

ONE MORE NEW SPECIES OF *OPISTHACANTHUS* PETERS, 1861 (SCORPIONES: HORMURIDAE) FROM THE LAVASOA FOREST, SOUT-HEASTERN MADAGASCAR

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Abstract: A new species, *Opisthacanthus lavasoa* sp. n., is described from the Lavasoa Forest, in south-eastern Madagascar. The new species shows affinities with both *Opisthacanthus madagascariensis* Kraepelin, 1894, known from the western portion of the island, and *Opisthacanthus ambanja* Lourenço, 2014, only known from the extreme north of the island. The new species and *O. madagascariensis* have similar external morphologies, whereas with *O. ambanja* the new species shares a similar morphology of the hemispermatophores. Moreover, *O. madagascariensis* is exclusively found in spiny forest thickets and savannah-like formations, whereas the new species was found in a humid forest. The total number of species in Madagascar is now raised to eleven.
Key words: Scorpiones, Hormuridae, *Opisthacanthus*, new species, PETM, Madagascar.

Una especie nueva de *Opisthacanthus* Peters, 1861 (Scorpiones: Hormuridae) del bosque de Lavasoa, sudeste de Madagascar

Resumen: Se describe una especie nueva, *Opisthacanthus lavasoa* sp. n., del bosque de Lavasoa, situado en el sureste de Madagascar. La especie nueva muestra afinidades tanto con *Opisthacanthus madagascariensis* Kraepelin, 1894, conocido del oeste de la isla, como con *Opisthacanthus ambanja* Lourenço, 2014, conocido sólo del extremo norte de la isla. La especie nueva tiene una morfología externa similar a la de *O. madagascariensis* y unos hemispermatóforos semejantes a los de *O. ambanja*. Por otra parte, *O. madagascariensis* está presente exclusivamente en manchas de bosque espinoso y formaciones de tipo sabana, mientras que la especie nueva se ha encontrado en un bosque húmedo. El número total de especies de Madagascar se eleva así a once.

Palabras clave: Scorpiones, Hormuridae, *Opisthacanthus*, especie nueva, PETM, Madagascar.

Taxonomy / Taxonomía: *Opisthacanthus lavasoa* sp. n.

Introduction

As previously outlined by Lourenço (2014a, b), scorpions of the genus *Opisthacanthus* Peters, 1861 have been the subject of several studies and revisions during the last three decades (Lourenço, 1987; Lourenço & Fé, 2003; Lourenço & Goodman, 2006). Nevertheless, new discoveries are always possible, as in the case of the descriptions of new species for the subgenus *Monodopisthacanthus* Lourenço, 2001 from Madagascar (Lourenço, 2001, 2014a, b; Lourenço & Goodman, 2006, 2008). For a precise Historical account readers can refer to Lourenço & Goodman (2006, 2008) and Lourenço (2014a, b).

The present study of new samples of hormurid scorpions of the genus *Opisthacanthus*, subgenus *Monodopisthacanthus* from Madagascar, has resulted in the discovery of one new species. These were collected from the extreme South-East of the Island, in the Lavasoa humid forest, and are related to *Opisthacanthus madagascariensis* Kraepelin, 1894 which is known from the western portion of the island. Nevertheless, *O. madagascariensis* is exclusively found in spiny forest thickets and savannah-like formations whereas the new species was found in the humid forest of Lavasoa. Some comments on the known geographic distribution, the biogeography and ecology of the Malagasy species of *Opisthacanthus* are included in this paper.

Historical account on *Opisthacanthus madagascariensis* Kraepelin, 1894.

As already outlined previously (Lourenço & Goodman, 2006) *Opisthacanthus madagascariensis* was described by Kraepelin (1894) from Majunga (Mahajanga). Subsequently, a second species, *O. punctulatus*, was described by Pocock (1896) from south central Madagascar. In a revision of the genus, Kraepelin (1911) considered *O. punctulatus* as a junior synonym of *O. madagascariensis*. This position was followed by subsequent authors, including Fage (1929) and Lourenço (1989).

In a monograph devoted to the scorpion fauna of Madagascar, Lourenço (1996), attempted to characterize these two species, based upon his observations on some old collections of the MNHN in Paris. In a subsequent publication (Lourenço, 2004), the question of the validity of these two species was reopened, and it appeared evident that the very broad distribution of the genus *Opisthacanthus* in Madagascar could not be correlated with a precise distribution pattern of a single species. The difficulty in resolving this taxonomic problem was associated with the fact that most of the specimens from older collections lacked precise details about their provenance.

Subsequently to these publications, the collections of important samples provided the necessary material to allow for the recognition of some intra-population variability in *O. madagascariensis*. This led to the confirmation of the synonymy: *O. punctulatus* = *O. madagascariensis*. Detailed study of these samples equally revealed a number of non-described species of *Opisthacanthus* in Madagascar. These new taxa were in previous studies misidentified as possible juvenile forms of *O. madagascariensis*, but the subsequent study of their internal genitalia confirmed that they are adults. Therefore, the broad distribution previously assigned to *O. madagascariensis* (Lourenço, 2002) corresponded in fact to several different taxa. The geographical distribution of *O. madagascariensis* ranges from the west of the Betsiboka watershed in the west to south of the Onilahy watershed in the southwest (Fig. 1). Some of the previous records of *O. madagascariensis* in the extreme south of the island, as for example the Parc National d'Andohahela (Lourenço & Goodman, 1999), corresponded in fact to new species (Lourenço & Goodman, 2006). Several new species subsequently described (Lourenço & Goodman, 2008; Lourenço, 2014a, b) proved, however to be totally new geographic records of the genus *Opisthacanthus* on Madagascar.

Methods

Illustrations and measurements were made with the aid of a Wild M5 stereo-microscope equipped with a drawing tube (camera lucida) and an ocular micrometer. Measurements follow Stahnke (1970) and are given in mm. Trichobothrial notations follow Vachon (1974) and morphological terminology mostly follows Hjelle (1990).

The present composition of the genus *Opisthacanthus* Peters, 1861

The classification given below takes into account the most recent taxonomic modifications proposed for the genus (Lourenço, 2014a, b). Since most historical aspects concerning Malagasy species of *Opisthacanthus* have already been presented in previous publications (Lourenço, 2014a, b; Lourenço & Goodman, 2006, 2008), these will not be further discussed here.

Family Hormuridae Laurie, 1896 Genus *Opisthacanthus* Peters, 1861

- Subgenus *Opisthacanthus* Peters, 1861, with 3 species groups:
 - I. *cayaporum* group, distributed in Tropical South America.
 - II. *lepturus* group, distributed in Tropical South and Central Americas and on the Great Antilles.
 - III. *lecomtei* group, distributed in Western Africa.
- Subgenus *Nepabellus* Francke, 1974, with 5 species groups:
 - I. *africanus* group, distributed in Southern, Western and Eastern Africa.
 - II. *asper* group, distributed in Southern and Eastern Africa.
 - III. *laevipes* group, distributed in Southern Africa.
 - IV. *rugulosus* group, distributed in Southern Africa.
 - V. *validus* group, distributed in Southern Africa.

- Subgenus *Monodopisthacanthus* Lourenço, 2001, with one species group:

I. *madagascariensis* group, distributed in Madagascar, with 11 species:

- Opisthacanthus madagascariensis* Kraepelin, 1894.
- Opisthacanthus lucienneae* Lourenço & Goodman, 2006.
- Opisthacanthus maculatus* Lourenço & Goodman, 2006.
- Opisthacanthus darainensis* Lourenço & Goodman, 2006.
- Opisthacanthus piceus* Lourenço & Goodman, 2006.
- Opisthacanthus milloti* Lourenço & Goodman, 2008.
- Opisthacanthus pauliani* Lourenço & Goodman, 2008.
- Opisthacanthus andohahela* Lourenço, 2014.
- Opisthacanthus antsiranana* Lourenço, 2014.
- Opisthacanthus ambanja* Lourenço, 2014.
- Opisthacanthus lavasoa* sp. n.

Opisthacanthus madagascariensis Kraepelin, 1894

DIAGNOSIS: Medium to large size scorpions: males 62 mm and females 68 mm in total length. Coloration; basically reddish brown to dark brown with some blackish zones on the pedipalp carinae and metasomal segments. Metasomal segments darker than prosoma and mesosoma; vesicle reddish-yellow; aculeus dark reddish on the tip. Chelicerae reddish-brown; base of fingers blackish; the whole surface with dark variegated spots; fingers dark with reddish teeth. Pedipalps blackish-brown. Venter and sternites reddish-yellow to reddish-brown; pectines and genital operculum paler than sternites; legs yellowish to reddish-yellow with strongly diffused spots. Morphology. Body and appendages weakly granulated, almost smooth and with punctuations. Sternum wider than long. Genital operculum formed by two semi-oval plates in males, and one single heart-like shaped plate in females, with a small incision in the base. Pectinal tooth count 7 to 8 in males and 6 to 8 in females; mode 8 in males, 7 in females. Trichobothriotaxy type C; orthobothriotoxic (Vachon, 1974). Legs: tarsi with 3 lateral rows of spines, surrounded by some long setae. Hemispermatophore with the distal lamina moderately long and very complex.

Opisthacanthus ambanja Lourenço, 2014

DIAGNOSIS: Medium to small size scorpions: male 43.2 mm in total length (subadult female paratype = 34.1). Coloration reddish-brown to dark brown, with some blackish zones. Pectines with 6 teeth in male and 5-6 in females; mode 6 in males and females. Hemispermatophore slender and thin; distal lamina weakly enlarged and less complex than in the other species. Female genital operculum larger than long, with an almost oval-shape, and with an incision in the base. Trichobothrial pattern of type C, orthobothriotaxy (Vachon, 1974).

Description of a new species

Opisthacanthus lavasoa sp. n.

Fig. 2-14.

TYPE MATERIAL: Madagascar, Toliara Province (Anosy Region), Forêt humide de Lavasoa (rainforest), VII/1972 (J. M. Betsch – RCP 225). 1 male holotype and 1 male (pre-adult) paratype. Deposited in the Muséum national d'Histoire naturelle, Paris.

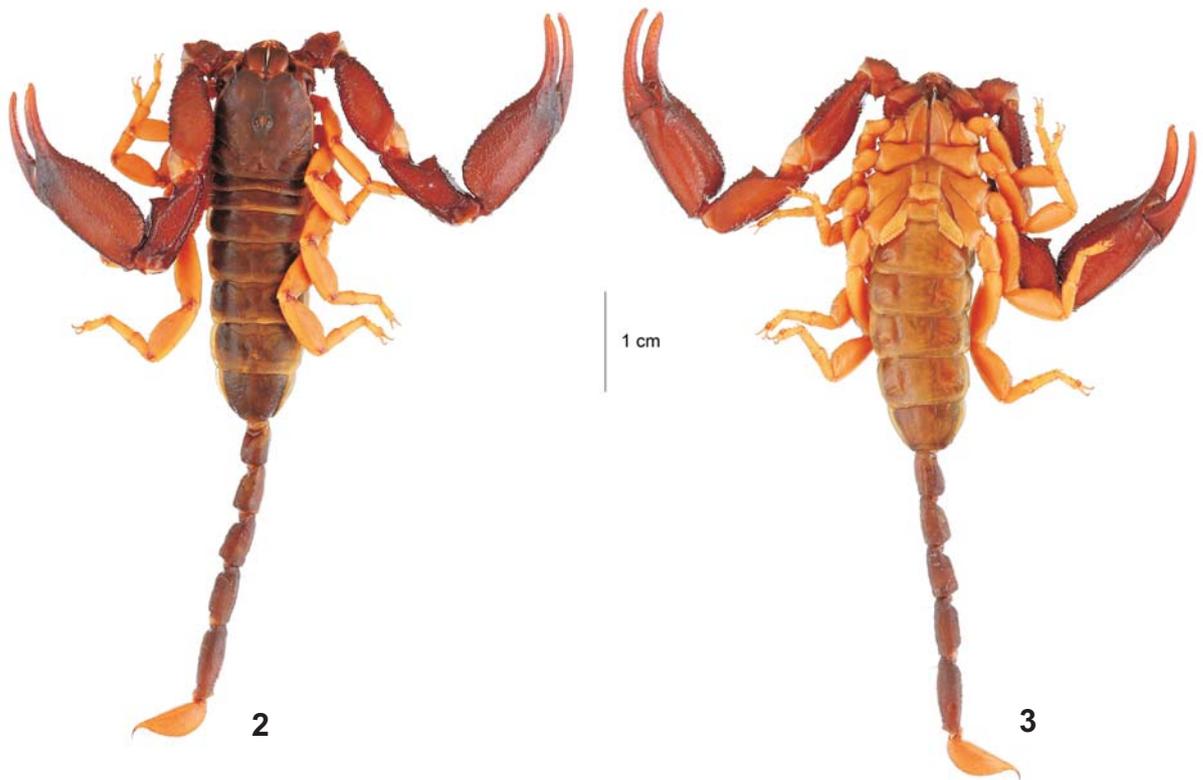
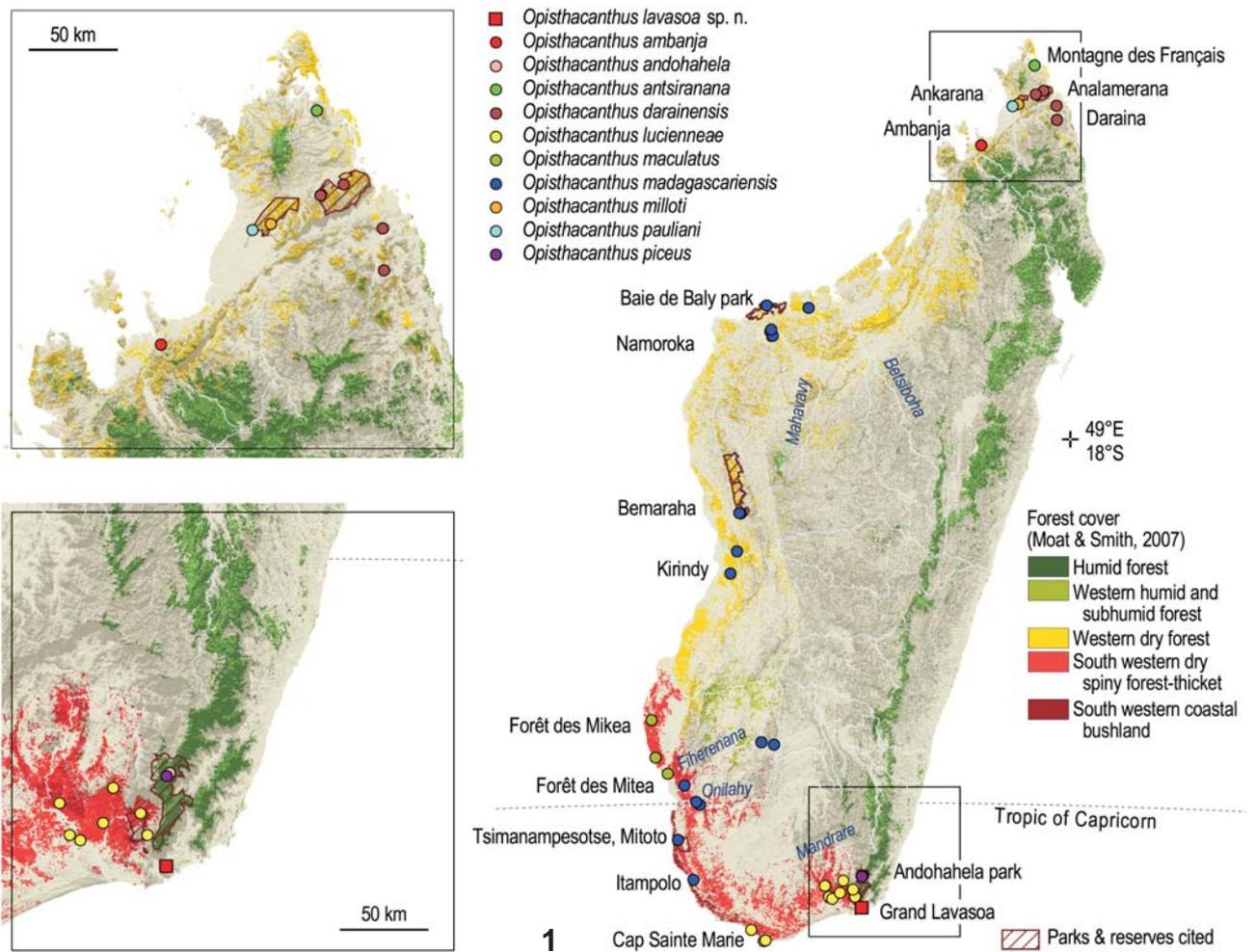


Fig. 1. Map showing the geographic distribution of extant Malagasy species of *Opisthacanthus*. **Fig. 2-3.** *Opisthacanthus lavasoa* sp. n. Male holotype, 2, dorsal and 3, ventral aspects.

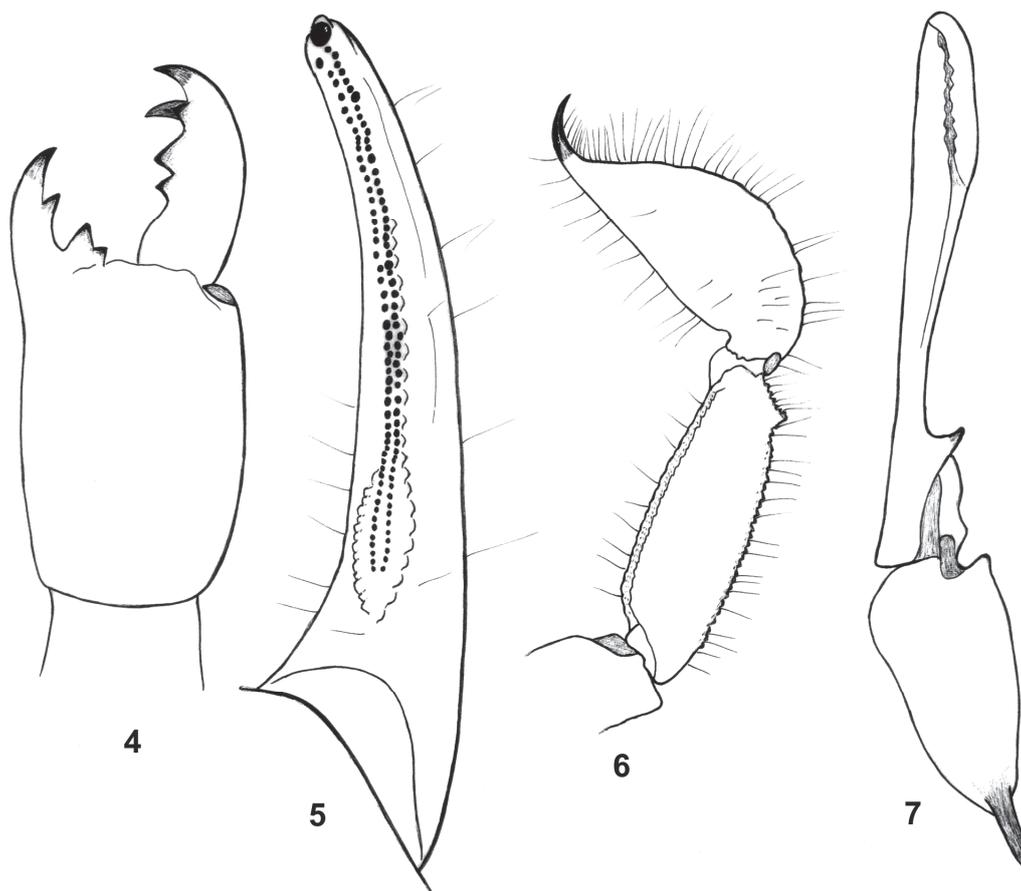


Fig. 4-7. *Opisthacanthus lavasoa* sp. n. Male holotype. 4. Chelicera. 5. Cutting edge of movable finger, showing the two series of granulations. 6. Metasomal segment V and telson, lateral aspect. 7. Hemispermatophore, external aspect.

ETYMOLOGY: The specific name is a noun in apposition to the generic name and refers to the region where the new species was found.

DIAGNOSIS: Medium to large size scorpion: male with 69.6 mm in total length. Coloration reddish-yellow to reddish-brown, with some dark variegated zones on chelicerae. Pectines with 7-8 teeth in males; mode 8 in males. Hemispermatophore very slender with an elongated distal lamina, weakly enlarged. Male genital operculum large, with a minute incision in the base. Trichobothrial pattern of type C, orthobothriotaxy.

DESCRIPTION BASED ON HOLOTYPE AND PARATYPE.

Coloration. Basically reddish-yellow to reddish-brown with some dark variegated zones on the chelicerae. Carapace reddish-brown; median and lateral eyes surrounded with black pigment. Tergites reddish-yellow to reddish-brown. Metasomal segments reddish-brown; vesicle yellow with a reddish lateral strip; aculeus dark reddish. Chelicerae reddish-brown; base of fingers darker; the whole surface with diffuse variegated spots; fingers yellowish-brown with reddish teeth. Pedipalps reddish-yellow to reddish-brown; most carinae blackish; chela fingers yellow. Venter and sternites yellow to reddish-yellow; pectines and genital operculum paler than sternites, sternum and coxapophysis; legs intensely yellow.

Morphology. Carapace with some rare granulations some punctuation and smooth zones; furrows shallow. Anterior margin with a strong concavity reaching as far as the level of

the 2rd lateral eye. Median ocular tubercle flattened and almost in the centre of the carapace; median eyes moderate, separated by one ocular diameter; three pairs of large lateral eyes. Sternum pentagonal, wider than long. Genital operculum formed by two semi-oval plates in males; with a minute incision in the base. Tergites with only a vestigial median carina, smooth and with punctuations. Pectinal tooth count 8-8 in male holotype (7-8 in paratype). Sternites smooth and shiny; VII acarinate with very few punctuations. Metasomal segments I to V longer than wide, with some thin but intense granulations. All carinae moderately marked in segments I-IV; segment V rounded with some weak spinoid granules on the ventral surface. All segments with moderate to weak chetotaxy. Telson with a pear-like shape; smooth and covered with strong chetotaxy. Pedipalps: femur with dorsal internal, dorsal external, ventral internal and ventral external carinae strong, tuberculate; dorsal face with thin granulation; ventral face with minute granulation; internal face moderately granulate. Patella with internal and external faces weakly granulated; dorsal and ventral faces smooth and lustrous; dorsal internal, ventral internal, ventral external and external carinae moderate to strong; other carinae less well marked. Chela strongly granular excepted on ventral face; dorsal marginal, external secondary, ventrointernal and ventral median carina strong; other carinae less well marked. Chelicerae typical of Scorpionoidea (Vachon, 1963); teeth strongly sharp. Trichobothriotaxy type C; orthobothriotaxy (Vachon, 1974). Legs: tarsi with two lateral rows of spines, surrounded by a few.

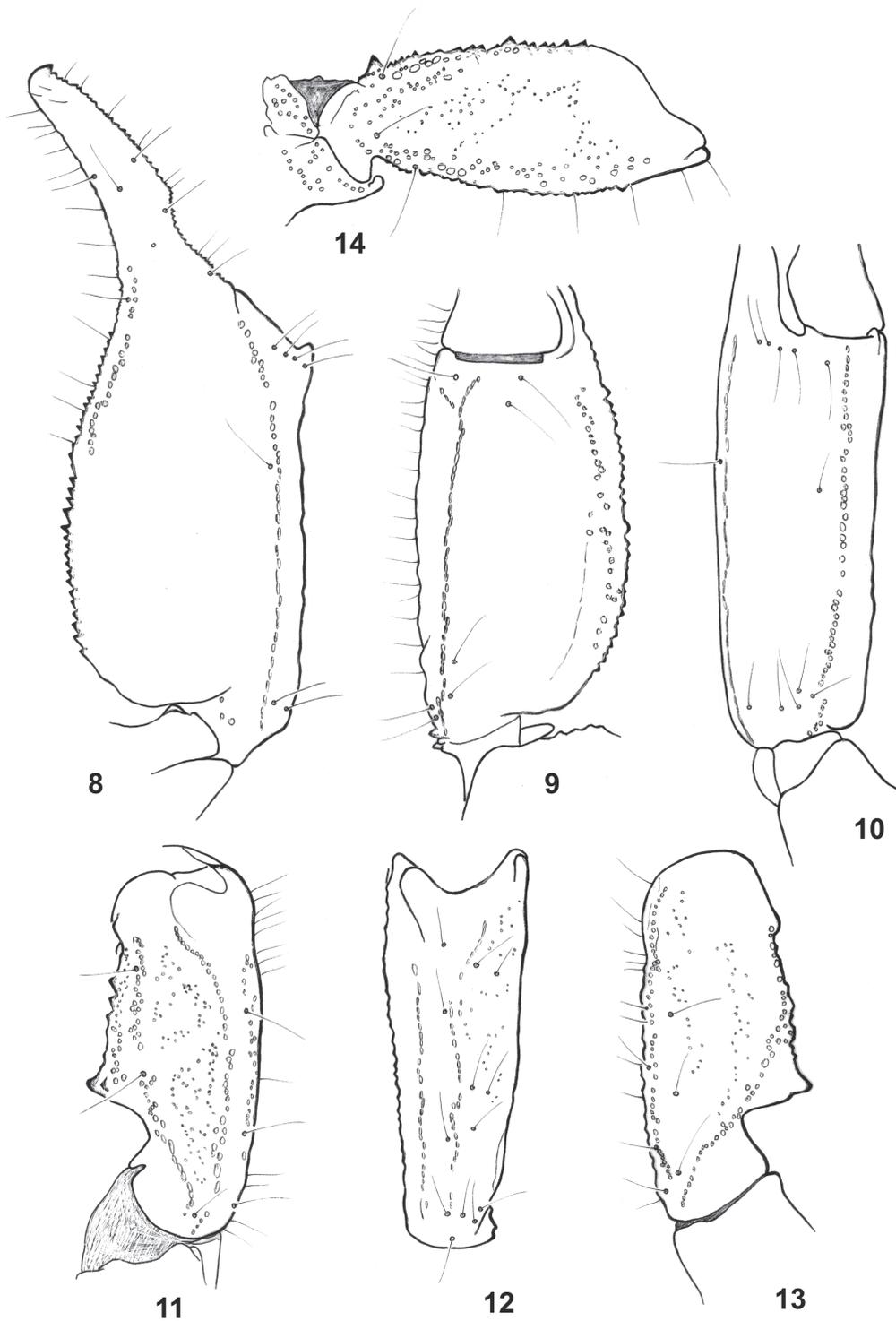


Fig. 8-14. *Opisthacanthus lavasoa* sp. n. Male holotype. Trichobothrial pattern. **8-10.** Chela, dorso-external, ventral and external aspects. **11-13.** Patella, dorsal, external and ventral aspects. **14.** Femur, dorsal aspect.

long setae. Spurs moderate. Hemispermaphore very slender with an elongated distal lamina, weakly enlarged.

Morphometric values (in mm) of male holotype. Total length (including telson) 69.6. Carapace: length 10.8; anterior width 6.8; posterior width 10.8. Mesosoma length 23.4. Metasomal segment I: length 4.0, width 2.9; II: length 4.4, width 2.5; III: length 4.9, width 2.4; IV: length 5.8, width 2.1; V: length 7.8, width 1.9, depth 2.5. Telson length 8.5. Vesicle: width 2.5, depth 3.2. Pedipalp: femur length 10.8, width 4.6;

patella length 11.1, width 4.8; chela length 21.2, width 6.3, depth 4.2; movable finger length 10.2.

RELATIONSHIPS: The new species is most certainly associated with *Opisthacanthus madagascariensis* and with *O. ambanja* but can be distinguished from these two species by a number of characters: (i) bigger global size and distinct morphometric values (ii) a globally paler coloration than that of *O. madagascariensis*, (iii) Hemispermaphore with a distinct morphology – very slender compared to that of *O.*

madagascariensis (see Lourenço & Goodman, 2006). In fact, the hemispermatothores of the new species show similarities only with the one of *Opisthacanthus ambanja* Lourenço, 2014, described from the extreme north of the island. Moreover, the three different populations inhabit quite distinct habitats.

Biogeographic considerations

The geographic distribution of extant Malagasy *Opisthacanthus*.

As already outlined by Lourenço (2014a), the taxonomy of *Opisthacanthus madagascariensis* remained unclear for a long time and, until the publication by Lourenço & Goodman (2006); the presence of one or two species (cf. *O. punctulatus*) was not precisely defined in Madagascar (Lourenço & Goodman, 1999). A similar situation also prevailed for a long period of time for two *Opisthacanthus* species distributed in the Neotropical region, namely *Opisthacanthus lepturus* (P. de Beauvois, 1805) and *Opisthacanthus elatus* (Gervais, 1844). Their status was finally clarified by Lourenço (1995). *Opisthacanthus madagascariensis* has a broad distribution across portions of South-central, Western, and Southern Madagascar (Fig. 1). Several of the collection sites are in zones of transitional humid and dry deciduous forest and often with canyons that create locally more mesic conditions (e.g., Analalava, Namoroka, Bemaraha) or specifically in riparian forests growing along major rivers (e.g., Mahavavy, Fiherenana) and bordered by distinctly drier formations. It is also known from the dry deciduous forests of Kirindy, north of Morondava and the park of Baie de Baly, as well as some of the driest regions of the island, including zones with spiny thicket (e.g., Itampolo, near Mitoho Cave in the Tsimanampetsotse park, or forêt de Mitea). The known range of the species extends from the Mahafaly region in the southwest to the west of the Betsiboka watershed (Fig. 1) which encompasses a diversity of forest types, including western dry forest, western humid forest, and south western dry spiny forest-thickets.

The remaining species belong to a northern group with five narrow-ranged species in the extreme North of the island, and to a southern group with four species distributed in Southern Madagascar (Fig. 1). Amongst these two groups, there are species found in the driest regions of the island, the Diego-Suarez micro-climate and the sub-arid bioclimate (Cornet 1974), namely *Opisthacanthus antsiranana* endemic to Montagne des Français in the North, and *O. maculatus* endemic to the forest of Mikea in the Southwest. *O. luciennae* is also found in the southern subarid region but has a larger range than the species mentioned before, and it also occurs in the Mandrare watershed where the forests are not as dry as in the Reserve of Cap Sainte-Marie. *O. luciennae* appears to have a parapatric distribution in relation to *O. madagascariensis*. The coastal winds have shaped the vegetation of this Southern Cap and dwarfed the trees and bushes of the reserve to a height below 2 to 3 m. In both, the northern and the southern groups of *Opisthacanthus*, species are distributed in the more humid forests, namely *O. ambanja* in the northern subhumid forests encountered in the Sambirano region, *O. piceus* and *O. andohahela* found at altitudes of 520 and 560 m in the humid forests of the park of Andohahela, and *O. lavasoa* sp. n. in the humid forests of Lavasoa (Fig. 1).

Opisthacanthus maculatus shows a somewhat sympatric distribution in relation to *O. madagascariensis*, but its range

is limited to the Mikea center of endemism limited by the Mangoby watershed to the north, and the Onilahy watershed to the south (cf. Wilmé *et al.*, 2012).

Opisthacanthus darainensis is an endemic species to the Daraina region and its nearby areas (Lourenço & Goodman, 2002).

Opisthacanthus piceus is only known from its type locality, the subtropical humid forest of the park of Andohahela.

Opisthacanthus andohahela is only known from its type locality, and represents another endemic species of the subtropical humid forest of the park of Andohahela.

Opisthacanthus antsiranana is only known from its type locality and inhabits the tropical dry forest and grasslands in the region of the Montagne des Français in the extreme north of Madagascar.

Opisthacanthus ambanja is only known from its type locality and inhabits the humid and subhumid forests located between Ambanja and Ambilobe along the north-western coast of Madagascar.

Opisthacanthus lavasoa sp. n. is only known from the type locality, the forest of Lavasoa which is the largest forest fragment of the Ambatotsirongorongo Mountain. The Lavasoa forest is a fragment of humid forest located at the southern tip of the Anosy watershed, and is also the southernmost humid forest of Madagascar, at a distance of some kilometres only from the dry spiny forest-thicket (Fig. 1).

Four scenarios to explain the current *Opisthacanthus* distributions.

We assume that the species in the subgenus *Monodopisthacanthus* have adapted to the drier regions of the island, with a tolerance to more mesic forests since the subgenus is mostly absent from the eastern rainforests but is present in some of the driest biomes on the west and south of the island. The collection localities in the humid forests of Andohahela and Lavasoa are subtropical, at some 125 and 175 km south of the Tropic of Capricorn respectively (Fig. 1). The shortest distance between the two sister species *Opisthacanthus lavasoa* sp. n. in the South and *O. ambanja* in the North is of some 1300 km. Vicariance has been proposed as a process to explain a similar pattern of distribution for species in the endemic Heteroscorpionidae family (Lourenço *et al.*, 2015). Vicariance could be an approach to explain geographic separation of the two *Opisthacanthus* sister species (henceforth the sister species) with similar hemispermatothores. However, we discard this hypothesis on the grounds that (i) these species belong to an old bradytelic group with slow evolution (*sensu* Lourenço *et al.*, 2016a); (ii) the geographic barrier between the two sister species represents 95% of the total area of the island.

The climatic context: Madagascar since the K–Pg.

Proto-elements to the Hormuridae family are documented by fossil material dating back some 110 million years ago (Ma) during the Lower Cretaceous to which the genus *Opisthacanthus* can be related (Carvalho & Lourenço, 2001). Following the Cretaceous–Paleogene (K–Pg) mass extinction at the end of the Cretaceous some 66 Ma, and during the early Paleogene, the ancestral *Monodopisthacanthus* was likely present in Madagascar and survived the K–Pg. Madagascar was already separated from Africa, and India was drifting to the north (Fig. 15). Madagascar was located at some 7 to 8 degrees to the south of its current position, its southern tip at

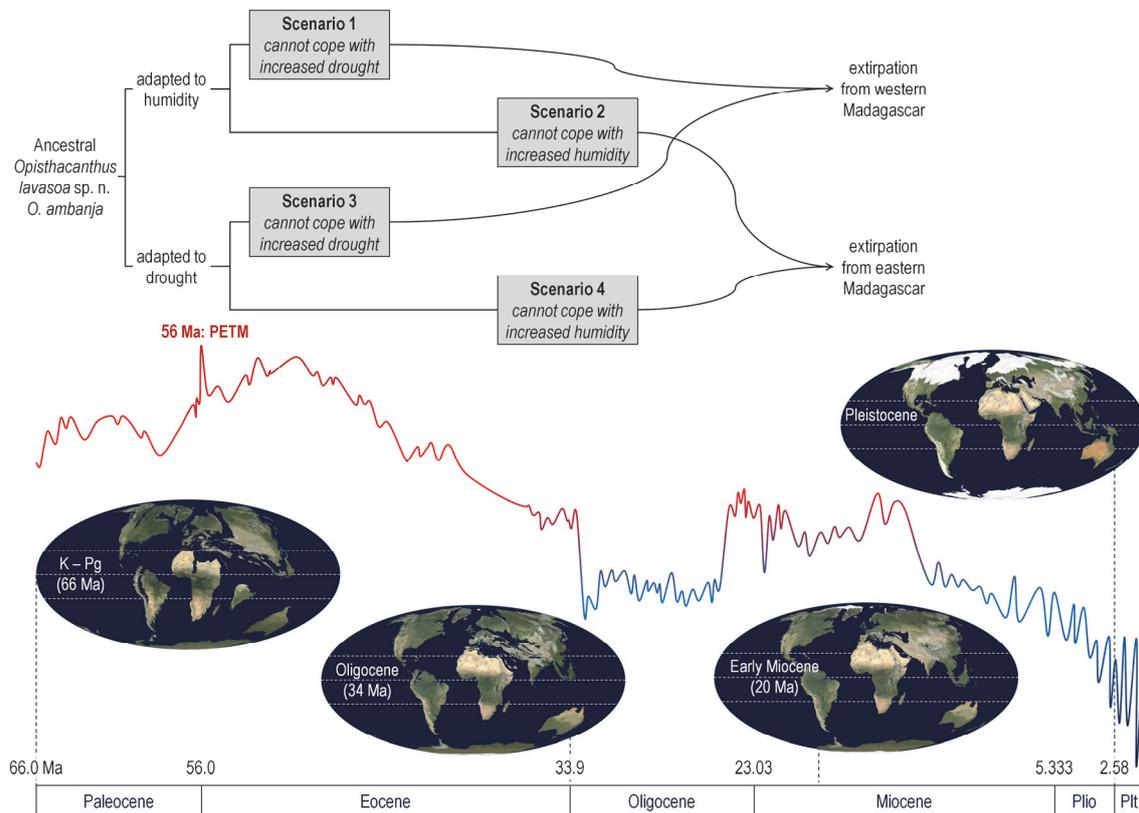


Fig. 15. Four climatic change scenarios elaborating the distribution of the two sister species (*Opisthacanthus lavasoa* sp. n. and *O. ambanja*). Climatic change during the past 66 million years. “Break up Gondwana” 66 Ma K–Pg, to 2.58 Ma Pleistocene, (modified from <http://jan.ucc.nau.edu/rcb77/mollglobe.html> (Blakey, 2008). © Ron Blakey, Colorado Plateau Geosystems, used with permission). Red-blue line indicates temperature change. PETM= Paleocene–Eocene thermal maximum; ages according to Cohen *et al.* (2013); temperatures modified from Zachos *et al.* (2001))

32.9°S (vs. current 25.6°S) and northern tip at 20.1°S (vs. current 12.0°S) (Wells, 2003).

During the Paleocene (66.0–56.0 Ma), Madagascar was isolated from Africa and India; the South-Indian drift was affecting the eastern coast of Madagascar which increased the rainfall, and Northern Madagascar entered the monsoon belt (Fig. 15). At the end of the Paleocene (56.0 Ma), a major global increase in temperature occurred, the Paleocene–Eocene thermal maximum (PETM), which lasted some 200,000 years (Zachos *et al.*, 2005). Only by the mid Oligocene, 29 Ma, has Madagascar completed its drift out of the arid belt and entered completely the trade wind regime (Wells, 2003; de Wit, 2003; Waeber *et al.*, 2015 and references therein).

- **SCENARIO 1:** the ancestral population of the sister species was adapted to humid conditions and could not cope with increased drought.

The rapid warming of the PETM could have eliminated most populations on the island since they were not adapted to increased drought. Ancestral populations would only have survived in pockets of increased humidity in the extreme north and extreme south. At the time of the PETM, Northern Madagascar already entered the Indian monsoon and the Sambirano could have experienced more mesic conditions as compared to the remaining western and southern portion of the island. Southern Madagascar was still in the arid belt (Fig. 15) and thus the conditions to find humid refugia were reduced. Hence, Scenario 1 is rather unlikely when considering the asynchronous events between the increasing humidity in

northern vs. southern Madagascar, which does not fit the PETM.

- **SCENARIO 2:** the ancestral population was adapted to humid conditions but could not cope with increased humidity.

This scenario would have the same early settings as described in Scenario 1, with ancestral populations of the sister species living along the eastern side of the island where humidity after the K–Pg increased over time (Fig. 15). With increased humidity during the Oligocene when the entire island entered the trade wind regime, the ancestral populations could have disappeared from the most humid parts of Madagascar and survived only in pockets of reduced humidity, as was the case in the Sambirano in the North, or in the coastal subtropical areas along the Southern part of the island. Scenario 2 is thus likelier than Scenario 1 given that the mesic conditions in the northwest and the southeast could have been synchronous.

- **SCENARIO 3:** the ancestral population was adapted to dry conditions and could not cope with increased drought.

Adaptation to dry conditions of the Madagascar *Opisthacanthus* lineage could be inferred from its current distribution in the dry biome of northern, western and southern Madagascar (Fig. 1), but especially from its ancient age and presence in Madagascar when the climate was a lot warmer and drier during the Paleogene (Fig. 15). At the time, a common ancestor of the sister species could have been distributed over the eastern belt of the island which was probably covered by some kind of dry forest and thickets (Wells, 2003).

The assumption here is that ancestral populations were adapted to dry conditions in western Madagascar. The subsequent increased drought associated with the PETM eradicated the populations from the driest parts of the west, while some survived in the more mesic pockets in the extreme north and south. As in Scenario 1 above, Scenario 3 refers to two asynchronous events with a time lag between the increasing humidity in Northern and Southern Madagascar, which does not fit the PETM.

- SCENARIO 4: the ancestral population was adapted to dry conditions but could not cope with increased humidity.

Ancestral *Monodopisthacanthus* populations adapted to dry conditions in Paleocene eastern Madagascar could have disappeared from the eastern belt of the island when Madagascar entered the trade wind regime with increased humidity along this portion of the island. We could hypothesize the survival of some populations at the limit of the new rainforest belt (Fig. 15), where humidity was not as important. This scenario seems more likely, especially when considering *O. andohahe-la* and *O. piceus* occurring in the humid subtropical forest of Andohahela, or *O. madagascariensis* in the subhumid forests occurring in the western tsingy formations as encountered in Namoroka, or Bemaraha, and *O. pauliani* in the subhumid forests of Ankarana (Fig. 1).

The four scenarios are based on large-scale catastrophic events limiting the distribution of ancestral scorpion populations, or their extirpations from large areas. The scenarios do not consider further dispersal. Over the course of millions of years, the ancestral populations have dispersed and also experienced further local extirpations as in the case of volcanism or earthquakes, but the current distribution of the two sister species is best explained in ancient times. Considering the currently wide range of *O. madagascariensis* in Western Madagascar, it is not farfetched to assume a wide range for an ancestral population of the sister species but the current information available for the group does not allow us to infer its location. The subgenus *Monodopisthacanthus* is currently recognized as monophyletic; therefore the 11 species in this subgenus share a single ancestor. At the time of the K–Pg, it is assumed that the phylum survived on the island but it is not known if the current species encountered in Madagascar originate from a single population or multiple populations which have survived the K–Pg.

The two regions with high *Opisthacanthus* diversity represent together less than 5% of the total area of the island, but they share the peculiarity to harbour the highest diversity of forest types ranging from humid rain forests to sub-arid forests and thickets. Interestingly the wide-ranged and unspecialized *O. madagascariensis* does not occur in the *Opisthacanthus* species rich area of extreme north and south of Madagascar (Fig. 1).

Conclusions

The current scorpion fauna of Madagascar is dominated by ancient groups with some humus dweller scorpions encountered in the humid rain forests on the eastern portion of the island (e.g., in the genus *Tityobuthus*, Lourenço *et al.*, 2016a). However, several current scorpion groups (e.g., the genera *Neogrosphus* or *Pseudouroplectes*) are absent from the humid and subhumid forests (Lourenço *et al.*, 2015, 2016b). The

four scenarios may serve as a guide to explain large-scale distribution patterns of other ancient endemic lineages. Lava-soa is also the type locality of another scorpion belonging to an ancient lineage *Heteroscorpion kaii* (Lourenço & Goodman, 2009), and harbours no less than nine species of Diplopoda in seven genera and three families (Wesener, 2009; Wesener *et al.*, 2009, 2014).

Acknowledgements

We are most grateful to Elise-Anne Leguin (Muséum, Paris) for her contribution to the preparation of the photos and plates.

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