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The geographical pattern of distribution of the genus *Tityobuthus* Pocock, 1890, a typical Ananterinae element endemic to Madagascar (Scorpiones: Buthidae)



Schéma de distribution géographique du genre Tityobuthus Pocock, 1890, Ananterinae endémique typique de Madagascar (Scorpiones: Buthidae)

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ABSTRACT

New comments are proposed for the Ananterinae (sensu Pocock) or the '*Ananteris* Group'. The worldwide pattern of distribution of the elements associated with the Ananterinae, as well as aspects of their ecology, is discussed. The biogeographic patterns presented by extant and fossil elements of this group confirm not only the characteristics of a lineage representing a typical Gondwanian distribution, but correspond also to older Pangean patterns. One new species is described in the genus *Tityobuthus* Pocock. This new species is also a possible endemic element to the Island of Nosy-Be or at least to the Sambirano region. Generally, the Madagascar pattern of *Tityobuthus* is following the *Neogrosphus* rule, showing typical high species richness with low dispersal when the ancestral population had a large niche breadth.

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R É S U M É

De nouvelles considérations sur les Ananterinae (sensu Pocock) ou le « groupe *Ananteris* » sont proposées. Le modèle très élargi de distribution des éléments associés aux Ananterinae, ainsi que des aspects de leur écologie, sont discutés. Les modèles biogéographiques présentés par des éléments, aussi bien fossiles que modernes, associés à ce groupe confirment non seulement les caractéristiques d'une lignée gondwanienne, mais aussi celles d'un groupe avec des traits datant de la Pangée. Une nouvelle espèce est décrite pour le genre *Tityobuthus* Pocock. Cette nouvelle espèce est également un possible élément endémique de l'île de Nosy-Be ou pour le moins de la région du Sambirano. Le genre *Tityobuthus* de Madagascar se conforme globalement à la « *Neogrosphus* rule » en

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montrant une richesse spécifique élevée, avec une dispersion limitée lorsque la niche de la population ancestrale était étendue.

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1. Introduction

The genus *Tityobuthus* appears as a particular element within the Malagasy scorpion fauna. Despite being an endemic element to Madagascar, *Tityobuthus* has a close relationship with other genera of the Ananterinae, or 'Ananteris Group' [1], which are only present in quite distinct geographical regions of the world. The most marked example is the genus *Ananteris* Thorell, 1891, an element of the Neotropical scorpion fauna, which, however, clearly appears as quite distinct from the other buthid elements of this fauna.

Tityobuthus was established by Pocock [2] for *Tityobuthus baroni* (Pocock, 1890) previously included in the genus *Rhoptrurus* Karsch, 1886, because this name was already preoccupied by that of a snake genus, *Rhoptrura* Peters, 1858 [3]. Confusion existed about the genera *Tityobuthus* Pocock, *Pseudobuthus* Pocock and *Odonturus* Karsch until they were revised by Vachon [3], who finally included only two species in the genus *Tityobuthus*: *Tityobuthus baroni* (Pocock, 1890) and *Tityobuthus 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 [4] as *Troglotityobuthus gracilis*. Subsequently, several other species of *Tityobuthus* have been described from the island [5].

In this current paper, we bring some new insights into the biogeographic patterns presented by the genus *Tityobuthus* in Madagascar. One new species is also described, attesting to the high levels of diversity

presented by this genus in Madagascar [5]. For further historical details about this genus and its increasing species richness, see Lourenço [5].

2. The Ananterinae or 'Ananteris Group'; history, composition and known distribution

As outlined in recent papers [1,6], the position of subfamilies within the family Buthidae has always been a controversial matter [7,8]. The subfamily Ananterinae was proposed by Pocock [9] to accommodate the genus *Ananteris* Thorell. Pocock wrote: 'I propose to eliminate from this subfamily (Buthinae) the isolated Neotropical genus *Ananteris*, which differs strikingly from the rest of the family in the structure of the pectines. The subfamily Ananterinae may be created for its reception'. Kraepelin [10] added Ananterinae, previously described by Pocock [9] and the Tityinae, within the Buthidae family. The definition of a subfamily Ananterinae, or of one 'Ananteris group', remains to be decided. For more details, see Lourenço [1,6].

A number of genera may be accommodated within the Ananterinae or 'Ananteris Group'. Some are strongly speciose, as *Ananteris*, *Tityobuthus* or *Lychas* C.L. Koch, and can be distributed over broad geographical ranges, whereas others may be represented by only one or two species such as *Lychasioides* Vachon or *Troglotityobuthus* Lourenço and are endemic to rather narrow ranges. The global extant distribution of the *Ananteris* group is tropical in South America, tropical and subtropical in Asia, Oceania

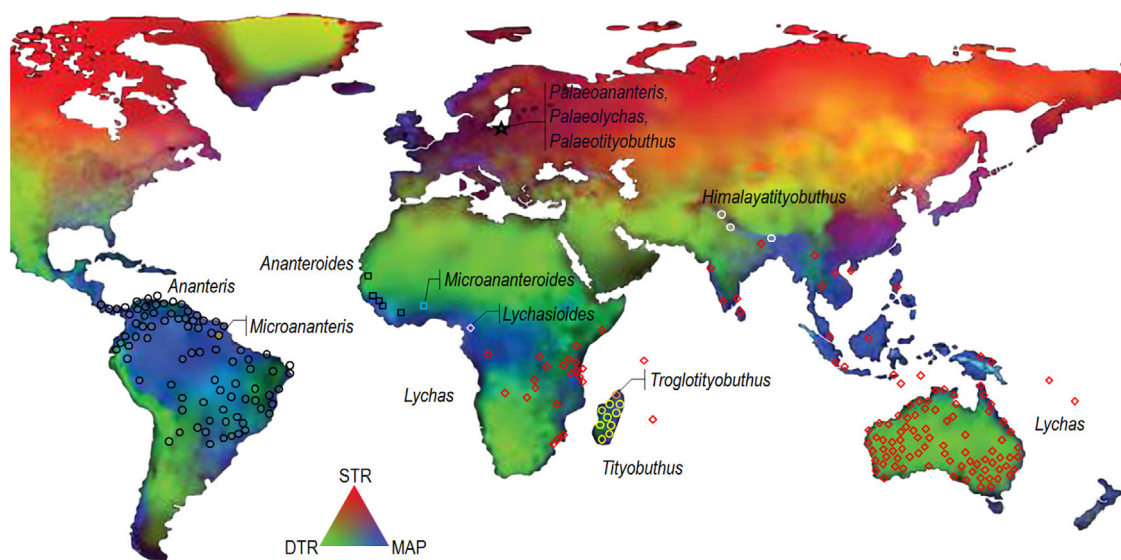


Fig. 1. Distribution of the nine genera in the *Ananteris* group, as well as the three fossil Cenozoic genera on the global map of climate variability modified from Chan et al. [11]. (STR: seasonal temperature range; MAP: mean annual precipitation; DTR: diurnal temperature range).

and Sub-Sahara Africa, in climatic conditions encompassing humid, dry and arid ones [11] (Fig. 1).

Ananteris Thorell, 1891 – Almost all the Neotropical region.

Ananteroides Borelli, 1911 – Africa; Guinea Bissau, Guinea, Ivory Coast, Mauritania, Sierra Leone.

Himalayotityobuthus Lourenço, 1997 – India and Nepal.

Lychas C.L. Koch, 1845 – Africa, India, Southeast Asia, Australia, Indian Ocean and Western Pacific Ocean islands.

Lychasioides Vachon, 1974 – Africa; Cameroun.

Microananteris Lourenço, 2003 – French Guiana.

Microananteroides Rossi & Lourenço, 2015 – Africa; Ghana.

Tityobuthus Pocock, 1893 – Madagascar.

Troglotityobuthus Lourenço, 2000 – Madagascar (cave species).

†*Palaeolychas* Lourenço & Weitschat, 1996 – Cenozoic fossil, Samland Peninsula, Baltic coast.

†*Palaeoananteris* Lourenço & Weitschat, 2001 – Cenozoic fossil, Samland Peninsula, Baltic coast.

†*Palaeotityobuthus* Lourenço & Weitschat, 2000 – Cenozoic fossil, Samland Peninsula, Baltic coast.

Among the several genera of Cenozoic fossil scorpions described from the Samland Peninsula along the Baltic coast (today Poland and Kaliningrad in Russia), most are related to the Ananterinae [12]. Some of these fossil specimens remain rather incomplete and their morphology cannot be globally known. Nevertheless, their affinities with the extant Ananterinae genera are well supported by a number of characters [12–15].

Several recent studies [4,5,16,17] attest that *Tityobuthus* shows closer affinities with the genus *Ananteris* than to the other Ananterinae genera. Another genus that shows affinities with *Tityobuthus* is *Himalayotityobuthus*, endemic to the Himalayas of India and Nepal [18]. The association of all these different genera within the subfamily Ananterinae clearly indicates a Gondwanian pattern of distribution for this undoubtedly ancient lineage of buthid scorpions. The discovery of the fossil elements from Baltic amber brought further evidence to support the biogeographic model of past distribution and the present observed pattern of distribution of the Ananterinae, which can be attributed to a model of panbiogeography [19,20].

It is interesting to notice that the genus *Lychas* is encountered in the Seychelles, on satellite islets of Mauritius in the Indian Ocean, and in Eastern and Southern Africa, but not in Madagascar. Most of the Seychelles, the so-called granitic Seychelles, were part of the Gondwana, while the coral portions are of much younger age [21]. Mauritius is a volcanic island. The endemic species only known from the satellite islets of Mauritius, Round Island and Gunner's Quoin, is extremely rare and currently of unknown affinities.

3. Methods

Illustrations and measurements were produced using a Wild M5 stereomicroscope with a drawing tube and an ocular micrometer. Measurements follow Stahnke [22] and

are given in millimetres. The trichobothrial notations follow Vachon [23], and the morphological terminology mostly follows Vachon [24] and Hjelle [25].

4. Taxonomic treatment

Family Buthidae C.L. Koch, 1837

Subfamily Ananterinae Pocock, 1900

Genus *Tityobuthus* Pocock, 1890

Tityobuthus lokobe sp. n. (Fig. 2)

Type material. Madagascar, Nosy-Be, R.N. Lokobe. 1 female holotype with 5 juvenile paratypes, 4 males & 1 female (one juvenile was removed by M. Vachon), IX/1947 (J. Millot leg.), battage (RS-1428), deposited in the Muséum national d'Histoire naturelle, Paris.

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

Diagnosis. Scorpion of moderate size, with respect to the genus, and with 31–32 mm in total length. General coloration pale yellow throughout, both the body and the appendages with some spots on the carapace, tergites, legs, and partially on pedipalps and metasomal segments. Carapace with a moderate concavity. Pectines large and less separate than in females of other species with 14 to 15 teeth; fulcra reduced. Telson moderately elongated, with a short and curved aculeus; subaculear tooth strong, between rhomboid and spinoid, with two subaculear granules. Internal face of the patella with 9–10 spinoid granules. Tibial spurs strongly reduced on leg IV, absent on leg III. Pedipalp fixed and movable fingers with 8–9 slightly oblique rows of granules. Trichobothrial pattern of type A- α (alpha) – orthobothriotaxic.

Relationships. From its general morphology and by the pattern of pigmentation, *Tityobuthus lokobe* sp. n. seems to be associated with *Tityobuthus darainensis* Lourenço & Goodman, 2002, described from the 'Forêt de Binara', located in Daraina. These two sites are situated in the extreme north of Madagascar at a similar latitude. The two species can be distinguished by a number of features:

- the new species shows only 14 to 15 teeth on pectines vs. 16–19 in *T. darainensis*;
- smaller global size of the new species;
- the new species has reduced fulcra in pectines;
- in the new species tibial spurs are reduced on leg IV and absent on leg III; these are present on legs III and IV of *T. darainensis*.

4.1. Description based on female holotype and paratypes

Coloration. Ground colour yellow throughout the body and appendages. Carapace yellowish with diffused dark spots, between median and lateral eyes, and with some dark zones on the lateral and posterior margins; eyes surrounded by black pigment. Mesosoma yellow, with three diffuse longitudinal dark stripes; the central is separated by a yellow band. Metasomal segments I to V yellowish; all segments with blackish spots, better marked

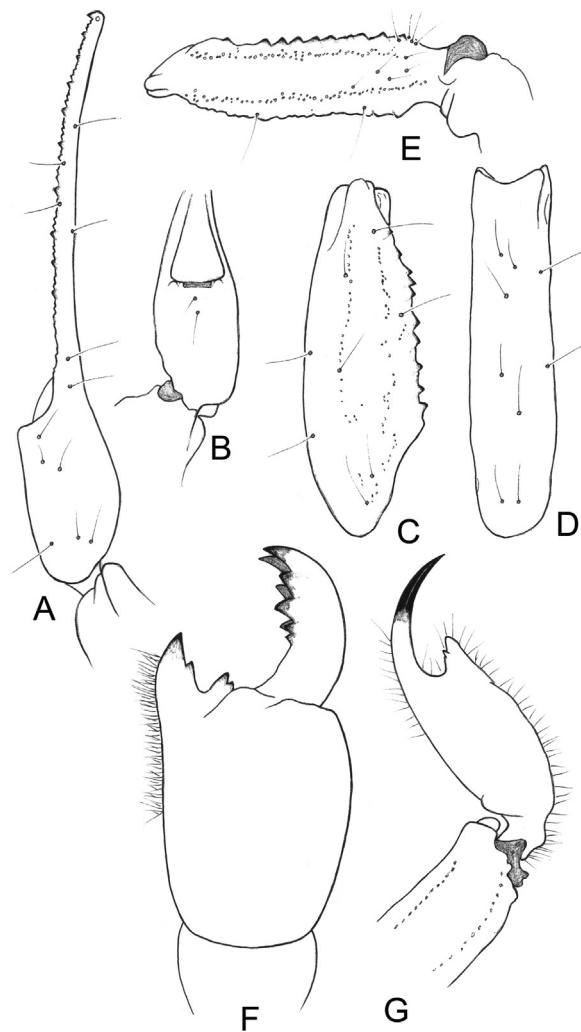


Fig. 2. *Tityobuthus lokobe* sp. n. Female holotype. A–E. Trichobothrial pattern. A–B. Chela dorso-external and ventral aspects. C–D. Patella, dorsal and external aspects. E. Femur, dorsal aspect. F. Chelicera, dorsal aspect. G. Metasomal segment V and telson, lateral aspect.

on IV and V; telson yellow with the tip of aculeus reddish. Venter yellowish. Chelicerae yellowish, with variegated pigmentation at the base of fingers; fingers intensely spotted with blackish; teeth reddish. Pedipalps yellowish, with dark spots on the femur and the patella; chela yellowish; fingers brown to blackish, with darker zones on their base. Legs yellowish, with diffuse dark spots.

Morphology. Carapace weakly to moderately granular; anterior margin with a moderately 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 in size, separated by about one ocular diameter. Three pairs of lateral eyes. Sternum subtriangular. Mesosoma: tergites weakly granular. Median carina moderate to weak on all tergites; absence of other carinae. Tergite VII pentacarinata. Venter: genital operculum divided longitudinally, each half being semi-oval in shape. Pectines large in size; pectinal tooth count 14 to 15; basal middle lamellae not dilated; fulcra present but reduced. Sternites

smooth, excepted for VII, which shows some minute granulations; spiracles small and elongate. Metasomal segments I and II with 10 carinae, crenulate; segments III and IV with 8 carinae, crenulate. Intercarinal spaces weakly granular. Segment V rounded, with five vestigial carinae and weakly granular. Telson with a pear-like shape and totally smooth; presence of some setations; aculeus moderately curved; subaculear tooth strong and from rhomboid to spinoid with two basal granules. Cheliceral dentition characteristic of the family Buthidae [26]; basal teeth of movable fingers reduced but not fused; ventral surfaces of finger and manus with long setae. Pedipalps: femur pentacarinata and crenulate; patella with some carinae, weakly crenulate; chela rounded and smooth; internal face of patella with 9–10 spinoid granules; all faces weakly granular; fixed and movable fingers with 8–9 almost linear rows of granules. Trichobothriotaxy; orthobothriotaxy A- α (alpha) [23,27]. Legs: tarsus with numerous fine median setae ventrally. Pedal spurs moderate; tibial spurs reduced on leg IV, absent on leg III.

Distribution and ecology. The species is only known from its type locality, the 'Parc National de Lokobe' on the Island of Nosy-Be, where rainforest formations predominate. Some authors consider the forests encountered on Nosy-Be as dry forests [28], but the forest in Lokobe is an evergreen rainforest, and subhumid forest would better qualify the vegetation of this small reserve. The bioclimate is subhumid, with an average of six months of hydric deficit per annum, a mean annual rainfall above 2000 mm and mean temperatures of the coldest month between 16 °C and 18 °C [29] (see also Fig. 3).

Morphometric values (in mm) of female holotype. Total length (including telson) 31.8. Carapace: length 3.5; anterior width 2.4; posterior width 3.4. Mesosoma length 9.2. Metasomal segment I: length 2.4, width 1.8; II: length 2.6, width 1.6; III: length 2.8, width 1.6; IV: length 3.2, width 1.5; V: length 4.3, width 1.4, depth 1.5. Telson length 3.8. Vesicle: width 0.5, depth 0.6. Pedipalp: femur length 3.3, width 0.5; patella length 4.3, width 0.7; chela length 6.4, width 0.5, depth 0.4; movable finger length 4.7.

5. Ecology and population densities of Ananterinae

The ecology and biology of Ananterinae are poorly known, but detailed inventories carried out during the last 40 years have significantly increased the number of described scorpion species [30]; from 3 to more than 70 in *Ananteris* and from 1 to almost 20 in *Tityobuthus*. However, in most cases, the species are extremely rare and narrow endemic, with limited ranges.

A few species of *Ananteris* proved to be more common [31,32]. Recent ecological studies using pitfall and Winkler traps showed remarkable results and clearly suggested that at least some species are much more common than was originally suspected [32]. The collection efforts in Madagascar have been opportunistic and not systematic, thus not allowing us to assess the geographic range and distribution of the scorpion species. However, some species of *Tityobuthus* may have larger ranges, as *T. dastychi* or *T. petrae*, but more studies are needed to understand the species circumscription as well as their precise ranges. *T. dastychi* is encountered in the dry forests growing above marls in the Bemaraha, and also in the dry forests of Ankarafantsika some 375 km to the northeast. Several species occur in forests growing above sedimentary reliefs where humidity can sometimes be maintained. Species like *T. rakotondravonyi*, *T. antsingy* and *T. pococki* occur in the forests growing above marls or limestones of Ankarana, Namoroka, or Bemaraha, respectively, and *T. chelbergorum* occurs in the Isalo sandstones where subhumid forests grow in the deep canyons (Fig. 3).

A peculiarity of the museum collections of *Ananteris* and *Tityobuthus* is the frequent absence of juveniles. Collections have been based mainly on the overturning of rocks and the use of ultra-violet light and pitfall traps. Only the use of extraction methods such as Berlese, Winkler and Kempson ones have resulted in the collection of juvenile forms [33]. Extraction methods also led to the discovery and description of new humicolous species [34,35]. These methods have been used more in Madagascar than in the

Neotropics and have resulted in the collection of juvenile forms of *Tityobuthus* [5], while there is still a big knowledge gap for the *Ananteris* [6]. The new species described here is based on one female collected together with a brood of five or six juveniles. Although almost nothing is known about the reproductive biology of the *Tityobuthus* species, these values seem to be in accordance with those already observed for other species of microbuthoid scorpions [36].

6. Distribution of *Tityobuthus* species

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 4000 mm. Only *T. baroni* is known from the central highlands at an elevation of 1500 m and 1650 m (Fig. 3). Other species are encountered in several mountainous areas, including Andringitra, Ivohibe, Andohahela, but only at low elevation. Some species from the eastern humid or subhumid forests are also occurring in the dry or subarid forests, e.g., *T. parrilloi* in Andohahela.

Few species of *Tityobuthus* are encountered in the subarid bioclimate of southern and southwestern Madagascar (Fig. 3). A notable exception is *T. judsoni*, which is only known from the type locality, the dry forest of Marofandilia. In the subarid southwest with its spiny forests and thickets, no *Tityobuthus* has been recorded to date. The only spiny forest hosting the genus is in the reserve of Cap Sainte-Marie. The Madagascar scorpion fauna has a high diversity, with most species being geographically extremely localized; only Cap Sainte-Marie harbours as many as six species (*Grosphus feti* Lourenço, 1996, *Neogrosphus griveaudi* (Vachon, 1969), *Pseudouroplectes bettschi* Lourenço 1995, *P. pidgeoni* Lourenço & Goodman, 1999, *Opisthacanthus luciennae* Lourenço & Goodman 2006, *Tityobuthus* cf. *petrae*) [37,38]. Some authors have argued that the 'chevrons' deposits occurring above the southern region of the island and visible on satellite imagery could be traces of a past Holocene megatsunami [39,40]. Such extreme events would have had an impact on the fauna and flora of the entire region that could still be visible nowadays. These historical conditions have to be carefully studied on the ground before any inferences can link past and current environmental settings to explain local scorpion fauna over the region in general, and Cap Sainte-Marie in particular [41].

Tityobuthus lokobe sp. n. is only known from the type locality in the subhumid forests protected on the satellite island of Nosy-Be (Fig. 3). Nosy-Be was connected to the mainland during several dry phases of palaeoclimate oscillations, when sea levels were at ca. 130 m below the current levels [42]. *T. lokobe* has not been recorded in the Sambirano region [38]. The absence of the genus in the Sambirano may be due to the paucity of inventories in the region, the conspicuous behaviour of some members of this group, the absence of suitable habitat, i.e. low elevation forests, or a combination of these factors [37: fig. 3].

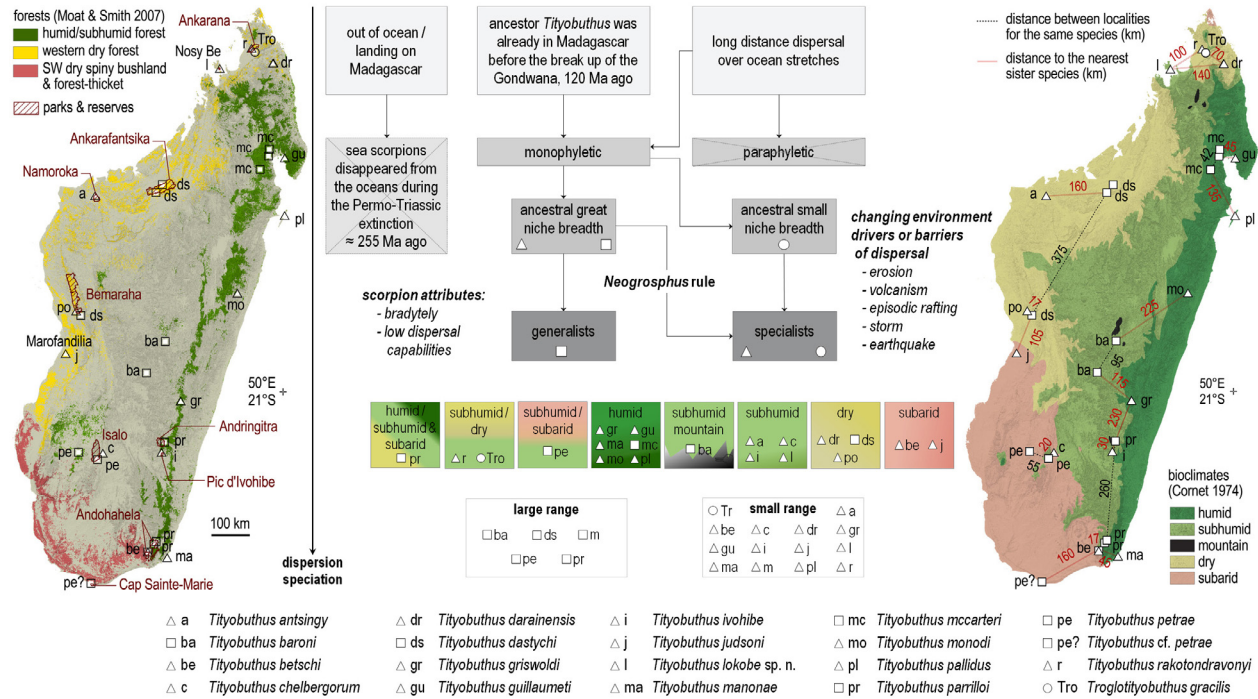


Fig. 3. Distribution of the Madagascar species of the *Ananteris* group according to forest cover (left) [28] and simplified bioclimates (right) [29], and logical flow chart summarizing the evolution of the group in Madagascar (center).

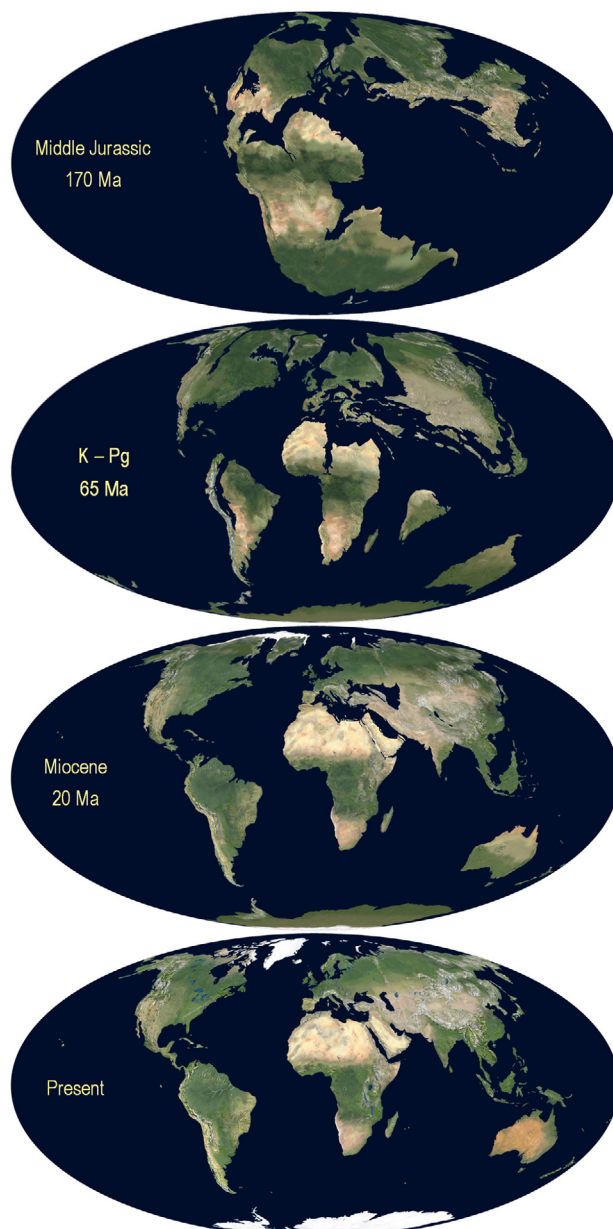


Fig. 4. Gondawana: breakup of the Gondwana 170 Ma.

Modified from <http://jan.ucc.nau.edu/rcb7/mollglobe.html> [43]. ©Ron Blakey, Colorado Plateau Geosystems, used with permission.

7. *Neogrosphus* rule reapplied

The species of the genus *Tityobuthus* belong to a group of scorpions of ancestral age [1]. To date it remains unclear how and where the ancestral Ananterinae survived at the K–Pg 65 Ma, or at the beginning of the Cenozoic (Fig. 4). However, three related fossils of the scorpion group from the Baltic coast, *Palaeoananteris*, *Palaeotityobuthus* and *Palaeolychas* allow for a glimpse of the ancestral's total range.

We put forth two possible explanations of the group's dispersal and speciation in Madagascar:

- the ancestor of *Tityobuthus* was already on Madagascar before it separated from the supercontinent;
- the ancestor of *Tityobuthus* arrived later by means of long-distance dispersal (LDD) over ocean stretches (Fig. 3).

The two Madagascar endemic genera *Tityobuthus* and *Troglotityobuthus* are phylogenetically more closely related to one another than to any other genus of scorpion in the *Ananteris* group [4,5,16,17], hence the consideration as monophyletic. If the ancestor reached Madagascar by means of LDD, one single case of successful colonization

could explain the entire group in Madagascar. The affinities of *Tityobuthus* and *Himalayativityobuthus* (Fig. 1) could also find an explanation in the Cretaceous when peninsular India was still attached to Madagascar before it drifted to the north some 80 Ma ago [43] (Fig. 4). Such a case could echo the Gondwana link of an Indian burrowing frog, a sister taxa of the family Sooglossidae only found on the granitic Seychelles of Gondwanan origin, but not in Madagascar [44]. The affinities between *Tityobuthus* and South-American *Ananteris* can be illustrated with another frog: the only Cretaceous frog known from Madagascar, *Beelzebufo ampinga* Evans et al., 2008, has a link with South America, but is unrelated to extant Madagascar frogs, or frogs found in the Seychelles or India [45]. South America and Indo-Madagascar have been separated before the Cretaceous (Fig. 4). The current distribution of the genus *Lychas* is best explained by LDD, in particular since the genus occurs on young volcanic islands. If LDD can be invoked to explain the presence of the genus in Africa, its absence in Madagascar is not understood, especially in context of its occurrence on the small islands of the Seychelles and the satellite islands of Mauritius. A southern Gondwana palaeo-distribution for *Lychas* cannot be excluded, but would be extremely ancient, since Antarctica was not connected to Africa and Australia anymore at the Early Cretaceous (Figs. 1 and 4).

Generally, scorpions are known to be bradytelic, i.e. they evolve at a slow rate when compared to other groups of animals, in particular if belonging to an old group such as the *Ananteris*. The ancestor of *Tityobuthus* and *Troglotityobuthus* have been on Madagascar for millions of years during which the Madagascar plate experienced rifting towards the north (Fig. 4) and was undergoing major climatic changes [42,46,47]. The ancient population was not adapted to dry or subarid environments; these traits are of recent adaptation only (see, for example, the case of modern buthids in the Sahara desert [33,35]). However, this does not rule out an ancestral large niche breadth allowing for adaptation. In such a scenario, the modern population could have colonized and survived in a variety of different environments (Fig. 3). In a small niche breadth scenario, the modern species could only have survived in a localized environmental setting with characteristics of a climatic refuge [42,48], i.e. be specialized and showing a narrow distribution range.

We hypothesize that the monophyletic ancestor of the Madagascar clade must have had a great niche breadth. The bradytelic ancestor, as all *Ananterinae* scorpions, had low dispersal capabilities. The *Neogrosphus* rule [38] states that 'the lower the species' dispersal ability and the greater the niche breadth of the ancestor taxum, the higher the species richness in a changing environment producing geographical barriers, and vice-versa.' Based on the extant distributions, we can infer that the ancestor of *Troglotityobuthus* had a small niche breadth. This monotypic cavernicolous genus is only known from its type locality, a cave in the sandstone formations of Northern Madagascar. The ancestor of *Tityobuthus* (Fig. 3) with its 19th species described here must have had a large niche breadth, with modern species occurring both on large ranges or narrow ranges, all over Madagascar in the various bioclimates, but mainly at lower elevations.

8. Conclusions

In the case that *Tityobuthus* would have kept ancestral features while most species are occurring in humid and subhumid forests, some species must have been able to cope with mesic environments. We can postulate a possible 'Tityobuthus pattern': The small ranged species of the group occur in every bioclimate, with the exception of mountains, while the large-ranged species occur also in mountains.

Disclosure of interest

The authors declare that they have no competing interest.

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Appendix 1. Checklist for the *Tityobuthus* species known from Madagascar

Tityobuthus monodi Lourenço, 2000

Distribution: only known from the type locality; Prov. Toamasina, F.C. Andriantantely (18°41,7'S–48°48,8'E), 530 m, 7–10/12/1998 (H.J. Ratsirarson leg.).

Tityobuthus guillaumeti Lourenço, 1995

Distribution: only known from the type locality; Iaraka, 'Baie d'Antongil', 700 m, rain forest 17/11/1969 (J.-M. Betsch).

Tityobuthus mccarteri Lourenço et al., 2008

Distribution: Toamasina Province, Akirindro mountain, NW of Ambinanitelo, [presumed to be 15°17'3"S–49°32'9"E, cf. Heterick, 2006], 600 m, 'forêt humide', 03/1969 (J.-M. Betsch); Réserve Spéciale d'Ambatovaky, 450 m, rain forest, 31/1/2006 (L.R. de Roland); plateau de Makira, forêt de Vohitaly (site F), 5 km SE of the Anjahely village (15°26'58"S–49°32'06"E), 540–680 m, pitfall vial marked "C9 site F Vohitaly", no date (V. Andrianjakarivelo).

Tityobuthus rakotondravonyi Lourenço & Goodman, 2003

Distribution: only known from the type locality; Antsiranana Province, 'Réserve spéciale d'Ankarana, Campement des Anglais' (Anilotra), 7.5 km NW of Mahamasina, 12°54,5'S–49°06,6'E, 125 m (S.M. Goodman).

Tityobuthus judsoni Lourenço, 1996

Distribution: only known from the type locality; Mad. W, route de Morondava, Belo-sur-Tsiribihina, 'forêt de Marofandilia, sous bois mort', 8/12/1969 (J.-M. Betsch).

***Tityobuthus pallidus* Lourenço, 2004**

Distribution: only known from the type locality; Sainte-Marie Island, Ambohidena Forest Station, 16°51'S–49°57'E, 27/12/1955 (IRSM leg.).

***Tityobuthus manonae* Lourenço, 2000**

Distribution: only known from the type locality; Mandena, Fort Dauphin, littoral forest 10 km north of Fort Dauphin, 6–12/01/1999 (J.-B. Ramanamanjato).

***Tityobuthus baroni* (Pocock, 1890)**

Distribution: this species was the subject of numerous misidentifications. Consequently, many wrong citations remained in the literature until the final clarification about the identity and the status of this species was published by Lourenço et al. (2008). Refer to this publication for further details on the species and type material. The present known distribution of *T. baroni* can be summarized as follows: Madagascar, type material, Rev. R. Baron. BM 1888–12. Parc de l'Est, Antsirabe, 16/09/1973 (C. Duval leg.) [male holotype and female allotype of *Tityobuthus lucileae*]. Fianarantsoa, forêt d'Atsirakambiaty, 7.6 km WNW from Itremo, 1550 m (20°35'36"S–46°33'48"E), montane rainforest (Fisher, Griswold et al.), 22–26/01/2003.

***Tityobuthus pococki* Lourenço, 1995**

Distribution: only known from the type locality; W. Bekopaka, Antsiny, 07/1970 (P. Griveaud).

***Tityobuthus ivohibe* Lourenço & Goodman, 1999**

Distribution: only known from the type locality; Prov. Fianarantsoa, exterior northern limit of the 'R. S. d'Ivohibe', along the Hefitany River, 7.5 km ENE of Ivohibe (22°28,2'S–46°57,6'E), 900 m, 6–13/10/1997 (S. Goodman).

***Tityobuthus griswoldi* Lourenço, 2000**

Distribution: only known from the type locality; Prov. Fianarantsoa, P.N. Ranomafana, Talatakely (21°15,3'S–47°25,9'E), 9–26/04/1998 (pitfall traps; C.E. Griswold, D.H. Kavanaugh, N.D. Penny & M.J. Raheirilalao leg.).

***Tityobuthus parrilloi* Lourenço, 1996**

Distribution: only known from the type locality; Madagascar Est, Prov. Fianarantsoa, 45 km south of Ambalavao (eastern bank of the Iantara River, along the Ambalamanenjana–Ambatomboay trail, edge of the 'Réserve Naturelle Intégrale n° 5 de l'Andringitra'), 22°13'40"S–47°00'13"E (720 m alt.), 19–20/11/1993 (S. Goodman).

***Tityobuthus dastychi* Lourenço, 1997**

Distribution: this species was also the subject of a number of misidentifications. Consequently, a number of sites attributed to this species in the SW of Madagascar should now be disregarded (see Lourenço & Goodman, 2003). In fact, the populations in the SW of the island proved to be a distinct

species yet to be described. Only the sites reported for the Province of Mahajanga should be retained for *T. dastychi*. Prov. Mahajanga, Ampijoroa, 03/1996 (P. Chouteau), [type material]; idem, 02/2001 (G. Garcia); 'Parc National de Bemaraha', southern bank of the Manambolo River, near Tombeau Vazimba, 3.5 km of Bekopaka, 19°08,4'S–44°49,7'E, 100 m, Tsingy forest (A. Raselimanana).

***Tityobuthus petrae* Lourenço, 1996**

Distribution: south of Madagascar, Tuléar Province, Vohibasia, 10/1995 (S. Goodman); a few paratypes also from Prov. Tuléar, Tanjon'i Vohimena (Cap Sainte-Marie), 'Réserve spéciale'.

The original type material was collected in two different sites; however, new elements led to believe that the material from Cap Sainte-Marie should be reconsidered as a possible distinct population. Only further material will allow the clarification of this situation.

***Tityobuthus betschi* Lourenço et al., 2008**

Distribution: only known from the type locality; Toliara Province, 'Parc National d'Andohahela' parcel 2, 'forêt de Manantalinjo', 24°49'01"S–46°36'36"E, 150–300 m, V/1972 (J.-M. Betsch); 'extraction dans forêt sèche' (spiny bush forest).

***Tityobuthus chelbergorum* Lourenço et al., 2008**

Distribution: only known from the type locality; Fianarantsoa Province, 'Parc National d'Isalo', 8–9 km north of Ranohira (22°28'59"S–45°27'38"E), 700–730 m, nearby 'forêt galerie', 8/11/2004 (W.R. Lourenço).

***Tityobuthus darainensis* Lourenço & Goodman, 2002**

Distribution: only known from the type locality; Antsiranana Province, 'Forêt de Binara, near Analamazava River, 7.5 km SW of Daraina (13°15,3'S–40°37,0'E), 325–600 m (S. Goodman).

***Tityobuthus lokobe* sp. n.**

Distribution: only known from the type locality; Nosy-Be, Parc National (e.g., 'Réserve Naturelle Intégrale') Lokobe, DINA region (formerly Province of Antsiranana).

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