]. Given their small size coupled with humicolous/cryptozoic behavior, species in the family Microcharmidae and in the genus *Pseudouroplectes* have extremely limited dispersal abilities.

If species diversity in any given area is caused by speciation, extinction and dispersal [24], there are only two processes driving the scorpion diversity: speciation and extinction [20,21]. As a global rule for the scorpions, and in particular for the humicolous micro-scorpions: *the lower the species' dispersal ability and the greater the niche breadth of the ancestor taxon, the higher the species richness in a changing environment producing geographical barriers, and vice-versa*. This translates into the following formula:

$$(A \wedge B) \leftrightarrow C$$

A: low dispersal, B: great niche breadth, C: high species richness.

The genus *Microcharmus* represents a typical case-1 taxon (Table 1), i.e., high species diversity in a rapidly changing environment of a taxon with an ancestor with great niche breath. Northern Madagascar has experienced volcanism at various ages, including during the Quaternary in Nosy Be and Montagne d'Ambre (Fig. 1). The region has entered the intense monsoonic system during the Pliocene with increased rain in the Sambirano region due to the local topography (Fig. 4) [19].

Within the humicolous micro-scorpions, *Neoprotobuthus intermedius* is the largest species (females up to 20 mm vs 13–18 for the females *Microcharmus*) [3,14]. *Neoprotobuthus* has the characteristics of a relict species with one species only occurring at high elevation, above 1200 m, on an old and eroded volcano (Manongarivo) in an area which has experienced major changes in recent times from which many groups have been extirpated (Sambirano). It has been shown that the Sambirano region (Fig. 1) has acted as a major barrier for scorpion species in several groups, including for species in the *Grosphus* or *Neogrosphus* genera, but also primates in the Indriidae family, or birds in the endemic order of the Mesithorniformes. *Neoprotobuthus intermedius* could be an extreme case 2

Table 1
The "Neogrosphus rule" in a changing environment producing geographical barriers, the lower the species' dispersal ability and the greater the niche breadth of the ancestor taxon, the higher the species richness, and vice-versa is equivalent to its contrapositive: the higher the species' dispersal ability or the smaller the niche breadth of the ancestor taxon, the lower the species richness, and vice-versa.

Case	A	B	C	A	∧	B	↔	C	(A ∧ B) ↔ C
1	True	True	True	Low dispersal	AND	Great niche breadth	EQV	High spp richness	True
2	True	False	False	Low dispersal	AND	Small niche breadth	EQV	Low spp richness	True
3	False	True	False	High dispersal	AND	Great niche breadth	EQV	Low spp richness	True
4	False	False	False	High dispersal	AND	Small niche breadth	EQV	Low spp richness	True
5	True	False	True	Low dispersal	AND	Small niche breadth	EQV	High spp richness	False
6	False	True	True	High dispersal	AND	Great niche breadth	EQV	High spp richness	False
7	False	False	True	High dispersal	AND	Small niche breadth	EQV	High spp richness	False
8	True	True	False	Low dispersal	AND	Great niche breadth	EQV	Low spp richness	False

In formulas: $(A \wedge B) \leftrightarrow C$ is equivalent to its contrapositive: $(\neg A) \vee (\neg B) \leftrightarrow (\neg C)$ with the following: A = low dispersal abilities; ¬A = high dispersal abilities; B = great ancient niche breadth; ¬B = small ancient niche breadth; C = high species richness; ¬C =low species richness; ∧ = AND; ∨ = OR; ↔ = equivalent (EQV). The *Neogrosphus* rule above applies to species with low mobility as the scorpions (cases 1 & 2), and to mobile species, as most of the birds or several groups of mammals with high dispersal abilities (cases 3 & 4).

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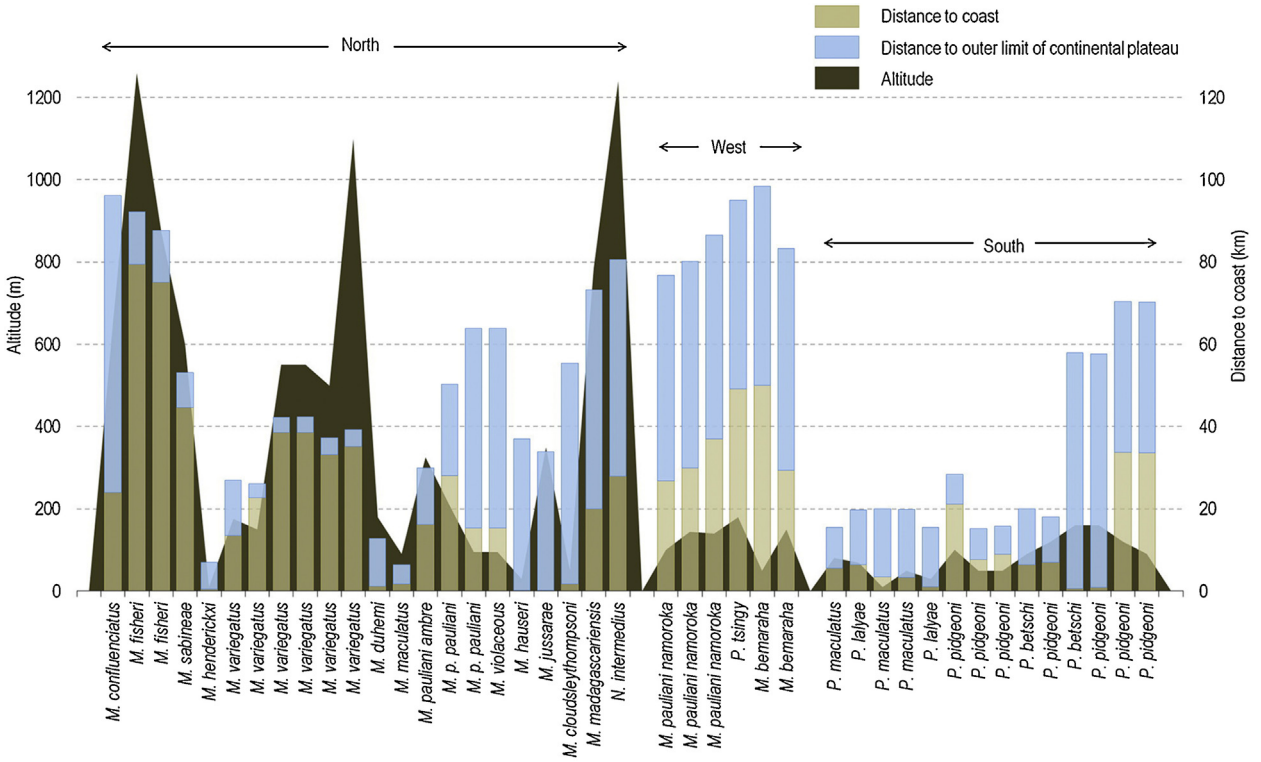

Fig. 4. Shortest distance to coast and to the outer limit of the continental plateau for every collection locality of humicolous micro-scorpions (see Fig. 1 map), and altitude of the collection localities (anti clockwise from northeast to southeast).

(box in the top right corner of Fig. 1), with a monotypic genus, therefore pointing towards a specialized ancestor.

The genus *Pseudouroplectes* occurring in the oldest biome of Madagascar [19] has lived in a "stable" environment, as compared to the members of the Microcharmidae in the north. The absence of the genus in subhumid or humid vegetation types (Fig. 1), may be explained by the limited niche breath of the ancestor taxa, only able to cope with arid to dry conditions. The humicolous behavior is considered as basal, dating back to the "out of aquatic environments" event of the ancient lineages of scorpions, sometimes between the Carboniferous and the Triassic ($[358.9 \pm 0.4]$–$[201.3 \pm 0.3]$ million years ago), at a time when scorpions were not adapted to the dry epigenous environments [21–23]. The four species occurring in southern Madagascar have large ranges as compared to the micro-endemic *Microcharmus* species. Given the collection effort in southern Madagascar, *Pseudouroplectes* scorpions are extremely rare or totally absent from most places through their range. Their extant coastal low altitudinal distribution (Fig. 4) may reflect an ancient extended range over the current continental plateau which has been emerged as recently as ca. 20,000 years ago during the Last Glacial Maximum. The southern extend of this continental plateau could have acted as a bridge between the populations of *P. pidgeoni* or *P. betschi* (Fig. 1). This may also explain why *P. tsingy* sp. n. is isolated; it could be a relict population which has survived in refugia within the former range of the species. The limestone tsingy formation found in the Bemaraha is a karstic residual landform where water is absent on the surface but can be maintained in caves or avens [25]. The lithology, tectonic and geomorphological evolution have sculpted the local landscape, allowing a diversity of micro-climates and the establishment of a variety of vegetation types. The modern large but patchy and coastal distribution of the members of the genus *Pseudouroplectes*, a typical class-2 taxon (Table 1), may constitute another argument to explain a reduced niche breath of the *Pseudouroplectes*.

9. Conclusion

The three groups of endemic humicolous micro-scorpions show distinct biogeographical features related to the pace and extent of environmental changes. With their extremely limited dispersal abilities at the time scale of scorpion evolution, the genus *Microcharmus* shows high species richness in the rapidly changing environment in northern Madagascar, while the monotypic *Neoprotobuthus* illustrates a relict population in the family Microcharmidae. The *Pseudouroplectes* have a littoral distribution along the driest region of southern Madagascar, with a relict population in the western Bemaraha limestone formation which is described here as *P. tsingy* sp. n. The extended distribution of the species in the genus *Microcharmus* in the most humid types of vegetation in northern Madagascar, together with the total absence of the genus *Pseudouroplectes* from the humid types of forest in southeastern Madagascar exemplifies the specialized features of the ancestor *Pseudouroplectes* vs plasticity of the

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Microcharmus ancestor. This may be an explanation for the absence of humicolous micro-scorpions in the eastern humid forests. The Microcharmidae, as well as the genus *Pseudouroplectes* follow the "*Neogrosphus* rule"; with a species richness related to dispersal ability and niche breadth of the ancestral taxa in a changing environment. The "*Neogrosphus* rule" does apply to scorpions but also to mobile species and does allow for biogeographic understanding at taxonomic higher levels.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgements

We are most grateful to Bernard Duhem (MNHN, Paris) for his contribution to the preparation of the drawings, and we would like to acknowledge constructive discussions and exchanges with Joerg Ganzhorn (University of Hamburg) and Jean-Luc Mercier (University of Strasbourg).

References

[1] W.R. Lourenço, S.M. Goodman, A reappraisal of the geographical distribution of the genus *Pseudouroplectes* Lourenço (Scorpiones: Buthidae) in Madagascar, C. R. Biologies 329 (2006) 117–123.
[2] W.R. Lourenço, E. Ythier, Another new species of *Pseudouroplectes* Lourenço, 1995 from Madagascar (Scorpiones Buthidae), ZooKeys 48 (2010) 1–9.
[3] W.R. Lourenço, S.M. Goodman, B.L. Fisher, A reappraisal of the geographical distribution of the endemic family Microcharmidae Lourenço (Scorpiones) in Madagascar and description of eight new species and subspecies, Proc. California Acad. Sci. 4th ser. 57 (2006) 751–783.
[4] W.R. Lourenço, Description de trois nouveaux genres et de quatre nouvelles espèces de scorpions Buthidae de Madagascar, Bull. Mus. Natn. Hist. Nat., Paris 4e ser. 17 (1995) 79–90.
[5] W.R. Lourenço, S.M. Goodman, Taxonomic and ecological observations on the scorpions collected in the Réserve Naturelle Intégrale d'Andohahela, Madagascar, in: S.M. Goodman (Ed), A floral and faunal inventory of the Réserve naturelle intégrale d'Andohahela, Madagascar: with reference to elevational variation, Fieldiana, Zool., n. ser. 94 (1999) 149–153.
[6] H.L. Stahnke, Scorpion nomenclature and mensuration, Entomol. News 81 (1970) 297–316.
[7] M. Vachon, Étude 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. Natl. Hist. Nat. 140 (1974) 857–958.
[8] J.T. Hjelle, Anatomy and morphology, in: G.A. Polis (Ed.), The biology of scorpions, Stanford University Press, CA, USA, 1990, pp. 9–63.
[9] M. Vachon, De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les Scorpions, Bull, Mus. Natl. Hist. Nat. 35 (1963) 161–166.
[10] M. Vachon, 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. Sci. Paris Ser. D 281 (1975) 1597–1599.
[11] J. Moat, P. Smith (Editors), Atlas of the vegetation of Madagascar, 124 p, Kew Publishing, Royal Botanic Gardens, Kew, UK, 2007.
[12] J.J. Wiens, C.H. Graham, Niche conservatism: Integrating evolution, ecology, and conservation biology, Annu. Rev. Ecol. Evol. Syst. 36 (2005) 519–539.
[13] J.J. Wiens, D.D. Ackerly, A.P. Allen, B.L. Anacker, L.B. Buckley, H.V. Cornell, E.I. Damschen, T.J. Davies, J.-A. Grytnes, S.P. Harrison, B.A. Hawkins, R.D. Holt, C.M. McCain, P.R. Stephens, Niche conservatism as an emerging principle in ecology and conservation biology, Ecol. Lett. 13 (2010) 1310–1324.
[14] W.R. Lourenço, Un nouveau genre de scorpion malgache, maillon possible entre les Microcharmidae et les Buthidae, C. R. Acad. Sci. Paris, Ser. III 323 (2000) 877–881.
[15] R.E. Dewar, A.F. Richard, Evolution in the hypervariable environment of Madagascar, Proc. Natl. Acad. Sci. USA 104 (2007) 13723–13727.
[16] P.O. Waeber, L. Wilmé, B. Ramamonjisoa, C. Garcia, D. Rakotomalala, Z.H. Rabemananjara, C. Kull, J.U. Ganzhorn, J.-P. Sorg, Dry forests in Madagascar, neglected and under pressure, Int. Forest. Rev. 16 (2015) 127–148.
[17] L. Wilmé, S.M. Goodman, J.U. Ganzhorn, Biogeographic evolution of Madagascar's microendemic biota, Science 312 (2006) 1063–1065.
[18] L. Wilmé, M. Ravokatra, R. Dolch, D. Schuurman, E. Mathieu, H. Schuetz, P.O. Waeber, Toponyms for centers of endemism in Madagascar, Madagascar Conserv. Dev. 7 (2012) 30–40.
[19] N.A. Wells, Approches paléoenvironnementales du Mésozoïque et du Cénozoïque, in: S.M. Goodman (Ed.), Paysages naturels et biodiversité de Madagascar, MNHN, Paris, 2007, p. 23-56 & 89-94.
[20] W.R. Lourenço, L. Wilmé, P.O. Waeber, More about the geographical distribution of the Malagasy genus *Neogrosphus* Lourenço, 1995 (Scorpiones: Buthidae) and description of a vicariant new species, C. R. Biologies 338 (2015) 768–776.
[21] W.R. Lourenço, Humicolous buthoid scorpions; a new genus and species from French Guiana, C. R. Biologies 326 (2003) 1149–1155.
[22] W.R. Lourenço, Humicolous buthoid scorpions: a new species from Brazilian Amazon, C. R. Biologies 328 (2005) 949–954.
[23] W.R. Lourenço, Humiculous scorpions: On the genera *Ananteris* Thorell, 1891 and *Microananteris* Lourenço, 2004 (Scorpiones: Buthidae), with the description of a new species from French Guiana, C. R. Biologies 335 (2012) 555–961.
[24] R.E. Ricklefs, Community diversity: relative roles of local and regional processes, Science 235 (1987) 167–171.
[25] J.-L. Mercier, L. Wilmé, The Eco-Geo-Clim model: explaining Madagascar's endemism, Madagascar Conserv. Dev. 8 (2013) 63–68.

Please cite this article in press as: W.R. Lourenço, et al., More about the geographical pattern of distribution of the genus *Pseudouroplectes* Lourenço, 1995 (Scorpiones: Buthidae) from Madagascar, C. R. Biologies (2015), http://dx.doi.org/10.1016/j.crvi.2015.11.001