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The genus *Opisthacanthus* Peters, 1861 (Scorpiones: Hormuridae), a remarkable Gondwanian group of scorpions

Le genre Opisthacanthus *Peters (Scorpiones : Hormuridae), un remarquable groupe de scorpions gondwaniens*

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ABSTRACT

New comments are proposed on the geographic distribution of genus *Opisthacanthus*, and the Gondwanian model is further supported. The diversity of the genus is extraordinary in Madagascar, with the same number of species as in continental Africa, but sub-Saharan Africa is home to six out of the nine groups currently recognized of *Opisthacanthus*. Given the affinities of the *Opisthacanthus* groups and their current distribution, a center of origin in Africa could be favored for these ancient scorpions. The proposed Gondwana model suggests that the Madagascar *Opisthacanthus* are closer to those of the New World, which is consistent with the affinities observed in morphological characters. A new species, *Opisthacanthus* titanus sp. n., is described from the Torotorofotsy Forest, located in Eastern Madagascar. The new species shows affinities with both *Opisthacanthus* madagascariensis Kraepelin, 1894 known from dry regions in the western portion of the island and *Opisthacanthus* lavasoa Lourenço, Wilmé & Waeber, 2016 only known from the extreme southeast of the island. The new species and *O. madagascariensis* have similar external morphologies but the morphometric values are markedly distinct. Moreover, *O. madagascariensis* is exclusively found in spiny forest thickets and open woodlands, whereas the new species was found in the humid forest of Torotorofotsy. The total number of species in Madagascar is now raised to twelve. Biogeographical scenarios are also proposed to infer the origin of the *Opisthacanthus* and better understand its distribution in the New World, in Africa and Madagascar.

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RÉSUMÉ

Une nouvelle réflexion est proposée sur la répartition géographique du genre *Opisthacanthus* avec la proposition d'un modèle gondwanien. La diversité du genre est extraordinaire à Madagascar, avec un nombre d'espèces qui égal celui de l'Afrique, mais l'Afrique sub-saharienne abrite six des neuf groupes actuellement reconnus d'*Opisthacanthus*. Compte tenu des affinités des groupes d'*Opisthacanthus* et leur répartition actuelle, un centre d'origine en Afrique pourrait être favorisé pour ces scorpions anciens. Le modèle gondwanien proposé suggère que les *Opisthacanthus* de Madagascar sont plus proches de ceux du Nouveau Monde, ce qui est cohérent avec les affinités observées à partir des caractères morphologiques. Une nouvelle espèce est décrite, *Opisthacanthus titanus* sp. n., connue de la forêt de Torotorofotsy, à l'est de Madagascar. La nouvelle espèce montre des affinités avec *Opisthacanthus madagascariensis* Kraepelin, 1894 connu des régions sèches de l'Ouest de l'île et *Opisthacanthus lavasoa* Lourenço, Wilmé & Waeber, 2016, qui n'est connu que de l'extrême Sud-Est de l'île. La nouvelle espèce et *O. madagascariensis* ont des morphologies externes similaires, mais leurs valeurs morphométriques sont nettement distinctes. De plus, *O. madagascariensis* se trouve exclusivement dans les fourrés épineux et les formations arborées ouvertes, tandis que la nouvelle espèce provient de la forêt humide de Torotorofotsy. Le nombre total d'espèces à Madagascar est maintenant porté à douze. Des scénarios biogéographiques sont proposés pour appréhender l'origine des *Opisthacanthus* et mieux comprendre leur distribution dans le Nouveau Monde, en Afrique et à Madagascar.

1. Introduction

As already discussed in several previous publications, the taxonomic history related to the genus *Opisthacanthus* Peters, 1861 is rather complex [1,2]. The genus was created by Peters [3], based on the species *Ischnurus elatus* Gervais, 1844 [= *Opisthacanthus elatus* (Gervais, 1844)], a species distributed from Colombia to Panama. Subsequently, the discovery in Africa of species with morphology closely related to *O. elatus* led some authors to accept the existence of this genus on both continents. By the end of the 19th century, the notion of Gondwanian groups was yet inexistent and consequently this model of discontinuous distribution appeared difficult to explain by that time. This complex situation led Pocock [4], in a new classification of scorpion, to propose a new genus *Opisthocentrus* for the African species, whereas *Opisthacanthus* remained associated exclusively with the Neotropical species. Nevertheless, in the following years Pocock himself took different decisions and first placed both American and African species under *Opisthacanthus* [5,6], but a few years later he split the species of the two continents again in two genera [7]. Other authors such as Kraepelin [8] considered *Opisthocentrus* as a synonym of *Opisthacanthus*, a position followed by several authors [9,10].

During the 1970s the question around the issue of one or two genera associated with *Opisthacanthus* was raised again by two authors: Newlands [11,12] and Francke [13]. Newlands [11,12] suggested the existence of a single genus, *Opisthacanthus* over two continents (America and Africa), but rejected any hypothesis about a Gondwanian distribution; based on the theory of "transoceanic rafting on driftwood", as defined by Darlington [14], Newlands [11,12] proposed the hypothesis of recent dispersion from Africa to America. To the contrary, Francke [13] rejected the idea of a single genus over two continents and revalidated the genus *Opisthocentrus*. However, since *Opisthocentrus* was already occupied by a fish genus, *Opisthocentrus* Kner, 1868 (Actinopterygii: Pholidae), he introduced a new replacement name *Nepabellus* Francke, 1974 for the African species.

The arguments suggested both by Newlands [11,12] and Francke [13] were entirely rejected by Lourenço [1,2], and a single genus *Opisthacanthus* was defined for all the American and African species, based on a Gondwanian model of distribution (cf. Lourenço [1,2] for further details). It is important to note that in their different analysis during the 1970s, authors such as Newlands [11,12] and Francke [13] totally ignored the existence of the Malagasy species *Opisthacanthus madagascariensis* described by Kraepelin, 1894 and the fact that this last species presents more morphological traits in common with American than African species. At the time of their analysis, *O. madagascariensis* was the only species described in the genus. Subsequently, in 1995, Lourenço [15] confirmed the model of a single Gondwanian genus, *Opisthacanthus*, but with two subgenera *Opisthacanthus* for the American species including also one species from Occidental Africa, *Opisthacanthus lecomtei* (Lucas, 1858) and *Nepabellus* Francke, 1974 for the other African species. The ever growing knowledge on the Malagasy scorpion fauna [16] led to the creation of a third subgenus for the Malagasy species of *Opisthacanthus*: *Monodopisthacanthus* Lourenço, 2001 [17].

One important question can however be addressed concerning the real phylogenetic affinities of the three different lineages defined at present. One group, *Opisthacanthus*, is clearly defined for the American species,

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