

New taxonomic considerations on the genus *Tityobuthus* Pocock, 1890, and description of a new species (Scorpiones, Buthidae)

Wilson R. LOURENÇO¹, Patrick O. WAEBER² & Lucienne WILME³

¹ Muséum national d'Histoire naturelle, Sorbonne Universités, Institut de Systématique, Évolution, Biodiversité (ISYEB), UMR7205-CNRS, MNHN, UPMC, EPHE, CP 53, 57 rue Cuvier, F – 75005 Paris, France
<wilson.lourenco@mnhn.fr>

² ETH Zurich, Department of ITES, Forest Management and Development (ForDev) Group,
Universitätstrasse 16, CH – 8092 Zurich, Suisse <patrick.waerber@usys.ethz.ch>

³ Missouri Botanical Garden, Madagascar Research & Conservation Program, BP 3391,
Antananarivo 101, Madagascar <lucienne.wilme@mobot-mg.org>

<http://zoobank.org/2C55465F-85B5-4D48-A1D4-C3933183024B>

(Accepté le 28.X.2020 ; publié le 10.XII.2020)

Abstract. – Some new taxonomic considerations are proposed for *Tityobuthus* Pocock, 1890, a Malagasy genus of the Ananterinae subfamily (*sensu* Pocock). *Tityobuthus* elements are only present in Madagascar, but the group does belong to a lineage representing a typical Gondwanian distribution. The number of known *Tityobuthus* species rose considerably in the last 25 years but most are rarely collected and only known from very few or even a single individual. The reanalysis of certain morphological traits of *Tityobuthus* species suggests the existence of two possible taxonomic groups within the genus, one comprising species with short chelae and another with long chelae. One new species, *Tityobuthus orangea* n. sp., is also described from a cave located in the reserve of Orangea in the North of Madagascar. The new species is a possible endemic element to this cave in Orangea.

Résumé. – **Nouvelles considérations taxonomiques pour le genre *Tityobuthus* Pocock, 1890, et description d'une nouvelle espèce (Scorpiones, Buthidae).** De nouvelles considérations taxonomiques sont proposées pour *Tityobuthus* Pocock, 1890, genre malgache de la sous-famille des Ananterinae (*sensu* Pocock). Les éléments appartenant à *Tityobuthus* ne sont rencontrés qu'à Madagascar, mais le groupe appartient à une lignée montrant typiquement une distribution gondwanienne. Le nombre connu d'espèces de *Tityobuthus* a considérablement augmenté au cours des 25 dernières années, mais la plupart sont rarement collectées et ne sont connues que de très peu ou même d'un seul individu. La réanalyse de certains traits morphologiques des espèces de *Tityobuthus* suggère l'existence de deux groupes taxonomiques possibles au sein du genre, l'un comprenant des espèces à pinces courtes et un autre à pinces longues. Une nouvelle espèce, *Tityobuthus orangea* n. sp., est également décrite d'une grotte située dans la réserve d'Orangea au nord de Madagascar. La nouvelle espèce est un élément endémique possible de cette grotte d'Orangea.

Keywords. – Madagascar, Ananterinae, taxonomy, morphology, cave, new species.

As already outlined in previous publications (LOURENÇO *et al.*, 2016, 2018), the genus *Tityobuthus* appears as a particular element among the scorpion groups found in Madagascar. As most of the Malagasy scorpion genera, it is an endemic element to the island. Nevertheless, *Tityobuthus* has a close relationship with other genera of the Ananterinae subfamily *sensu* Pocock (LOURENÇO, 2011), which are present in quite distinct geographical regions of the world, such as the genera *Ananteris* Thorell, 1891, a typical element of the Neotropical scorpion fauna, *Lychasioides* Vachon, 1974, distributed in Western Africa or *Himalayotityobuthus* Lourenço, 1997, only known from the Himalayan mountains of Nepal and India (LOURENÇO *et al.*, 2016). In all cases, these Ananterinae elements appear as peculiar among the other buthid groups also

present in these distinct regions. It is also noticeable to remark that some Ananterinae elements have also been recorded and described from Cenozoic fossil amber, found in Samland Peninsula, Baltic Coast (LOURENÇO, 2009).

The genus *Tityobuthus* was established by Pocock (1893) for *Rhoptrurus baroni* Pocock, 1890. *Rhoptrurus* Karsch, 1886, was introduced as a new replacement name for *Odonturus* Karsch, 1879, which was believed to be a homonym of *Odontura* Rambur, 1841 (Orthoptera). These two names are not however homonyms. Subsequently, Pocock (1893) synonymized *Rhoptrurus* Karsch, 1886, with *Odonturus* Karsch, 1879. In the following publications (e.g. Fage, 1946: 256), the species *baroni* was cited both under *Tityobuthus* and *Odonturus*, and this confusion remained until the revision by Vachon (1980), who finally included only two species in the genus *Tityobuthus*: *Tityobuthus baroni* (Pocock, 1890) and *T. gracilis* (Fage, 1946). The latter was originally described in the genus *Babycurus* Karsch, 1886. *T. gracilis* was finally accommodated in its own genus by Lourenço (2000) as *Troglotityobuthus gracilis*. Subsequently, several other species of *Tityobuthus* have been described from the island (LOURENÇO *et al.*, 2016, 2018).

In this study, we bring new insights about some morphological characteristics presented by the species of the genus *Tityobuthus*. We further describe one new species from a cave located in the region of Orangea in the North of Madagascar, attesting to the high levels of diversity presented by this genus on the island. For further details on the taxonomy and biogeography of Ananterinae elements readers can refer to Lourenço *et al.* (2016).

METHODS

Illustrations and measurements were produced using a Wild M5 stereomicroscope with a drawing tube and an ocular micrometre. Measurements follow Stahnke (1970) and are given in mm. Trichobothrial notations follow Vachon (1974) and morphological terminology mostly follows Vachon (1952) and Hjelle (1990).

RESULTS

CHELAE MORPHOMETRIC VALUES IN *TITYOBUTHUS* SPECIES

AND DEFINITION OF TWO POSSIBLE INFORMAL TAXONOMIC GROUPS WITHIN THE GENUS

Until the middle of the 1990s, the genus *Tityobuthus* was represented by only two species, *T. baroni* and *T. gracilis*. Starting with the contribution by Lourenço (1995), the total number of species knew a major growing to reach 20 species at present. Meanwhile, *T. gracilis* was transferred to a distinct genus *Troglotityobuthus* (LOURENÇO, 2000). Although the number of contributions to the genus *Tityobuthus* was significant, no previous attention was paid to the possible existence of species-groups within the genus. A recent analysis of all described species of *Tityobuthus* suggested the possible existence of two distinct species-groups: one composed by species with short chelae and the other by species with long chelae. The ratio of chela length vs chela width indicates species with values inferior to 6.0 and others with values superior to 6.0 (fig. 1). Naturally, the samples used in the analysis, composed mainly of the type material of the known species, are in many cases weak, since most species are rarely collected and only known by very few individuals and in some cases by a single sex. Nevertheless, the observed existence of two possible species-groups seems to be clear. Moreover, the totality of the species belonging to the group with long chelae are distributed in the northern range of the island (fig. 2). The analysis of more important samples should confirm the existence of the two suggested species-groups, and identify the limit between the two groups.

Species-groups within several buthid genera are not uncommon. Several characters have been used to define these groups. In the case of variation of chela dimensions, this can be observed in genera such as *Androctonus* Ehrenberg, 1828, *Isometrus* Ehrenberg, 1828, or *Lychas* Koch, 1845. Nevertheless, the most expressive variation for this character is found in the genus *Tityus* Koch, 1836. For this extremely speciose genus with more than 220 known species, an impressive number of species-groups was suggested (MELLO-LEITÃO, 1945; LOURENÇO, 2006). Several of these groups were finally assumed in a more formal way and defined as subgenera (LOURENÇO, 2006). This should not be the case for *Tityobuthus* and the possible defined species-groups should remain informal.

The evolutionary meaning of this variation is not always clear. Size and length of chelae should normally be associated with foraging behaviour, but in a number of cases, it is observed as a typical sexual dimorphism strongly expressed in some species of *Tityus* such as *Tityus vaissadei* Lourenço, 2002, from Colombia (LOURENÇO, 2002). Adaptation to cave life also implies elongation of appendages. The new species described here was found in a cave and belongs to the species-group with long chelae. However, *Tityobuthus ivohibe* was also found in a cave (LOURENÇO & WILMÉ, 2019), but this species is to be placed in the species-group with short chelae. *T. lokobe* found in the rain forest of the north-western satellite island Nosy Be shows the greatest value of the ratio length/width of chela, followed by the two species located on the extreme north of the island *T. rakotondravonyi*, and the cave dwelling *T. orangea* n. sp. (fig. 1-2).

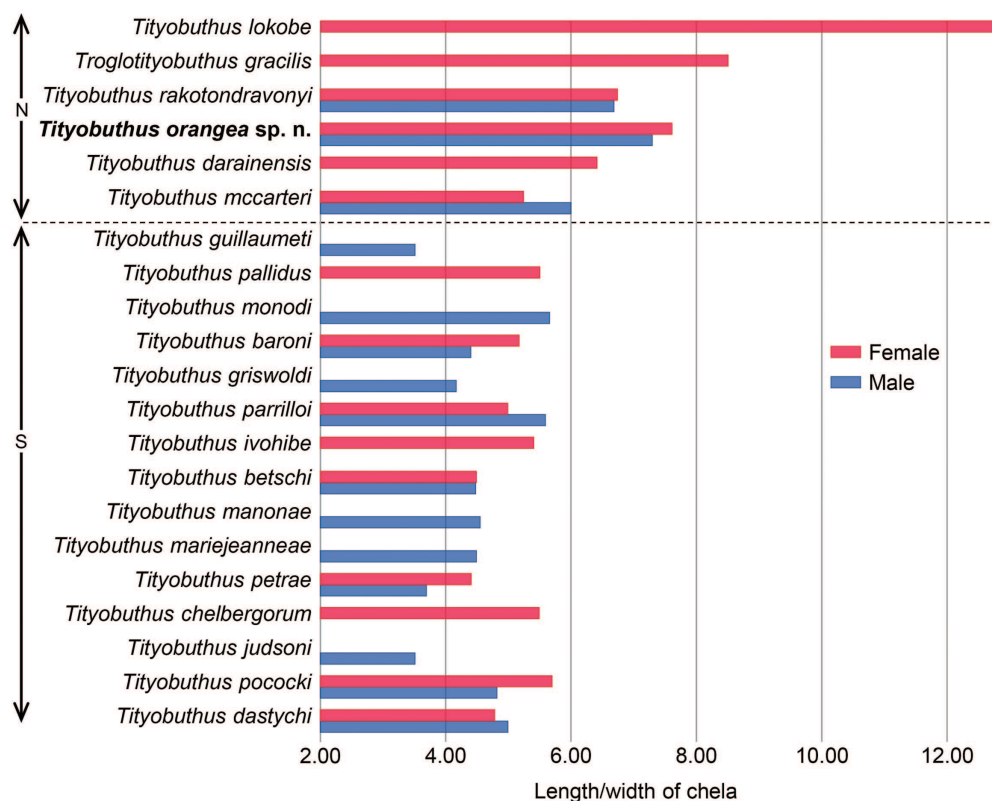


Fig. 1. – Distribution of the two groups of *Tityobuthus* according to the ratio of length/width of their chela, and the position of *Troglotityobuthus gracilis* in the Northern group.

CHECKLIST FOR SPECIES OF *TITYOBUTHUS* KNOWN FROM MADAGASCAR

For details on geographical distribution, refer to LOURENÇO *et al.* (2016).

Family **Buthidae** Koch, 1837Subfamily **Ananterinae** Pocock, 1900Genus ***Tityobuthus*** Pocock, 1890

Tityobuthus baroni (Pocock, 1890)

T. pococki Lourenço, 1995

T. guillaumeti Lourenço, 1995

T. judsoni Lourenço, 1996

T. parrilloi Lourenço, 1996

T. petrae Lourenço, 1996

T. dastychi Lourenço, 1997

T. ivohibe Lourenço & Goodman, 1999

T. manonae Lourenço, 2000

T. griswoldi Lourenço, 2000

T. monodi Lourenço, 2000

T. darainensis Lourenço & Goodman, 2002

T. rakotondravonyi Lourenço & Goodman, 2003

T. pallidus Lourenço, 2004

T. mccarteri Lourenço, Qi & Goodman, 2008

T. betschi Lourenço, Qi & Goodman, 2008

T. chelbergorum Lourenço, Qi & Goodman, 2008

T. lokobe Lourenço, Waeber & Wilmé, 2016

T. mariejeanneae Lourenço, Waeber & Wilmé, 2018

T. orangea n. sp.

TAXONOMIC TREATMENT

***Tityobuthus orangea* n. sp.** (fig. 3-11)

<http://zoobank.org/A3644248-500D-4322-9E93-B2129408B868>

HOLOTYPE: ♀, Madagascar, Orangea, Grotte des Pintades, XII.1946, *J. Millot leg.*, deep inside the cave (MNHN-RS-1430).

PARATYPES: 1 ♂ and 11 first instar juveniles, *idem* holotype (MNHN-RS-1430).

Type locality. – The cave's entrance is located at 49°22'00"E 12°14'18"S, at an altitude of ~ 30 m.

Diagnosis. – Scorpion of moderate size, with respect to the genus, and with 37.1 and 32.5 mm in total length for female and male respectively. General colouration pale yellow throughout, both the body and the appendages with some marbled zones on the carapace and tergites of male. Carapace with a moderate to strong concavity. Pectines large and less separate than in other species with 16 or 17 teeth in both sexes; fulcra moderately marked. Telson moderately elongated, with a short and curved aculeus; subaculear tooth strong and slightly spinoid, with two subaculear granules; presence of an important setation all over the telson. Internal face of patella with 12 - 13 spinoid granules. Tibial spurs moderate to strong on leg IV, reduced on leg III. Pedipalp fixed and movable fingers with 8-8 slightly oblique rows of granules. Trichobothrial pattern of type A-α (alpha) – orthobothriotaxic.

Description. – **Colouration.** Ground colour yellow throughout the body and appendages. Carapace yellowish without spots; only some vestigial marbled zones are present; eyes surrounded by black pigment. Mesosoma yellow, with tergites slightly marbled on male. Metasomal segments I to V yellow; all segments without spots; telson yellow with the aculeus slightly reddish. Venter yellow to pale yellow; pectines and genital operculum whitish. Chelicerae pale yellow without any pigmentation; fingers pale yellow with reddish teeth. Pedipalps pale yellow, without any spots; series of granulations on fingers slightly reddish. Legs pale yellow without spots.

Carapace weakly to moderately granular; anterior margin with a moderately to strongly pronounced median concavity. Anterior median and posterior median carinae weak to obsolete; furrows moderate to weak. Median ocular tubercle distinctly anterior to the centre of the carapace; median eyes large, separated by about one ocular diameter. Three pairs of lateral eyes. Sternum subtriangular.

Mesosoma. Tergites moderately granular. Median carina moderate to weak on all tergites; absence of other carinae. Tergite VII pentacarinat.

Venter. Genital operculum divided longitudinally, each half being semi-oval in shape. Pectines large; pectinal tooth count 16-16 for female holotype and male paratype (variation on juvenile paratypes 16(19) and 17(3); basal middle lamellae not dilated; fulcra present and conspicuous. Sternites smooth, excepted for VII, which shows some minute granulations; spiracles small and elongate.

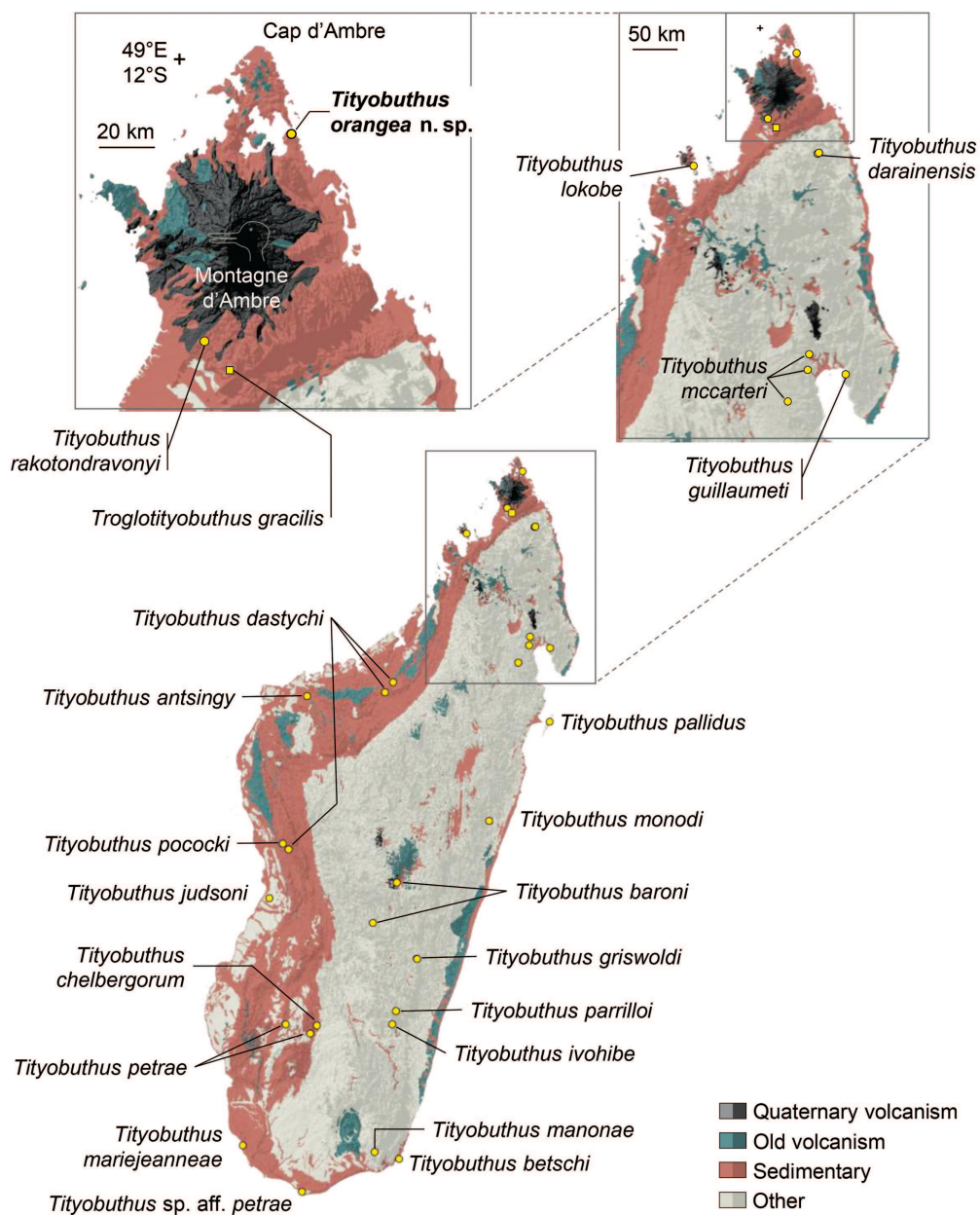


Fig. 2. – Distribution the *Tityobuthus* species and *Trogloityobuthus gracilis* according to lithology and volcanism. (The localities of the species belonging to the northern group are detailed on the insets on the right).

Metasomal segments I to III with 10 carinae, crenulate; segment IV with eight carinae, crenulate. Intercarinal spaces weakly granular. Segment V rounded, with five weak carinae and weakly granular.

Telson with a pear-like shape and completely smooth; presence of a strong setation; aculeus moderately curved; subaculear tooth strong and mainly spinoid with two basal granules. Cheliceral dentition characteristic

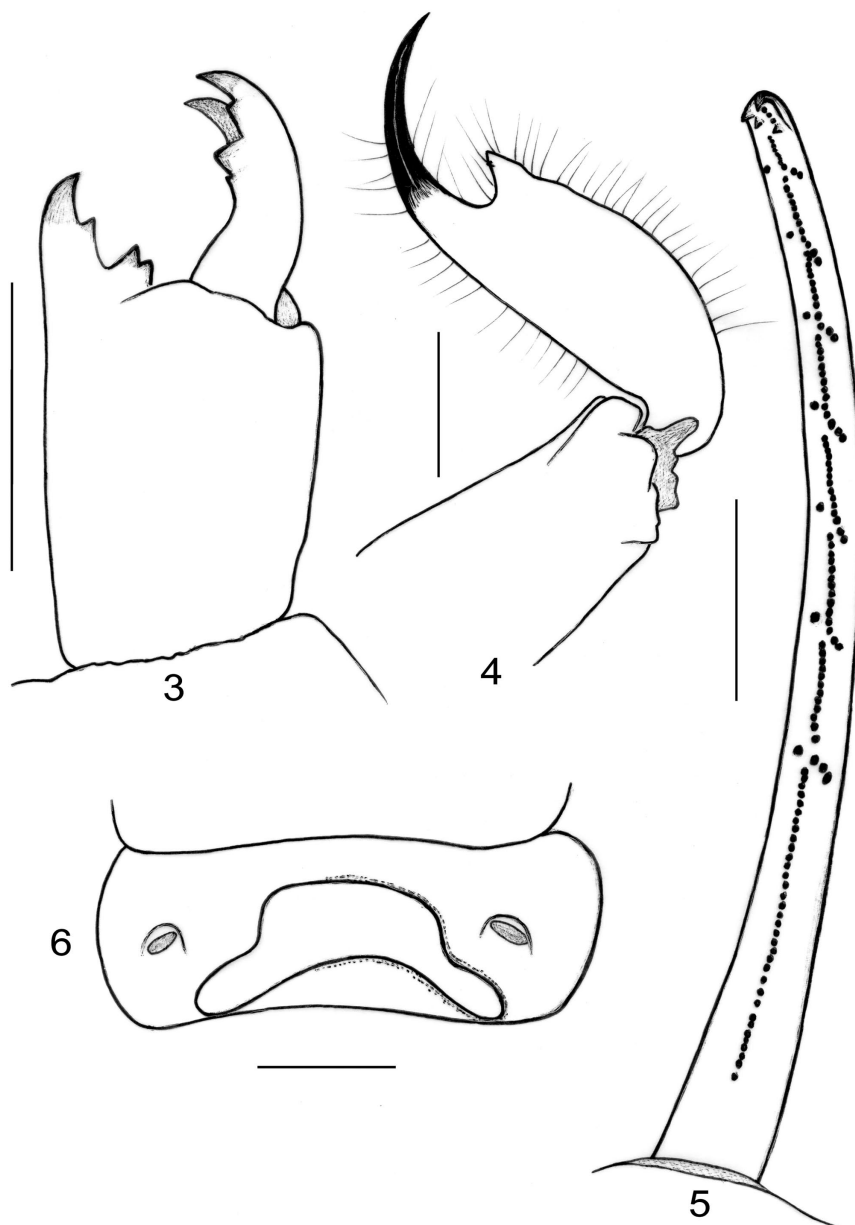


Fig. 3-6. – *Tityobuthus orangea* n. sp. – 3-5, Female holotype: 3, chelicera, dorsal aspect; 4, metasomal segment V and telson, lateral aspect; 5, cutting edge of movable finger, with rows of granules. – 6, Male paratype, sternite V showing the presence of the conspicuous white zone. Scale bars = 1 mm.

of the family Buthidae (VACHON, 1963); basal teeth of movable fingers not reduced but fused; ventral surfaces of finger and manus with long setae.

Pedipalps. Femur pentacarinat and crenulate; patella with some carinae, weakly crenulate; chela rounded and smooth; internal face of patella with 12-13 spinoid granules; all faces weakly granular; fixed and movable fingers with 8-8 almost linear rows of granules.

Trichobothriotaxy. Orthobothriotaxy A- α (alpha) (VACHON, 1974, 1975). **Legs:** tarsus with numerous fine median setae ventrally. Pedal spurs moderate; tibial spurs moderate on leg IV, reduced on leg III.

Morphometric values (in mm) of female holotype and male paratype. – Total length (including telson) 37.10/32.50. Carapace: length 4.20/3.80; anterior width 2.90/2.60; posterior width 4.30/4.10. Mesosoma length 11.40/8.60. Metasomal segment I: length 2.50/2.40, width 2.10/2.00; II: length 3.00/2.80, width 1.90/1.80; III: length 3.30/3.10, width 1.80/1.70; IV: length 3.80/3.50, width 1.70/1.60; V: length 4.90/4.50, width 1.70/1.50, depth 1.80/1.60. Telson length 4.00/3.80. Vesicle: width 1.10/1.10, depth

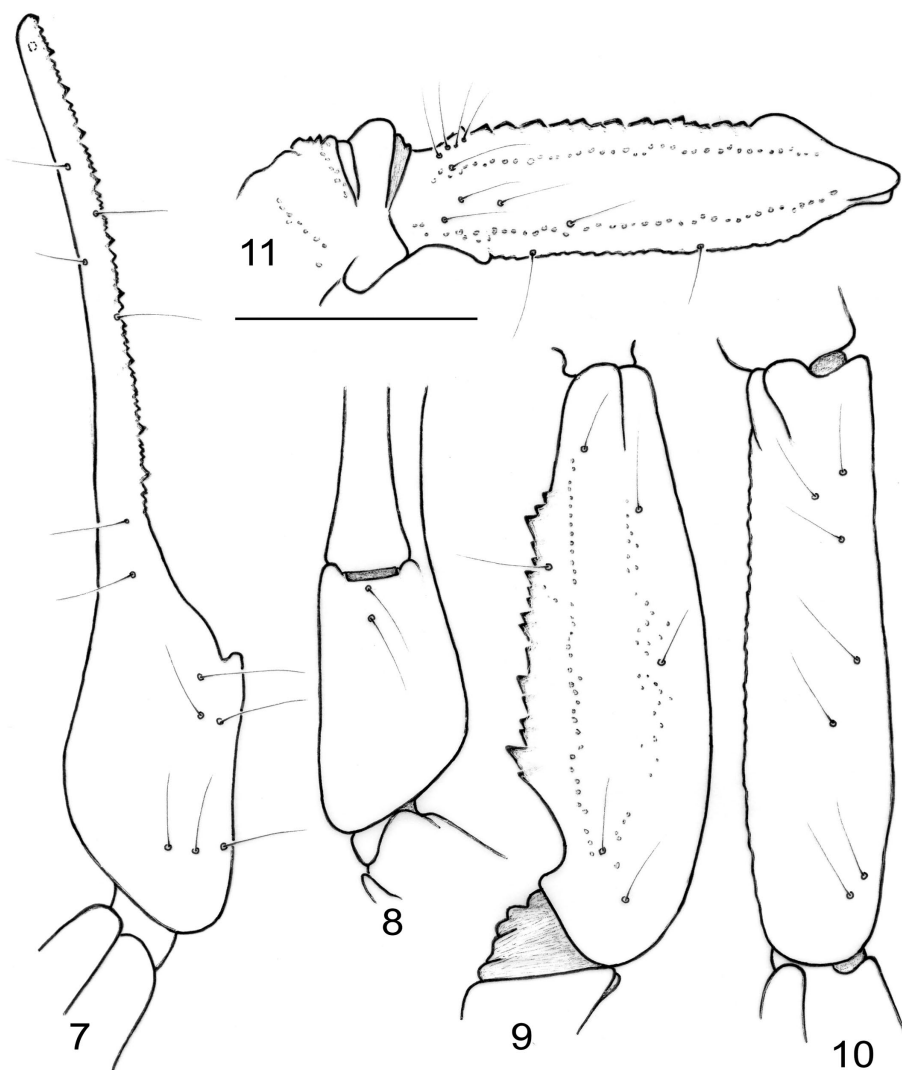


Fig. 7-11. – *Tityobuthus orangea* n. sp., female holotype, trichobothrial pattern. – 7-8, Chela dorso-external and ventral aspects. – 9-10, Patella, dorsal and external aspects. – 11, Femur, dorsal aspect. Scale bar = 2 mm.

1.20/1.20. Pedipalps: femur length 4.20/3.90, width 1.10/1.00; patella length 5.00/4.70, width 1.60/1.40; chela length 8.00/7.30, width 1.05/1.00, depth 1.00/1.00; movable finger length 5.60/5.40 (average size of juveniles 13 to 14 mm).

Etymology. – The specific epithet is a noun in apposition to the generic name and refers to the locality where the new species was collected.

Relationships. – The general morphology of the new species recalls that of *Tityobuthus lokobe* described from the rainforest of Lokobe, Nosy-Be Island. To be noticed is that the original sites where the two species were found are located in the extreme north of Madagascar. The two species can however be distinguished by a number of features:

- both species show distinct morphometric values and the ratio chela length vs width is different (fig. 1);
- the new species shows a paler general pattern of coloration almost without any pigments;
- the new species has much more conspicuous fulcra in the pectines, whereas in *T. lokobe* these are vestigial;
- in the new species, tibial spurs are moderate to strong, whereas these are reduced on *T. lokobe*;
- in the new species, the anterior margin of carapace shows a strong concavity;
- in the new species, the internal face of patella has 12-13 spinoid granules, whereas in *T. lokobe* these are only 9-10;
- setation in telson is markedly important in the new species.

Moreover, the microhabitat of both species is distinct since the new species was collected inside a cave, whereas *T. lokobe* was collected in a dense rainforest.

DISCUSSION AND CONCLUSION

Tityobuthus orangea n. sp. is encountered in one of the most arid regions of Madagascar. The region is known to experience the “*climat local de Diégo-Suarez*” which is a local climate characterized by high mean annual temperatures (> 20°C) and high climatic hydric deficit (> 1200 mm per year) —mean annual precipitations minus potential evapotranspiration (CORNET, 1974). The Grotte des Pintades is situated some 500 meters from the shoreline of the Indian Ocean with its entrance at 30 m.a.s.l. (fig. 2). It is a deep cave with an exit at the shoreline (L. J. Razafitsalama, pers. comm.). This cave is part of the karstic system of northern Madagascar, with stable temperatures as compared to the daily variable temperatures outside, and high hygrometry given the presence of a perennial stream going through the cave (fig. 12). Renaud Paulian collected invertebrates and bats in March 1948 from the Grotte des Pintades. The cave is currently encompassed in the Oranjia Park, a protected area of category IUCN V, and is managed by the Missouri Botanical Garden (<http://mobot.mg/conservation/oranjia/>). The vegetation of the park —growing mainly on sand— constitutes a dry forest of low stature. The type specimens of *Tityobuthus orangea* n. sp. have been collected deep into the Grotte des Pintades.

The geomorphology of the extreme north of the island is characterized by sedimentary series shaped in limestone layers, partially covered by the Montagne d’Ambre volcanism since the Miocene (12.1-0.83 Ma) and more recently during the Pleistocene (EMERICK & DUNCAN, 1982; CUCCINIELLO *et al.*, 2011). The volcanic activity continued during the upper Quaternary, making one of the most tectonically unstable regions of the island during recent geological times. The Orangea Peninsula lies to the northeast of the Montagne d’Ambre (fig. 2). While Madagascar is considered tectonically stable —due to its very slow migration eastwards relative to Africa— coastal rims in the southwest and extreme north show recent dynamic topography,

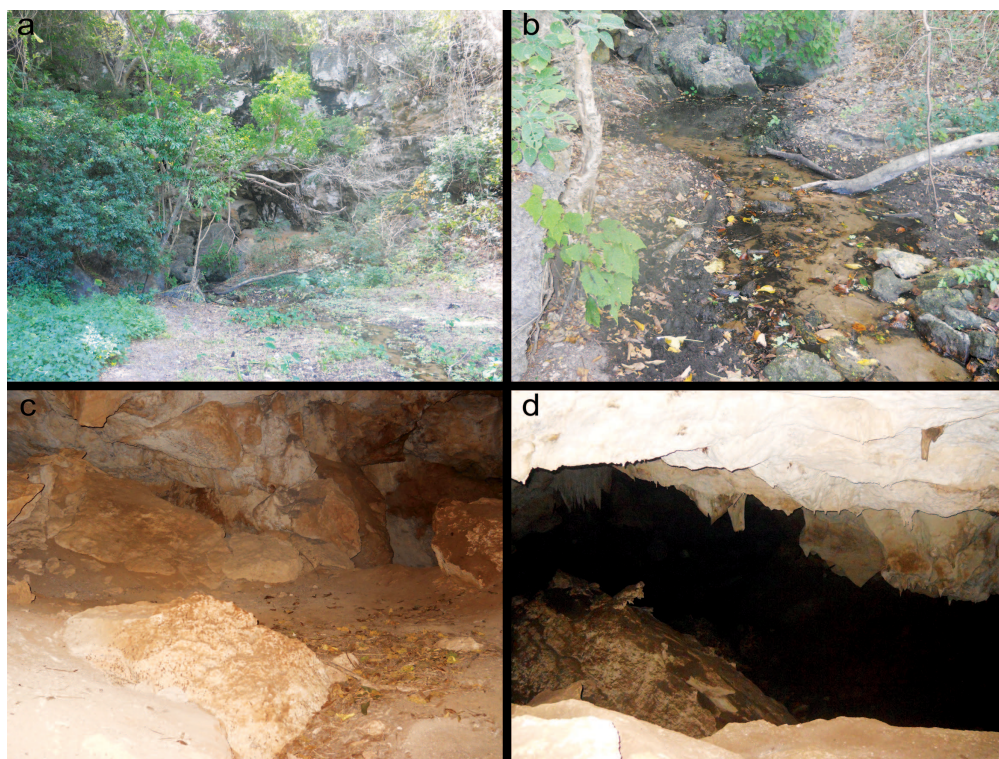


Fig. 12. – Grotte des Pintades : **a**, degraded dry deciduous forest in the vicinity of the cave entrance; **b**, small perennial stream near the entrance; **c**, inside the cave, shortly after the entrance with vegetation debris; **d**, deep in the cave, which probably is the habitat of the new species. (Photos by J. L. Veny, T. Hafany, D. Randriamahazomanana, N. S. Amady).

with uplifted margins (BATTISTINI, 1965a, b; STEPHENSON *et al.*, 2019). The Orangea Peninsula exhibits an upper terrace along the coastline of coarse sandstone and corals at an altitude of 6.6 m of LIG age —Last Inter-Glacial, commonly understood as an interval with climate as warm or warmer than today, 128,000-116,000 years ago (KUKLA *et al.*, 2002)— *i.e.*, the land has been uplifted by 6.6 meters over some 100,000 years —maximum of 9.3 m at Cap d’Ambre (fig. 2). An upper terrace, 600 m to the north-north-east of the entrance of the Grotte des Pintades, at Cap Miné, has an elevation of 29.5 m and is followed inland by a peneplaine, where the entrance of the Grotte des Pintades is situated. The peneplaine has been proposed as representing Middle Pliocene sea level —3.6 Ma. The top 5-10 m of this deposit have been altered to red laterite (STEPHENSON *et al.*, 2019).

TITYOBUTHUS RANGE

The majority of the members of the genus *Tityobuthus* are encountered in lowland humid forests, with an elevation range from sea level to 900 m a.s.l. where there is no hydric deficit and mean annual precipitation can be up to 4,000 mm. Few species of *Tityobuthus* are encountered in the subarid bioclimate of southern and south-western Madagascar (fig. 2). In the subarid southwest with its spiny forests and thickets, a single species has been collected in a region of spiny forest on red sand, *Tityobuthus mariejeanneae* Lourenço, Waeber & Wilmé, 2018. The only other spiny forest hosting the genus is in the small reserve of Cap Sainte-Marie, a hotspot of diversity for scorpions both at species and generic levels (LOURENÇO *et al.*, 2020). Scorpions

usually show patchy distributions, a common feature encountered in Madagascar for the group and already shown for the species in the genus *Tityobuthus*. *Tityobuthus orangea* n. sp. is assumed to be endemic from Grotte des Pintades, Orangea, given:

- the characteristics of the type locality;
- the stable micro-climate in a subarid region of extreme northern Madagascar;
- the dramatic changes through which the Orangea peninsula together with its cave system have gone through over the last three to four million years, and also more recently since the last inter-glacial age.

The species of *Tityobuthus* encountered in extreme northern Madagascar exhibit long chela and have patchy distributions in humid or subhumid forests, and caves in drier bioclimates. New discoveries of species in the genus *Tityobuthus* are needed to better define the Northern group, and to assess the cave dwelling of some of the species, and its possible relation with the chelae size.

ACKNOWLEDGEMENTS. – We are most grateful to Jean-Luc Veny, Tombondray Hafany, Daniel Randriamahazomanana, Nasser Said Amady, patrollers in the Reserve Oranjia for collecting and reporting field information about the Grotte des Pintades, and Lalao Jeremi “Jimmy” Razafitsalama, Missouri Botanical Garden, for organizing the team, photos and compilation of the information.

REFERENCES

- BATTISTINI R., 1965a. – Problèmes géomorphologiques de l'extrême Nord de Madagascar. *Revue de Géographie*, **7** : 1-61.
- BATTISTINI R., 1965b. – Le Quaternaire littoral de l'extrême nord de Madagascar. *Bulletin de l'Association Française pour l'Étude du Quaternaire*, **2** (2) : 133-144. <https://doi.org/10.3406/quate.1965.991>
- CORNET A., 1974. – *Essai de cartographie bioclimatique à Madagascar. Notice explicative N° 55*. Paris : ORSTOM, 28 p.
- CUCCINIELLO C., MELLUSO L., MORRA V., STOREY M., ROCCO I., FRANCIOSI L., GRIFA C., PETRONE C. M. & VINCENT M., 2011. – New ⁴⁰Ar-³⁹Ar ages and petrogenesis of a tholeiitic to strongly alkaline volcanic complex: the Massif d'Ambre, Northern Madagascar. *Geological Society of America Special Papers*, **478** : 257-282. [https://doi.org/10.1130/2011.2478\(14\)](https://doi.org/10.1130/2011.2478(14))
- EMERICK C. M. & DUNCAN R. A., 1982. – Age progressive volcanism in the Comores Archipelago, western Indian Ocean and implications for Somali plate tectonics. *Earth and Planetary Science Letters*, **60** : 415-428. [https://doi.org/10.1016/0012-821X\(82\)90077-2](https://doi.org/10.1016/0012-821X(82)90077-2)
- FAGE L., 1946. – Complément à la faune des Arachnides de Madagascar. *Bulletin du Muséum national d'Histoire naturelle*, (2) **18** : 256-267.
- HJELLE J. T., 1990. – Anatomy and morphology (p. 9-63) In : Polis G. A. (éd.), *The Biology of Scorpions*. Stanford Univ. Press, xxvi + 587 p.
- KUKLA G. J., BENDER M. L., DE BEAULIEU J.-L., BOND G., BROECKER W. S., CLEVERINGA P., GAVIN J. E., HERBERT T. D., IMBRIE J., JOUZEL J., KEIGWIN L. D., KNUDSEN K.-L., McMANUS J. F., MERKT J., MUHS D. R., MÜLLER M., POORE R. Z., PORTER S. C., SERET G., SHACKLETON N. J., TURNER C., TZEDAKIS P. C. & WINOGRAD I. J., 2002. – Last interglacial climates. *Quaternary Research*, **58** : 2-13. <https://doi.org/10.1006/qres.2001.2316>
- LOURENÇO W. R., 1995. – Description de trois nouveaux genres et de quatre nouvelles espèces de scorpions Buthidae de Madagascar. *Bulletin du Muséum national d'Histoire naturelle, Paris*, (4) **17** : 95-106.
- LOURENÇO W. R., 2000. – More about the Buthoidea of Madagascar, with special references to the genus *Tityobuthus* Pocock (Scorpiones, Buthidae). *Revue Suisse de Zoologie*, **107** : 721-736. <https://doi.org/10.5962/bhl.part.80145>
- LOURENÇO W. R., 2002. – Nouvelles additions à la faune de scorpions néotropicaux (Arachnida). *Revue Suisse de Zoologie*, **109** : 127-141. <https://doi.org/10.5962/bhl.part.79582>
- LOURENÇO W. R., 2006. – Nouvelle proposition de découpage sous-générique du genre *Tityus* C. L. Koch, 1836 (Scorpiones, Buthidae). *Boletín de la Sociedad Entomológica Aragonesa*, **39** : 55-67.

- LOURENÇO W. R., 2009. – A synopsis of the amber scorpions, with special reference to the Baltic fauna. *Denisia*, **26**, *Zugleich Kataloge der oberösterreichischen Landermuseen*, (N. S.) **86** : 131-136.
- LOURENÇO W. R., 2011. – The 'Ananteris group' (Scorpiones: Buthidae); suggested composition and possible links with other buthids. *Boletín de la Sociedad Entomológica Aragonesa*, **48** : 105-113.
- LOURENÇO W. R., ROSSI A., WILMÉ L., RAHERILALAO M. J., SOARIMALALA V. & WAEBER P. O., 2020. – The remarkable diversity of the genus *Grosphus* Simon, 1880 (Scorpiones: Buthidae) in Southern Madagascar and in particular in the region of Cap Sainte Marie. *Arachnida – Rivista Aracnologica Italiana*, **27** : 2-35.
- LOURENÇO W. R., WAEBER P. O. & WILMÉ L., 2016. – The geographical pattern of distribution of the genus *Tityobuthus* Pocock, 1890, a typical Ananterinae element endemic to Madagascar (Scorpiones: Buthidae). *Comptes Rendus Biologies*, **339** : 427-436. <https://doi.org/10.1016/j.crv.2016.06.003>
- LOURENÇO W. R., WAEBER P. O. & WILMÉ L., 2018. – One more new species of *Tityobuthus* Pocock, 1890 (Scorpiones: Buthidae) from the SW of Madagascar with comments on the distributions of associated species. *Arachnida – Rivista Aracnologica Italiana*, **18** : 15-25.
- LOURENÇO W. R. & WILMÉ L., 2019. – Scorpions from the Parc National du Tsingy de Namoroka, Madagascar and description of a new species of *Opisthacanthus* Peters, 1861 (Scorpiones: Hormuridae). *Revista Ibérica de Aracnologia*, **34** : 13-20.
- MELLO-LEITÃO C., 1945. – Escorpiões Sul-Americanos. *Arquivos do Museu Nacional, Rio de Janeiro*, **40** : 468 p.
- POCOCK R. I., 1893. – Notes on the classification of scorpions, followed by some observations on synonymy, with descriptions of new genera and species. *Annals and Magazine of Natural History*, **12** : 303-330. <https://doi.org/10.1080/00222939308677626>
- STAHNKE H. L., 1970. – Scorpion nomenclature and mensuration. *Entomological News*, **81** : 297-316.
- STEPHENSON S. N., WHITE N. J., LI T. & ROBINSON L. F., 2019. – Disentangling interglacial sea level and global dynamic topography: Analysis of Madagascar. *Earth and Planetary Science Letters*, **519** : 61-69. <https://doi.org/10.1016/j.epsl.2019.04.029>
- VACHON M., 1952. – *Études sur les scorpions*. Alger : Publications de l'Institut Pasteur d'Algérie, 482 p.
- VACHON M., 1963. – De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les Scorpions, *Bulletin du Muséum national d'Histoire naturelle*, **35** : 161-166.
- VACHON M., 1974. – 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. *Bulletin du Muséum national d'Histoire naturelle*, (3) **140** : 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. *Comptes Rendus de l'Académie des Sciences, Paris*, (D) **281** : 1597-1599.
- VACHON M., 1980. – Remarques biogéographiques sur la faune des Scorpions de Madagascar à propos de l'utilisation de caractères trichobothriotaxiques permettant la distinction des genres *Odonturus* Karsch, 1879 et *Tityobuthus* Pocock, 1893 (p. 217-224). In : *Comptes Rendus du 5^e Colloque d'Aracnologie d'Expression française*, 1979. Barcelone : Ediciones de la Universidad de Barcelona.