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Review of the leaf-litter skinks (Scincidae: *Panaspis*) from the Gulf of Guinea Oceanic Islands, with the description of a new species

Leonor B. Soares^{a,b}, Luis M. P. Ceriaco ^{b,c}, Mariana P. Marques^{b,d}, Cristiane Bastos-Silveira^b, Lauren A. Scheinberg^e, D. James Harris^d, António Brehm^f and José Jesus^{d,f,g}

^aDepartamento de Biologia, Universidade de Évora, Pólo da Mitra, Apartado 94, 7002-554 Évora, Portugal; ^bDepartamento de Zoologia e Antropologia (Museu Bocage), Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Rua da Escola Politécnica, 58, 1269–102 Lisboa, Portugal.; ^cDepartment of Biology, Villanova University, 800 Lancaster Avenue, Villanova, PA 19085-1699, USA; ^dCentro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO/UP), Campus Agrário de Vairão, 4485-661 Vairão, Portugal; ^eCalifornia Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, USA; ^fFaculdade de Ciências da Vida, Universidade da Madeira, Campus da Penteada, 9000-390 Funchal, Portugal; ^gCIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos – Polo dos Açores, Faculdade de Ciências e Tecnologias, Universidade dos Açores, R. Mãe de Deus 13A, 9501-801 Ponta Delgada, São Miguel, Açores, Portugal.

ABSTRACT

Leaf-litter skinks of the genus *Panaspis* are currently represented in the oceanic islands of the Gulf of Guinea by two species, *Panaspis africana* and *P. annobonensis*. Here we describe a third species, *Panaspis thomensis* sp. nov., endemic to São Tomé Island. Data from previous studies and a new phylogenetic analysis using the mitochondrial 16S gene shows that the new species is genetically divergent and reciprocally monophyletic with respect to *P. africana*. Morphological data (scalation and morphometry) identify consistent, yet subtle, phenotypic differences between the two island populations. We also confirm that *P. annobonensis* represents a valid species, sister to the species pair *P. africana* + *P. thomensis* sp. nov., based on both molecular and morphological evidence. This description raises the number of known *Panaspis* species in the Gulf of Guinea oceanic islands to three, with consequences for the interpretation of local endemism.

ZooBank—*Panaspis thomensis*:

lsid: zoobank.org:act:A1E69D28-CF4C-4070-BBCC-91E39C21DBA6

KEYWORDS

endemism; *Panaspis africana*;
Panaspis annobonensis;
Panaspis thomensis sp. nov.

Introduction

The forests of West Africa, including the oceanic islands of the Gulf of Guinea – São Tomé, Príncipe, and Annobon, and the surrounding islets – comprise one of the world's biodiversity hotspots (Myers et al. 2000; Burgoyne et al. 2005). These islands have never been connected to the mainland and correspond to the offshore portion of the 1 600 km Cameroon Volcanic Line (Déruelle et al. 1991; Aka et al. 2001; Burke 2001; Caldeira & Munhá 2002),

which initiates in mainland Africa at Mount Cameroon, extends southwest through Bioko (the only non-oceanic island of the Cameroon Volcanic Line), Príncipe, São Tomé and ends at Annobon (Lee et al. 1994). Príncipe, with an area of 128 km² and an estimated age of 31 million years, lies about 220 km southwest of Bioko, whereas São Tomé, with an area of 836 km² and an estimated age of 14 million years old, is about 146 km southwest of Príncipe (Lee et al. 1994). The most distant island, Annobon, 180 km southwest of São Tomé, is also the smallest and the youngest, with an area of about 17 km² and an estimated age of 4.8 million years old (Lee et al. 1994).

Given their isolation, the rates of speciation on these islands are particularly rapid (Melo et al. 2011), with a high number of endemics among vertebrates (Drewes & Stoelting 2004; Measey et al. 2007; Uyeda et al. 2007; Leventis & Olmos 2009; Miller et al. 2012; Ceriaco 2015; Ceriaco et al. 2015, 2016, 2017; Bell 2016), invertebrates (Mendes & Bivar-De-Sousa 2012; Sluys et al. 2017), and plants (Figueiredo 2005; Garcia et al. 2012; Stoelting et al. 2014). For their small size, the islands present a remarkable diversity of reptiles. Excluding marine turtles, the three islands harbour a total of 24 different species of reptiles, the majority endemic (Ceriaco et al. in press). However, this number represents a considerable underestimation, because ongoing research is both revealing new species and reviving formerly synonymised names (for a list of on going work, see Ceriaco et al. in press). Among this diversity, eight species of skinks (Family Scincidae), of three different genera, are known to occur on the oceanic islands of the Gulf of Guinea – the many scaled *Feylinia*, *Feylinia polylepis* Bocage, 1887, endemic to the Island of Príncipe; the Príncipe skink, *Trachylepis principensis* Ceriaco, Marques & Bauer, 2016, endemic to the Island of Príncipe; the São Tomé skink, *Trachylepis thomensis* Ceriaco, Marques & Bauer, 2016, endemic to the Island of São Tomé, Santana and Rolas islets; the Adamastor skink, *Trachylepis adamastor* Ceriaco, 2015, endemic to the islet of Tinhosa Grande; Osório's skink, *Trachylepis ozorii* (Bocage, 1893), endemic to the Island of Annobon; the São Tomé and Príncipe leaf-litter skink, *Panaspis africana* (Gray, 1845), endemic to the islands of São Tomé, Príncipe and Rolas islet; and finally the Annobon leaf-litter skink, *Panaspis annobonensis* (Fuhn, 1972), endemic to the Island of Annobon.

The taxonomic and nomenclature history of *Feylinia polylepis* has been stable since its original description, its taxonomic identity was confirmed by both molecular and morphological data (Brygoo & Roux-Esteve 1983; L. Ceriaco, unpubl. data), and the Gulf of Guinea oceanic island skinks of the genus *Trachylepis* were addressed in a review by Ceriaco et al. (2016). However, the current taxonomic and nomenclatural history of the leaf-litter skinks is problematic. The phylogenetic relationships of the Gulf of Guinea leaf-litter skinks were initially addressed by Jesus et al. (2007) using a combination of three mitochondrial genes (12S, 16S, and cytb) and one nuclear gene (c-mos). This study first provided evidence that the São Tomé and Príncipe populations were genetically distinct from one another, with high levels of divergence, supporting the recognition of three distinct species, one on Príncipe, one on São Tomé and one on Annobon. Fuhn (1972) had already described the Annobon form as different subspecies of the São Tomé-and-Príncipe form, *Panaspis africana annobonensis*, which then was recognized as a full species by Perret (1973) and subsequent authors (e.g. Schätti & Loumont 1992; Haft 1993; Jesus et al. 2007). It is, however, important to note that until Fuhn's description of *annobonensis*, the Annobon form was also considered as member of the nominotypical form by Bocage (1903) and Boulenger (1906). However, for both São Tomé and Príncipe, all past authors have referred

to both island populations as belonging to *P. a. africana* (Bocage 1866, 1889, 1903, 1905; Vieira 1886; Bedriaga 1892; Boulenger 1906; Henriques 1917; Smith 1937; Mittleman 1952; Manaças 1958; Fuhn, 1972; Perret 1973; Schätti & Loumont 1992; Haft 1993; Hofer 2002; Drewes & Stoelting 2004). The species was originally described by Gray (1845) as *Mococa africana*, based on a juvenile specimen from “West Africa”, without further data on the precise collection locality or collector. The second record for the species was made by Peters (1874), based on a specimen from Príncipe collected by “Dr Dhorn” (= Anton Dhorn, 1840–1909). Subsequent reports the species for the Rolas Islets, on the south coast of São Tomé Island, as indicated by Greef (1884), and numerous subsequent records exist for São Tomé (Bocage 1866, 1889, 1905; Vieira 1886; Bedriaga 1892; Boulenger 1906; Henriques 1917; Smith 1937; Mittleman 1952; Manaças 1958; Perret 1973; Schätti & Loumont 1992; Haft 1993; Hofer 2002) and Príncipe (Boulenger 1887, 1906; Bocage 1903; Manaças 1958; Perret 1973; Schätti & Loumont 1992; Haft 1993; Hofer 2002). Because of the uncertainties regarding the geographical origin of the holotype, Jesus et al. (2007) suggested that the original name should be retained by the Príncipe lineage, whereas the São Tomé form should be considered as a new lineage. In the same article, the authors noted that a description was being prepared, however a chain of unfortunate events precluded this and delayed it considerably.

The study of Jesus et al. (2007) also showed that all three forms constitute a monophyletic group, which suggests a single initial colonisation followed by the colonisation of the other islands (stepping stone colonisation). This scenario is similar to the colonisation of São Tomé and Príncipe by reed frogs of the genus *Hyperolius* (Bell et al. 2015) and house snakes of the genus *Boaedon* (L. Ceriaco unpub. data). Because of the limited sampling Jesus et al. (2007) followed the ideas of Schmitz et al. (2005) and considered the Gulf of Guinea oceanic island leaf-litter skinks as members of *Afroablepharus*. More recently Medina et al. (2016), with a larger sampling across the distribution of *Panaspis* and *Afroablepharus* and using a combination of both mitochondrial (16S and cytb) and nuclear genes (PDC and RAG1), found that *Afroablepharus* was embedded within *Panaspis*, and synonymised the two. These authors also found that both Príncipe and Annobon leaf-litter skinks were collectively sister to *Panaspis cabindae* (Angola and western Democratic Republic of the Congo, Bocage 1866). However, no specimens from São Tomé were used in their study.

Combining the molecular evidence produced by Jesus et al. (2007) with new molecular data from and morphological comparisons between the leaf-litter skinks of the three islands, and between insular and mainland populations, we here describe the São Tomé leaf-litter skink as a new species. External morphology and natural history data are presented both for the newly described species, as well as for the Príncipe endemic, *P. africana*, and Annobon endemic, *P. annobonensis*. Because the original description of *P. africana* did not give a specific location (“West Africa”) and the morphological differences between *P. africana* and the newly described form are very subtle, we assign the nomen *africana* to Príncipe population based on the limited diagnostic characters available. We also provide an account for the Annobon endemic, *P. annobonensis*.

Materials and methods

Specimens collected for the current study were preserved in 10% buffered formalin in the field and transferred to 70% ethanol at the conclusion of each expedition. Liver tissue was

removed before formalin fixation and preserved in 95% ethanol. For mensural and meristic comparisons, we examined high quality photos of the holotype of *Mocoo africana* Gray, 1845, from the collections of the British Museum of Natural History (BMNH), London (United Kingdom), as well as other Gulf of Guinea *Panaspis* specimens deposited in Museu Nacional de História Natural e da Ciência (MUHNAC), Lisbon (Portugal); Instituto de Investigação Científica Tropical (IICT), Lisbon (Portugal); California Academy of Sciences (CAS), San Francisco (USA); Muséum d'Histoire Naturelle de la Ville de Genève (MHNG)

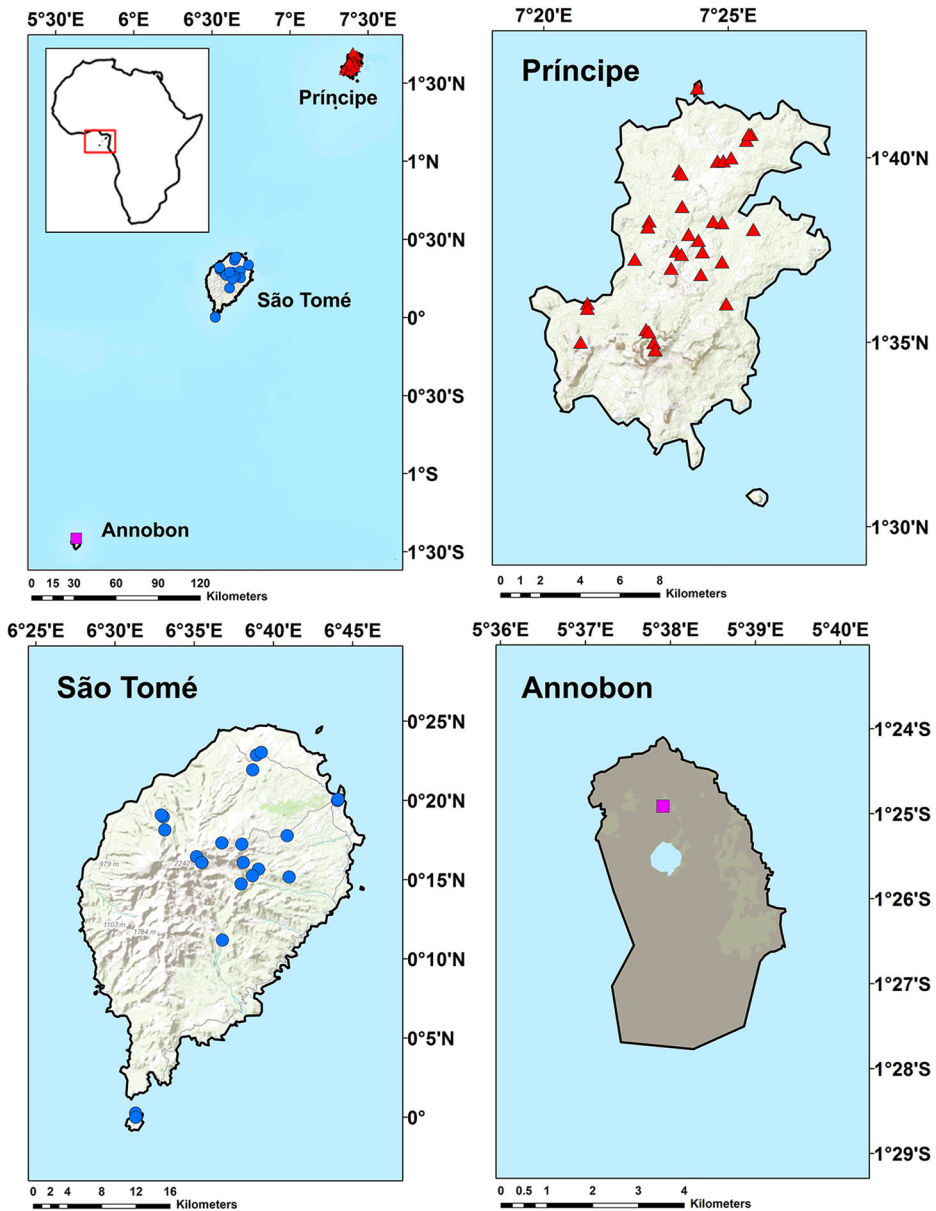


Figure 1. Geographic distribution of the specimens examined. Red triangles – *Panaspis africana*; Blue dots – *Panaspis thomensis* sp. nov.; Purple square – *Panaspis annobonensis*

(Switzerland), Zoologische Staatssammlung München (ZSM) (Germany), Zoologisches Museum der Universität Hamburg (ZMH) (Germany); and the Museum für Naturkunde der Humboldt- Universität zu Berlin (ZMB) (Germany), as well as available sequences from Genbank (Fig. 1; see Appendix 1).

Molecular methods

We obtained sequence data for the 16S mitochondrial gene from tissue samples preserved in 95–99% ethanol. The 16S region of mtDNA has been proven to be useful for identifying species level divergences in the genus *Panaspis* (Schmitz et al. 2005; Jesus et al. 2007; Medina et al. 2016). We constructed phylogenetic trees using 13 new sequences of *P. africana sensu lato* from both São Tomé and Príncipe islands. For comparison, 57 DNA sequences representing other *Panaspis* species and lineages (from Medina et al. (2016)), and a sequence of *Leptosiaphos vigintiserierum* used as an outgroup, were obtained from GenBank, in order to make the analyses more robust (Table 1). The number and geographic locations of the leaf-litter skinks included in genetic study are given in Table 1. Total genomic DNA for the new 13 samples was extracted from tissues of thirteen skinks using the Qiagen DNeasy tissue extraction kit (Qiagen Inc.) following the manufacturer's instructions. PCR primers used in both amplification and sequencing were 16SL and 16SH (Simon et al. 1990). The PCR cycling procedure was as follows: an initial denaturation step of 5 min at 85 °C; followed 35 cycles of denaturation 35 s at 94 °C, primer annealing for 3 s at 50 °C and extension for 1 min at 72 °C; and a final step of 5 min at 72 °C. PCR fragments were sequenced in an ABI 310 sequencer (Applied Biosystem DNA Sequencing Apparatus). Sequences were aligned using ClustalW (Thompson et al. 1994) as implemented in MEGA version 7 (Kumar et al. 2016) sequence alignment editor and subjected to visual inspection when necessary. Because phylogenetic reconstruction is based on positional homologies, only the regions that could be unambiguously aligned were included in analysis (about 13 bp of 16S). The dataset used for phylogenetic analyses consisted of 424 bp for 16S. The alignment is available on request from the corresponding author. True evolutionary relationships may be obscured or skewed in DNA sequence data sets if sites have become saturated by multiple substitutions (Swofford et al. 1996). To test for saturation, observed pairwise proportions of transitions and transversions were plotted against sequence divergence and calculated using DAMBE version 5 (Xia 2013). The data were imported to PAUP* 4.0b10 (Swofford 2002) and MEGA version 7 (Kumar et al. 2016).

We performed a Maximum Likelihood (ML) analysis on the 16S dataset, using MEGA 7 (Kumar et al. 2016). The optimum substitution models were selected by ModelTest 3.7 (Posada & Crandall 1998) using the Akaike information criterion (Posada & Buckley 2004). Based on the results, phylogenetic analyses were performed with a random starting tree under the HKY + G + I model. Phylogenetic robustness was estimated in the ML analyses by running 1 000 random addition bootstrap replicates (Felsenstein 1985). We regarded tree topologies with bootstrap values (bs) of 70% or greater as well supported (Huelsenbeck & Hillis 1993). To assess the level of divergence between the new species and the other closely related species, p-uncorrected pairwise distances between the sequences of *P. cabindae*, *P. africana*, *P. thomensis* sp. nov. and *P. annobonensis* were estimated using MEGA version 7 (Kumar et al. 2016).

Table 1. Details of material and sequences used in the genetic analyses; origin of sequences and samples, specimens' codes, and GenBank Accession Nos. DRC = Democratic Republic of Congo, E = east, GG = Gulf of Guinea, Moz = Mozambique, N = north, NW = northwest, SW = southwest, S = south, SA = South Africa.

	Field number	Catalog number	Locality	Accession numbers	Source
<i>Panaspis breviceps</i>	---	ZFMK 75380	Mt. Nlonako, Cameroon	KU236796	Medina et al. (2016)
<i>Panaspis</i> sp.	---	PEM R20799	Arusha, Tanzania	KU236718	
<i>Panaspis maculicolis</i>	MCZF 38733	CAS 234099	Farm Vrienden, Limpopo SA	KU236720	Medina et al. (2016)
<i>Panaspis wahlbergi</i>	MCZF 38868	CAS 234209	Limpopo, SA	KU236721	Medina et al. (2016)
<i>Panaspis togoensis</i>	DCB 34707		Gashaka Gumti National Park, Nigeria	KU236725	Medina et al. (2016)
<i>Panaspis</i> sp.	ELI 295	UTEP 21175	Mulongo, Katanga, DRC	KU236729	Medina et al. (2016)
<i>Panaspis</i> sp.	JHK 26	Uncatalogued	Kisanfu Camp, Katanga, DRC	KU236726	Medina et al. (2016)
<i>Panaspis</i> sp.	AMB 7634	MCZ R183767	Sesfontein, Namibia	KU236727	Medina et al. (2016)
<i>Panaspis</i> sp.	WRB 568	PEM R20247	Sombani Trail, Mt. Mulanje, Malawi	KU236732	Medina et al. (2016)
<i>Panaspis</i> sp.	WRB 572	PEM R16769	Klein's Camp, Serengeti, Tanzania	KU236734	Medina et al. (2016)
<i>Panaspis</i> sp.	SVN 693		Gorongosa National Park, Moz	KU236754	Medina et al. (2016)
<i>Panaspis</i> sp.	WC 1358	Uncatalogued	Quiterajo, Cabo Delgado, Moz	KU236776	Medina et al. (2016)
<i>Panaspis</i> sp.	WC 1051	No voucher	NW of Rapale, Nampula, Moz	KU236772	Medina et al. (2016)
<i>Panaspis</i> sp.	WRB 855	PEM R20569	Syran graphite mine, Balama, Moz	KU236766	Medina et al. (2016)
<i>Panaspis</i> sp.	DMP 187	MVZ 266148	Serra Jeci, Moz	KU236739	Medina et al. (2016)
<i>Panaspis cabindae</i>	MBUR 2128	Uncatalogued	S Leba Pass, Huila District, SW Angola	KU236740	Medina et al. (2016)
<i>Panaspis cabindae</i>	ANG 21	PEM R19467	Lagoa Carumbo, Angola	KU236741	Medina et al. (2016)
<i>Panaspis cabindae</i>	PM 049	Uncatalogued	Luango-Nzambi, Bas-Congo, DRC	KU236750	Medina et al. (2016)
<i>Panaspis cabindae</i>	PM 050	Uncatalogued	Luango-Nzambi, Bas-Congo, DRC	KU236751	Medina et al. (2016)
<i>Panaspis cabindae</i>	ELI 1722	UTEP 21173	Bombo-Lumene Reserve, Kinshasa, DRC	KU236753	Medina et al. (2016)
<i>Panaspis cabindae</i>	WRB 810	PEM R21594	Riverine Forest, Bengo, Angola	KU236765	Medina et al. (2016)
<i>Panaspis cabindae</i>	WRB 804	PEM R20256	Soyo, NW Angola	KU236768	Medina et al. (2016)
<i>Panaspis cabindae</i>	ANL 52	MTD 48612	Kimpa Vita Uni Campus, Uíge, N Angola	KU236771	Medina et al. (2016)
<i>Panaspis</i> sp.	MCZ-A 27176	Uncatalogued	Hoedspruit, Limpopo, SA	KU236743	Medina et al. (2016)
<i>Panaspis</i> sp.	TJC 264	Uncatalogued	Oromia, western Ethiopia	KU236752	Medina et al. (2016)
<i>Panaspis africana</i>	Pt1	MB03-001120	Terreiro Velho, Príncipe, GG	EU164462	Jesus et al. (2007)
<i>Panaspis africana</i>	Pt2	MB03-001121	Terreiro Velho, Príncipe, GG	EU164463	Jesus et al. (2007)
<i>Panaspis africana</i>	Pt3	MB03-001122	Terreiro Velho, Príncipe, GG	EU164464	Jesus et al. (2007)
<i>Panaspis africana</i>	Pt4	MB03-001123	Terreiro Velho, Príncipe, GG	EU164465	Jesus et al. (2007)
<i>Panaspis africana</i>	Pt5	MB03-001124	Terreiro Velho, Príncipe, GG	EU164466	Jesus et al. (2007)
<i>Panaspis africana</i>	Pt6	MB03-001125	Terreiro Velho, Príncipe, GG	EU164467	Jesus et al. (2007)

(Continued)

Table 1. Continued.

	Field number	Catalog number	Locality	Accession numbers	Source
<i>Panaspis africana</i>	Pt7	MB03-001126	Terreiro Velho, Príncipe, GG	EU164468	Jesus et al. (2007)
<i>Panaspis africana</i>	Pp1	MB03-001127	Ponta do Sol, Príncipe, GG	EU164469	Jesus et al. (2007)
<i>Panaspis africana</i>	Pp2	MB03-001128	Ponta do Sol, Príncipe, GG	EU164470	Jesus et al. (2007)
<i>Panaspis africana</i>	Pp3	MB03-001129	Ponta do Sol, Príncipe, GG	EU164471	Jesus et al. (2007)
<i>Panaspis africana</i>	Pp4	MB03-001130	Ponta do Sol, Príncipe, GG	EU164472	Jesus et al. (2007)
<i>Panaspis africana</i>	Pp5	MB03-001131	Ponta do Sol, Príncipe, GG	EU164473	Jesus et al. (2007)
<i>Panaspis africana</i>	Pp6	MB03-001132	Ponta do Sol, Príncipe, GG	EU164474	Jesus et al. (2007)
<i>Panaspis africana</i>	Pm1	MB03-001133	Montalegre, Príncipe, GG	EU164475	Jesus et al. (2007)
<i>Panaspis africana</i>	Pm2	MB03-001134	Montalegre, Príncipe, GG	EU164476	Jesus et al. (2007)
<i>Panaspis africana</i>	Pm3	MB03-001135	Montalegre, Príncipe, GG	EU164477	Jesus et al. (2007)
<i>Panaspis africana</i>	L1-P3	MB03-000935	Road near Quarry, Príncipe, GG	MG593139	This study
<i>Panaspis africana</i>	L2-P4	MB03-000944	Praia Caixão, Príncipe, GG	MG593141	This study
<i>Panaspis africana</i>	L3-P27	MB03-000936	Campo Político, Príncipe, GG	MG593138	This study
<i>Panaspis africana</i>	L5-P33	MB03-000940	Campo Político, Príncipe, GG	MG593137	This study
<i>Panaspis africana</i>	L6-P34	MB03-000941	Príncipe, GG	MG593140	This study
<i>Panaspis africana</i>	L7-16S-P38	MB03-000946	Santo Cristo, Príncipe, GG	MG593136	This study
<i>Panaspis africana</i>	L10-16S-P35	MB03-000942	Campo Político, Príncipe, GG	MG593135	This study
<i>Panaspis africana</i>	L11-16S-P36	MB03-000943	Maria Correia, Príncipe, GG	MG593134	This study
<i>Panaspis africana</i>	L16-P28	MB03-000937	Campo Político, Príncipe, GG	MG593133	This study
<i>Panaspis annobonensis</i>	An1	MB03-001104	Annobon, GG	EU164480	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An2	MB03-001105	Annobon, GG	EU164481	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An3	MB03-001106	Annobon, GG	EU164482	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An4	MB03-001107	Annobon, GG	EU164483	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An5	MB03-001108	Annobon, GG	EU164484	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An6	MB03-001109	Annobon, GG	EU164485	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An8	MB03-001110	Annobon, GG	EU164487	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An9	MB03-001111	Annobon, GG	EU164488	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An10	MB03-001112	Annobon, GG	EU164489	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An11	MB03-001113	Annobon, GG	EU164490	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An12	MB03-001114	Annobon, GG	EU164491	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An13	MB03-001115	Annobon, GG	EU164492	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An14	MB03-001116	Annobon, GG	EU164493	Jesus et al. (2007)
<i>Panaspis annobonensis</i>	An15	MB03-001117	Annobon, GG	EU164494	Jesus et al. (2007)
<i>Panaspis thomensis</i> sp. nov.	Sv1	MB03-001118	Vale do Contador, São Tomé, GG	EU164478	Jesus et al. (2007)
<i>Panaspis thomensis</i> sp. nov.	Sv2	MB03-001119	Vale do Contador, São Tomé, GG	EU164479	Jesus et al. (2007)
<i>Panaspis thomensis</i> sp. nov.	L12-ST49	MB03-000948	Jardim Botânico, São Tomé, GG	MG593145	This study
<i>Panaspis thomensis</i> sp. nov.	L13-ST50	MB03-000949	Jardim Botânico, São Tomé, GG	MG593143	This study
<i>Panaspis thomensis</i> sp. nov.	L14-ST51	MB03-000950	Jardim Botânico, São Tomé, GG	MG593144	This study
<i>Panaspis thomensis</i> sp. nov.	L15-16S-58	MB03-000947	Lagoa Amélia, São Tomé, GG	MG593142	This study
<i>Leptosiaphos vigintiserierum</i>		ZFMK 69429	Mt. Nlonako, Cameroon	AY308258	Schmitz (2003)

Morphological methods

Specimens were measured with a digital calliper. Lepidosis was observed with a stereomicroscope. All specimens used in the morphological analyses are listed in the Appendix. Scale nomenclature, scales counts and measurements used in the description follow Broadley (2000) and Jacobsen & Broadley (2000). We measured the following 23 characters: snout–vent length (SVL), from the snout to the vent; tail length (TL), from cloaca to tip of tail, measured only in specimens with complete original tails; head length (HL), from tip of snout to anterior tympanum border; head height (HH), from the base of the maxilla to the top of head; head width (HW), at the widest part of the maxilla; eye-diameter (ED); eye-tympanum distance (ET); eye-snout distance (ES), from the front of the eye to the tip of the snout; length of the arm (LA); length of the forearm (LFA); length of the leg (LL); length of the foreleg (LFL); distance between limbs (LD), minimum distance between the insertion of the anterior and posterior limbs; number of scale rows at midbody (MSR); number of scales dorsally (SAD), from the nuchal (excluded from count) to base of the tail; number of scales ventrally (SAV), from the mental (excluded from count) to the anal plate (excluded); number of subdigital lamellae under Finger-IV (LUFF); number of subdigital lamellae under Toe-IV (LUFT); number of supralabials (SL), with those widened in subocular position indicated between brackets; number of supraciliaries (SC); kind of contact between parietals (CP); kind of contact between frontoparietals (CFP); kind of contact between prefrontals (CPF); kind of contact between prefrontal and preoculars (CPF/PO). Finally, coloration pattern was reported, and high-resolution photographs of preserved specimens taken. These data were compared with relevant literature on the group (Bedriaga 1892; Fuhn 1972; Perret 1973).

Results

The aligned dataset contained 405 bp with 107 variable sites, of which 86 were parsimony informative (Table 2). Plots of observed pairwise divergences of haplotypes for transitions and transversions against total sequence divergence revealed negligible saturation (data not shown). Our data suggests that there is no gene flow among species of the clade *P. cabindae* + *P. annobonensis* + *P. africana* + *P. thomensis* sp. nov., which was expected, because of the isolation of the islands. Phylogenetic analyses recover the group composed as *P. africana*, *P. thomensis* sp. nov., *P. cabindae* and *P. annobonensis* as monophyletic (Fig. 2). Within this group, there are two strongly supported monophyletic clades, one composed of the São Tomé population and *P. africana*, and the other *P. cabindae* and *P. annobonensis*. Within the first clade, *P. africana* and the São Tomé form was strongly supported as being reciprocally monophyletic, with a genetic distance of 4.3–5.1% (average = 4.6%) for the mitochondrial marker 16S. The second clade, composed by *P. cabindae* and *P. annobonensis* is also strongly supported as being reciprocally monophyletic (Fig. 2), with a genetic distance of 2.4–3.2% (average = 2.7%) for the same gene. These average values fall within the values founded between the other species of the Gulf of Guinea and mainland (see Table 3). *P. africana*, *P. annobonensis* and the São Tomé population didn't show any particular signs of internal structure, whereas this structure is evident in *P. cabindae*. The number of haplotypes and the number of individuals of the species *P. cabindae*,

Table 2. Subset of variable sites of the partial sequences of 16S. In this table, only *Panaspis cabindae* (Pc) *Panaspis africana* (Paf), *Panaspis annobonensis* (Pan) and *Panaspis thomensis* (Pt) are considered. Additional data are available through the GenBank sequences.

Haplotype	Variable sites	Number of individuals per species bearing a haplotype			
		Pc	Paf	Pan	Pt
H1	ATCAATGAAA AGACCGACAC GGCCAGGCAA CCGAT----- -AAGACTA	1			
H2 A A A ----- - CG	2			
H3	. C G A A ----- - G	2			
H4	. C A A ----- - G	1			
H5 GG AG . G A ----- - G	1			
H6	. C A A ----- - CG	1	15		
H7	. . GC . A CTCT GC . . CCCACAA ACCAG . G		1		
H8	. . GC . A T . CTCT GC . . CCCACAA ACCAG . G		6		
H9	. . GC . A CT . T GC . . CCCACAA ACCAG . G		1		
H10	. . . C . A G . . CT . T GC . . CCCACAA ACCAG . G		1		
H11	G . GC . A CTCT GC . . CCCACAA ACCAG . G		1		
H12	. . GC . A G . . CT . T GC . . CCCACAA ACCAG . G		1		
H13	G . T . C . A TA . CTCT . AAAGACT . T ATCCAAAAC T ACCAGT . G				2
H14	G . T . C . A TA . CTCT . AAAGATT . T ATCCAAAAC T ACCAGT . G				3
H15	G . T . C . A A . CTCT . AAAGATT . T ATCCAAAAC T ACCAGT . G				1
H16	G . T . GC G A C . ACCCG - C . C . . . CG			1	
H17	G . T . GC G G A C . ACCCG - C . C . . . CG			2	
H18	G . T . GC G A C . ACCCG - C . C . . . CG			10	
H19	G . T . GC G A C . ACCCGG C . C . . . CG			1	

P. africana, *P. thomensis* sp. nov. and *P. annobonensis*, carried a particular haplotype and are shown in Table 2. No haplotypes are shared among species of the clade *P. cabindae* + *P. annobonensis* + *P. africana* + *P. thomensis* sp. nov., Mensural and meristic data for the specimens of the genus *Panaspis* from Príncipe, São Tomé and Annobon are presented in Table 4. São Tomé and Príncipe forms are morphologically similar, but easily separated genetically. Detailed diagnoses for the different forms are given in the taxonomic accounts below. A list of all the different chresonyms that have been applied to the taxon in each of the Islands is presented in all accounts, each of the chresonyms is followed by a list of references (including author, date and page) where they were used. Combining the morphological and molecular evidence presented above, we adopt the general lineage species concept (de Queiroz 1999) and recognise one additional species of the genus *Panaspis* from São Tomé Island. Our results confirm the specific identity of *P. annobonensis* from Annobon Island.

Systematics

Panaspis thomensis Ceriaco, Soares, Marques, Bastos-Silveira, Scheinberg, Harris, Brehm & Jesus, sp. nov. (Figs 3, 4)

Mococa africana (Gray 1845: 83; Greef 1884: 48; Bocage 1886: 68; 1889: 34; Vieira 1886: 237)

Lygosoma africanum (Bedriaga 1892: 814; Bocage 1905: 92; Boulenger 1906: 206; Manaças 1958: 185; Henriques 1917: 143)

Lygodactylus [sic] *africanus* (Henriques 1917: 81)

Riopa africanum (Smith 1937: 229)

Panaspis africana africana (Fuhn 1972: 261)

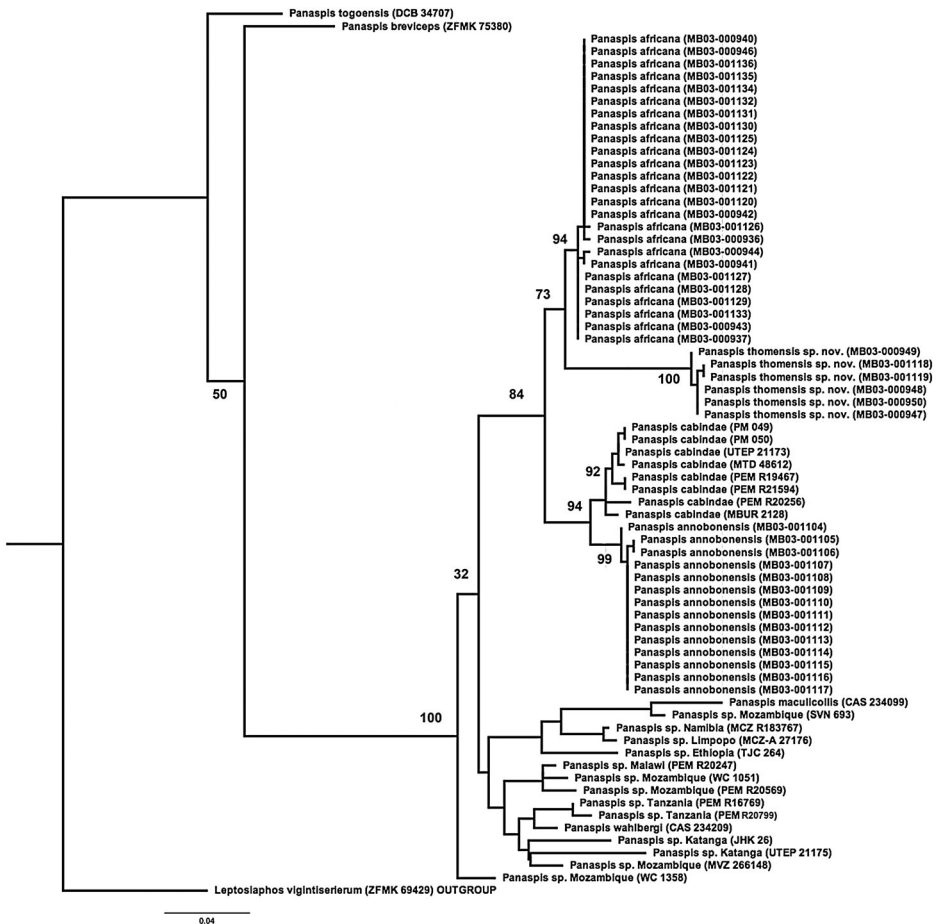


Figure 2. Tree derived from Maximum Likelihood analysis of 16S fragment. Average posterior probabilities are shown near nodes. The tree was rooted using *Leptosiaphos vigintiserierum*.

Panaspis africana (Schätti & Loumont 1992: 29; Perret 1973: 605)

Leioliopisma africana (Mittleman 1952: 10)

Leptosiaphos africana (Haft 1993: 59, 65)

Afroablepharus africana (Jesus et al. 2007)

Table 3. Descriptive statistics of 16S p-uncorrected pairwise distances between the sequences of the four species, *Panaspis cabindae*, *Panaspis africana*, *Panaspis thomensis* and *Panaspis annobonensis*. In each cell, the upper line gives mean \pm standard deviation; the lower line gives the maximum and minimum.

	<i>Panaspis cabindae</i>	<i>Panaspis africana</i>	<i>Panaspis thomensis</i>	<i>Panaspis annobonensis</i>
<i>Panaspis cabindae</i>	0.010 \pm 0.006 [0.018; 0]	0.044 \pm 0.002 [0.048; 0.037]	0.046 \pm 0.001 [0.076; 0.068]	0.027 \pm 0.002 [0.032; 0.024]
<i>Panaspis africana</i>		0.002 \pm 0.002 [0.008; 0]	0.046 \pm 0.001 [0.051; 0.043]	0.045 \pm 0.002 [0.051; 0.042]
<i>Panaspis thomensis</i>			0.002 \pm 0.002 [0.005; 0]	0.065 \pm 0.002 [0.068; 0.062]
<i>Panaspis annobonensis</i>				0.001 \pm 0.001 [0.05; 0]

Table 4. General comparison between *Panaspis* species from Príncipe, São Tomé and Annobon Islands. Data presented as Mean [rounded to the nearest whole number] (min–max; standard deviation). All mensural characters are in mm. Abbreviations are the same as those described in Materials and methods.

	<i>Panaspis africana</i> – Príncipe (n = 32)	<i>Panaspis thomensis</i> sp. nov. – São Tomé (n = 19)	<i>Panaspis annobonensis</i> – Annobon (n = 12)
SVL	35 (22–42.5; 4.9)	39.5 (31.1–47.7; 4.6)	32.5 (28–37.3; 2.4)
TL	30.2 (16–47.9; 7.1)	38 (23.2–60.4; 10.4)	-
HL	7.3 (5.6–9.3; 0.8)	7.4 (6.1–8.8; 0.7)	6.6 (5.8–7.4; 0.4)
HH	3.2 (1.8–4; 0.5)	3.5 (2.6–4.7; 0.5)	2.8 (2–3.1; 0.3)
HW	4.8 (3.3–5.6; 0.7)	4.9 (4–6.3; 0.6)	4 (3.2–4.4; 0.4)
LA	2.4 (1.5–3.6; 0.5)	2.3 (1.1–3.4; 0.6)	2.6 (1–3.2; 0.8)
LFL	2.4 (1.4–3.2; 0.4)	2.1 (1.2–3.4; 0.6)	2.8 (2–3.2; 0.5)
LL	3.3 (1.8–4.3; 0.6)	3.3 (2.1–4.3; 0.6)	3.2 (1.9–3.9; 0.7)
LFL	3 (1.5–4.5; 0.7)	3 (1.6–4.8; 0.9)	3.2 (1.8–4.5; 0.8)
LD	17.9 (9.8–31; 3.9)	21.7 (16.5–26.3; 3.1)	16.7 (13.7–19.7; 1.7)
ED	1.6 (0.9–2.9; 0.4)	1.4 (0.8–1.8; 0.2)	1.7 (1–3.5; 1)
ET	3.1 (2.3–3.8; 0.4)	3.1 (2.4–3.8; 0.4)	2.8 (2.2–4.4; 0.7)
ES	2.5 (1.7–3.2; 0.4)	2.7 (2.1–3.1; 0.3)	2.4 (1.8–3.1; 0.4)
MSR	25 (23–28; 1.1)	26 (24–29; 1.3)	25 (24–27; 1.2)
SAV	46 (29–54; 6.6)	49 (37–64; 7.9)	37 (25–40; 4)
SAD	53 (47–64; 3.1)	57 (46–62; 3.1)	54 (52–59; 1.9)
LUFT	12 (7–15; 1.5)	12 (10–14; 0.9)	16 (12–17; 1.4)
LUFF	8 (6–10; 1)	8 (7–10; 0.8)	11 (9–12; 0.9)
SC	5 (4–6; 0.6)	5 (5–6; 0.3)	5 (5–6; 0.3)
SL	6 (5–6; 0.5)	6 (5–6; 0.2)	6 (6–7; 0.3)
CP	Always in contact	Always in contact	Always in contact
CFP	Always in contact	Always in contact	Half times separated. half times in contact
CPF	Always separated	Usually separated, but sometimes in contact in a single point	Half times separated. half times in contact
CPF/PO	Always separated	Always in contact	Always in contact

Holotype—MB03-000947, adult male collected on a trail between Bom Sucesso Botanical Garden and Lagoa Amélia (N: 0.28825, E: 6.608466; WGS-84), São Tomé Island, Republic of São Tomé e Príncipe, by Luis Ceriaco and Mariana Marques on 15 February 2015 (Fig. 3).

Paratypes—All specimens from the Island of São Tomé, Republic of São Tomé and Príncipe. Eight specimens: MB03-00948 and MB03-00949, adult male, with the same collecting locality, collectors and date as the holotype; IICT 47-1954 adult male collected in Roça Monte Café (N: 0.30015, E: 6.63986; WGS-84) by Fernando Frade on 25 November 1954; IICT 50-1954, adult male collected in Roça Nova Moka (N: 0.28738, E: 6.63334; WGS-84) by Fernando Frade on 26 November 1954; MHNG 2496.11, adult female collected in Roça Monte Café (N: 0.30015, E: 6.63986; WGS-84) by Fernando Frade on 25 November 1954; MHNG 2540.63, adult unsexed collected in “São Tomé” (no precise locality) by Adolfo Moller on an unknown date (possibly 1885); CAS 219046 adult unsexed collected in trail between Bom Sucesso and Lagoa Amélia (N: 0.26800, E: 6.59131; WGS-84) by Robert C. Drewes, Ricka E. Stoelting and Jens V. Vindum on 14 April 2001; CAS 233693 adult unsexed collected in 0.8 km west (by road) from Abade (N: 0.25411, E: 6.64458; WGS-84) by Robert C. Drewes, J. Uyeda and Jens V. Vindum on 16 May 2006.

Diagnosis—*Panaspis thomensis* sp. nov. can be distinguished from other Gulf of Guinea Oceanic Islands *Panaspis* by the following characteristics 1) preocular and prefrontal

scales in contact; 2) a medium SVL (31.1–47.7 mm); 3) the limbs do not touch each other when addressed to the body; 4) an high number of paraventral scales (37–64); 5) between 10 to 14 lamellae under the fourth toe and 7 to 10 under the fourth finger; 6) an orange-brown coloration on the body.

Description of the holotype—Adult male in good condition. Arrangement and relative size of head, body and tail scales typical for *Panaspis* (Fig. 3). Robust and cylindrical body with short pentadactyl limbs. Fore- and hind-limbs do not overlap when addressed against the body. SVL 35.9 mm, tail length 39 mm. Head length 7.3 mm, with relatively acuminate snout (HL 155.4% HW). Other relevant measurements are presented in Table 5. Rostral wider than long. Rostral visible from above, nostrils set posteriorly so that post-nasal effectively borders nostril. Frontonasal wider than long, in contact with postnasal, two prefrontals and frontal. Prefrontals slightly hexagonal, separated by the frontal, and in contact with the following head shields: frontonasal, loreal, preocular, first supraoculars, and frontal. Two loreals, the posterior and dorsal margins of the largest loreal border one enlarged preocular. Frontal diamond-shaped, length 1.6 times the distance between anterior tip of frontal and tip of snout, in contact with prefrontals, the two anterior supraoculars and with both frontoparietals.

Frontoparietals two, in contact with each other, the frontal, second, third and fourth supraoculars, parietal and interparietal. Frontoparietal plus interparietal length is 1.25 times the length of the frontal. Interparietal with visible parietal foramen; parietals about two times larger than frontoparietals and in contact at the anterior point of the interparietal. Parietals in broad contact. A pair of large, broad nuchals collectively bordered by a total of six dorsals. Supraciliaries six, fifth largest. Supralabials seven, the fifth being the subocular. Infralabials seven. Transparent scale present in lower eyelid.



Figure 3. Holotype (MUHNAC/MB03-000947) of *Panaspis thomensis* sp. nov. (Photograph: Luis Ceriaco).



Figure 4. Live photograph of *Panaspis thomensis* sp. nov. (Photograph by Dong Ling).

Two pre-temporals. Tympanum visible, approximately the same height as eye. Dorsal scales smooth, without keels. Ventral scales smooth. MSR 27, SAD 56, SAV 57. Limbs with five digits; scales on soles of hands and feet smooth. Relative length of fingers III > IV > II > I > V, relative length of toes IV > III > V > II > I. Finger-IV lamellae 8 (right side), Toe-IV lamellae 12 (right side). Tail long, robust and tapering smoothly. In preservative, background colour of flanks and upper side of head, neck, dorsum, legs and tail dark-brown, with darker dorso-lateral lines, and some light-coloured speckles in the limits of those lines. Between the dorso-lateral lines, incomplete and thinner dark lines run on the midbody. A thin dark lateral line runs from the tympanum to the beginning of the tail. Supralabials present a distinctive whitish blotch, surrounded anteriorly and posteriorly by scattered small dark spots. Infralabials present some dark-brown dots that extend to the chin. Venter uniformly whitish-yellow, although in the transition from venter to dorsal sides of the body, there is a dark-brown pigmentation, forming small disperse patches.

Variation—Variation in scalation and body measurements of the paratypes of *P. thomensis* are reported in [Table 5](#). The majority of the paratype agree entirely with the holotype, except regarding the contact between the prefrontals, which are separated, but not in the case of IICT 50-1954, MB03-00949 and MHNG 2496.11, where the prefrontals contact narrowly at a single point.

Colour—Colour in life ([Fig. 4](#)): orange-brown background on flanks and upper side of head, neck, dorsum, legs and tail, with a distinctive dark dorsolateral band, speckled with some light-coloured scales, starting near the tympanum and running along the entire dorsum to the anterior half of the tail. In some specimens, there are some irregular

Table 5. Measurements (in mm) and scale counts of the holotype and paratypes of *Panaspis thomensis* sp. nov. Abbreviations are the same as those described in Materials and methods.

	MB03 000947 (holotype)	MB03 000948 (paratype)	MB03 000949 (paratype)	IICT 47-1954 (paratype)	IICT 50-1954 (paratype)	MHNG 2496.11 (paratype)	MHNG 2540.63 (paratype)	CAS 219046 (paratype)	CAS 233693 (paratype)
SVL	35.9	44.6	43.3	33.9	43	45.5	47.7	50.1	40.9
TL	39	29.6	31.7	43.1	-	55.2	60.4	54.2	48.0
HL	7.3	7.8	7.9	6.6	8.3	8.1	8.8	8.6	7.9
HH	3.3	3.1	3	3.4	3.7	3.7	4.6	4.3	3.5
HW	4.7	5.9	5.1	4.5	5.4	5.6	6.3	6.5	5.5
LA	3.2	3.4	2.4	2.3	2.3	1.7	3	4.0	3.4
LFA	2.1	2.9	2.7	2.2	3	2.7	2.3	3.3	3.1
LL	3.7	4.3	3.7	2.7	4.1	4.2	4	5.1	4.1
LFL	2.9	3.9	4.1	2.7	4.3	3.1	3.9	4.1	4.0
LD	20.2	25.1	23.8	19.2	22.7	26.1	26	27.7	24.6
ED	1.6	1.8	1.2	1.4	1.2	1.2	1.5	1.7	1.3
ET	3	3.5	2.7	3	3.5	3.1	3.8	4.2	3.8
ES	2.8	2.6	2.9	2.3	2.9	3.1	3	3.8	3.1
MSR	24	29	25	26	24	26	27	25	25
SAV	56	56	56	46	55	59	56	52	54
SAD	38	39	40	40	37	64	51	58	58
LUFT	12	13	12	10*	12	12	13	12	12
LUFF	8	9	8	7*	8	10	9	10	10
SC	6	5	5	5	5	5	5	6	6
SL	6	6	6	6	6	6	5	6	6

dark-brown lines in the dorsum, between the two dorsolateral bands. A dark-brown line starts on the top of the prefrontal and extends until the temporal, across the supraciliaries. Upper labials have a distinctive whitish blotch, surrounded anteriorly and posteriorly by scattered small dark spots. This pattern extends to the infralabials, and the small dark spots briefly enter into the limits of ventral side of the mandibula. Venter whitish, spotless. The underside of the tail bears scattered dark speckles. Female specimens have a vivid orange coloration between the cloaca and the anterior part of the tail.

Comparison with other Gulf of Guinea *Panaspis*—Table 4 summarises the most important distinguishing characteristics between *P. thomensis* and all other Gulf of Guinea oceanic island *Panaspis*. Comparing *P. thomensis* with *P. africana*, *P. thomensis* the preocular scale is in contact with the prefrontal scale, whereas in *P. africana* the preocular is separated from the prefrontal by the obtusion of the posterior supraciliar and the loreal. In *P. thomensis* the subocular (5th supralabial) is twice as long as wide, whereas in *P. africana* it is approximately as long as wide. In the new species has a larger SVL (31 to 47 mm in *P. thomensis* versus 22 to 42 mm in *P. africana*), and a higher number of ventral scales between the mental and the cloaca (37 to 64 in *P. thomensis* versus 29 to 54 in *P. africana*). The two species do not exhibit any consistent differences in color, although Príncipe individuals tend to be darker than the São Tomé species. Despite the differences cited in the morphological and meristic cranial between *P. thomensis* and *P. africana*, both species are morphologically very similar. Comparing *P. thomensis* with the Annobon endemic *Panaspis annobonensis*, the new species has a higher number of MSR (24 to 29 in *P. thomensis* versus 24 to 27 in *P. annobonensis*), a slightly lower number of LUFT (10 to 14 in *P. thomensis* versus 13 to 17 in *P. annobonensis*) and lower number of LUFF (7 to 9 in *P. thomensis* versus 9 to 12 in *P. annobonensis*). In *P. thomensis* the upper palpebrals (usually 7) are roughly the same size, whereas in *P. annobonensis* the fifth upper palpebral is considerably larger, extending along almost the entire upper region of the eye. In *P. thomensis* the preocular scale is in contact with the prefrontal scale, whereas in *P. annobonensis* the preocular is separated from the prefrontal by the obtusion of the posterior supraciliar and the loreal. In terms of coloration, *P. annobonensis* is considerably darker than *P. thomensis*, and has a well defined dark subocular band. The throat of *P. annobonensis* is homogeneously speckled with dark-brown speckles, whereas in *P. thomensis* these speckles only occur in the margins.

Distribution—Endemic to São Tomé Island, Rolas Islet and Santana Islet, Republic of São Tomé & Príncipe, West Africa.

Habitat and natural history notes—The newly described species occurs in the leaf litter of primary and secondary forests of São Tomé Island. It can sometimes be found along the limits of the forests, in more opened areas. Manaças' analysis of stomach contents revealed a diet composed of Dermaptera and other unidentified insects (Manaças 1958).

Etymology—The specific epithet "*thomensis*" refers to the Island of São Tomé and is applied here as a substantive in apposition. We propose the English name of "São Tomé Leaf-litter Skink" and the Portuguese name "Lagartixa da manta morta de São Tomé".

***Panaspis africana* (Gray, 1845)**

(Figs 5, 6)

Mocoo africana (Gray 1845: 83)*Lygosoma* (*Mocoo*) *africanum* (Peters 1874: 162)*Lygosoma africanum* (Boulenger 1887: 265; Bocage 1903: 53; Boulenger 1906: 206; Manaças 1958: 185)*Riopa* (*Panaspis*) *africanum* (Smith 1937: 229)*Panaspis africana africana* (Fuhn 1972: 261)*Panaspis africana* (Schätti & Loumont 1992: 29; Perret 1973: 605)*Leptosiaphos africana* (Haft 1993: 59, 65)*Afroablepharus africana* (Schmitz et al. 2005; Jesus et al. 2007)

Despite the taxonomic and nomenclatural issues regarding its identity, *Panaspis africana* is probably one of the most studied and well known species of the Príncipe herpetofauna (see for example Perret 1973 and Haft 1993). The abundance of the species on Príncipe, in forested areas, agricultural fields, but also wherever there is leaf litter, makes it one of the easiest species to locate in the Island of Príncipe.

As noted above and shown in Table 4, all mensural, and the majority of meristic characters overlap considerably, turning problematic the decision regarding the allocation Gray (1845) holotype, which type locality is imprecise, to one of the two islands. Almost all of mensural and meristic characters of the holotype falls among the overlapping range. The only character that allows a tentative allocation of the original Gray holotype (Fig. 5) to Príncipe population is the separation between the preocular and prefrontal,



Figure 5. Holotype (BMNH 1946.8.18.05) of *Mocoo africana* Gray, 1845, from "West Africa" (Photograph: Natural History Museum, London).



Figure 6. ABOVE: Live photograph of a specimen (MUHNAC/MB03-000937) of *Panaspis africana* (Gray, 1845) (Photograph: Luis Ceriaco) BELOW: Live specimen of *Panaspis africana* from Príncipe Island presenting a bifurcated tail (Photograph: Luis Ceriaco).

because of the obtrusion of the posterior supraciliar and the loreal, as noted above, in the São Tomé population the preocular and the prefrontal contact. Consequently, we follow the original suggestion by Jesus et al. (2007), and restrict *Mocoo africana* type locality to Príncipe Island.

Diagnosis—*Panaspis africana*. can be distinguished from other Gulf of Guinea Oceanic Islands *Panaspis* by the following characteristics 1) preocular and prefrontal scales not in contact; 2) a medium SVL (22–47.5 mm); 3) the limbs do not touch each other when adpressed to the body; 4) an high number of paraventral scales (29–54); 5) between 7 to 15 lamellae under the fourth toe and 6 to 10 under the fourth finger; 6) an orange-brown coloration on the body.

Variation—*Panaspis africana* are characterised as small to medium-sized skinks (SVL 22–42.5 mm) with tail length approximately the 90% of SVL, robust and tapering smoothly. Head wide and not very acuminate (HW /HL 65,6%), approximately 21% of SVL. Prefrontals always separated. Supraciliaries usually 4, sometimes 5 and rarely 6; 4 supralabials anterior to subocular; enlarged subocular in direct contact with the lip and not reduced basally by the intrusion of adjacent supralabials. Midbody scales rows 23–28, paravertebral scales 47–64, and paraventral scales 29–54. Lamellae beneath the fourth finger 6–10, beneath the fourth toe 7–15.

Colour—Dark-brown background on flanks and upper side of head, neck, dorsum, legs and tail, with a distinctive dark dorsolateral band, speckled with some light-coloured scales, starting near the tympanum and running along the entire dorsum to the anterior half of the tail (Fig. 6). In some specimens, there are some irregular dark-brown lines in the dorsum, between the two dorsolateral bands. A dark-brown line starts on the top of the prefrontal and extends to the temporal, across the superciliaries. Upper labials exhibit a small whitish blotch, limited anteriorly and posteriorly by a dark band. This blotch extends to the infra labials, and the small dark spots briefly enter into the limits of ventral side of the mandibula. Venter and underside of the tail whitish, immaculate. Female specimens have vivid orange coloration between the cloaca and the anterior part of the tail.

Distribution—Endemic to Príncipe Island, Republic of São Tomé & Príncipe, West Africa.

Habitat and Natural History notes—Similar to the São Tomé form, *Panaspis africana* occurs in under the fallen leaves of the primary and secondary forests of Príncipe Island. It can sometimes be found at the limits of the forests, in more opened areas. The species is very abundant in areas with leaf litter. These skinks are usually more active during the mornings (until 14:00) and the maximum known altitudinal occurrence is at 528 m, on Pico Papagaio (specimen MB03-001035). There are no explicit dietary data for the species, but specimens have been seen consuming small arthropods (LMPC pers. obs.). Two of the collected or observed specimens had a bifurcated tail (Fig. 6).

***Panaspis annobonensis* (Fuhn, 1972)**

(Fig. 7)

Lygossoma africanum (Bocage 1903: 59; Boulenger 1906: 206)

Panaspis africana annobonensis (Fuhn 1972: 262; Jesus et al. 2003: 20)

Panaspis annobonensis (Perret 1973: 605)

Leptosiaphos annobonensis (Haft 1993: 59)

Similar to all other Annobon endemics, little is known about *P. annobonensis*. Because of the isolation of the island and difficulty of access, few specimens of this species exist in collections. The first record of this species, at the time considered by Bocage (1903) as conspecific to *africana*, was collected in the late 1880s by Francisco Newton, whose specimens were then deposited in the collections of the Natural History Museum of Lisbon. These specimens were lost in the fire that destroyed the collections of Museu Bocage in 1978. Some years later, during his expedition to the Gulf of Guinea and West Coast of Africa, Leonardo Fea collected additional specimens, also classified by Boulenger (1906) as *africana*, which were deposited in both the British Museum of Natural History (England) and the Museo Civico di Istoria Naturale di Genova (Italy). Alfred Stauch in 1963 and Roger Taufflieb in 1964 collected 21 and 5 specimens, respectively, of *annobonensis*, which they deposited in the collections of the Muséum national d'Histoire Naturelle in Paris (France), and were later used by Fuhn (1972) to describe the subspecies (plus two specimens from Fea collection, housed in the British Museum). More recently, a team from the University of Madeira, led by D.J. Harris, visited the island in 2002 (Jesus et al. 2003) and collected several specimens ($n = 12$), currently housed in the collections of MUHNAC.

P. annobonensis belongs to the same clade as *P. africana* and *P. cabindae*, and are both sister to other *Panaspis* from central, eastern and southern Africa (Medina et al. 2016). This explains the morphological similarity between the species. According to the original description (Fuhn 1972), the main characters that distinguish *P. annobonensis* from *africana sensu lato* (including *P. thomensis*) are its longer limbs, which touch each other when adpressed along the midbody, an higher number of subdigital lamellae under the fourth finger and fourth toe, the presence of a large first loreal scale, darker coloration,



Figure 7. Specimen (MUHNAC/MB03-001104) of *Panaspis annobonensis* (Fuhn, 1972) (Photograph: Luis Ceriaco).

a well marked dark subocular band, and a black speckled throat speckled. In the majority of the specimens of the type series (16 out of 26) the frontonasals are not in contact, whereas in a smaller number the frontonasals are in contact at a single point.

Given its rarity and the lack of data regarding the species, we present here a diagnosis to the species and data concerning the specimens currently deposited in MUHNAC collections.

P. annobonensis are small to medium-sized skinks (SVL 28–37.3 mm) with a robust smoothly tapered tail. Head wide and not much acuminate (HW /HL 60%), approximately 20% of SVL. Prefrontals separated or in contact. Supraciliaries separated or in contact, usually 5 and rarely 6; 4 supralabials anterior to subocular; wide subocular in direct contact with the lip and not reduced basally by the intrusion of adjacent supralabials. Midbody scale rows 24–27, paravertebral scales 52–59, and paraventral scales 25–40. Lamellae beneath the fourth finger 9–12, beneath the fourth toe 13–17. All examined specimens have faded colouration resulting from preservation, although some patterns are visible in all specimens, such as a well-marked dark subocular band and a black speckled throat. General colouration is orange-brown, with dorsal surfaces of the head being much more homogeneous than the other two species. A distinctive dark dorsolateral band starts near the tympanum and runs along the entire dorsum to the anterior half of the tail, with some irregular dark-brown lines in the dorsum, between the two dorsolateral bands.

Distribution—Endemic to Annobon Island, Republic of Equatorial Guinea, West Africa.

Habitat and natural history notes—According to Jesus et al. (2003), the species has a restricted distribution in the island, usually found among leaf litter in the forest, and very rarely in dry places or near the coast. However, according to the authors, the species is abundant and present in relatively high densities in the areas where it occurs.

Discussion

In the past five years, the rate of discovery and description of new species of vertebrates in the Gulf of Guinea Oceanic islands has risen considerably. This can be explained, in part, by the increased use of molecular techniques, which has uncovered neglected cryptic diversity, but also to an increase in fieldwork on the islands by various teams and institutions. The works of Jesus et al. (2005a, 2005b, 2005c, 2007, 2006, 2009) and Measey et al. (2007) provided an important background on the phylogeography and phylogenetic relationships of the islands' herpetofauna, which was later complemented by the description of new taxa and the review of forgotten *nomina* by Uyeda et al. (2007), Miller et al. (2012), Ceriaco (2015) and Ceriaco et al. (2015, 2016, 2017). The current status of our knowledge of the terrestrial vertebrate diversity on the islands of Príncipe, São Tomé and Annobon, indicates that the majority of the occurring species are endemic to each specific island, whereas only a very small minority represent widespread species recently introduced/arrived to the islands. However, current data also indicates that despite this "endemicity pattern" in each island, colonisation and speciation processes are diverse across taxa. Species from the same genus, for example the two endemic shrews of the genus *Crocidura* (Mammalia: Insectivora) that inhabit São Tomé (*Crocidura thomensis* Bocage 1887) and

Príncipe, (*Crocidura fingu*i Ceriaco et al. 2015) are the result of two independent colonisation events, from different geographic sources (Ceriaco et al. 2015). This also appears to be the case for the five skinks species of the genus *Trachylepis* (Squamata: Scincidae; Ceriaco et al. 2016), the leaf-litter skink *Panaspis annobonensis* (current study), and the two puddle frogs of the genus *Phrynobatrachus* (Anura: Petropedetidae; Uyeda et al. 2007). Conversely, there are several examples of sister species, which occur one on each island, whose ancestral colonisation was initially one island and from there to the other/others, through a “stepping stone” process. This is clearly the case of some reed frogs species of the genus *Hyperolius* (Anura: Hyperoliinae; Bell et al. 2015), house-geckos of the genus *Hemidactylus* (Squamata: Gekkonidae; Miller et al. 2012), brown-house snakes of the genus *Boaedon* (Squamata: Lamprophiidae) and the leaf-litter skinks of the genus *Panaspis* from São Tomé and Príncipe islands (Jesus et al. 2007; this paper). Thirdly, there is the case of the remaining endemics, which are the single representatives of their genus/lineage on the islands (for example the caecilian *Schistometopum thomensis* from São Tomé Island, or the Príncipe Island legless skink *Feylinia polylepis*), which most likely represent a single and independent colonisation event (Stoelting et al. 2014).

According to our analysis, the four species (*P. africana*, *P. cabindae*, *P. thomensis* and *P. annobonensis*) form a single, highly supported clade and the relationships between *P. africana*, *P. cabindae* and *P. annobonensis* are similar to those found by Medina et al. (2016). However, our results contradict Jesus et al. (2007), which stated that the Gulf of Guinea leaf-litter skinks form a monophyletic group, which most likely resulted from a single colonisation event to the islands. The inclusion of *P. cabindae* (which is itself a species complex in need of revision, L. Ceriaco pers. obs.) demonstrates that the colonisation of the Gulf of Guinea Islands by *Panaspis* occurred at least twice: an initial colonisation by the common ancestors of *P. africana* and *P. thomensis* to one island first, as stated by Jesus et al. (2007), followed by dispersal from the initial island through a “stepping stone” process; and then a second colonisation event to Annobon directly from the mainland, reflected in the sister relationship between *P. annobonensis* and *P. cabindae*. This latter situation presents remarkable biogeographic similarities to that of the snake, *Philothamnus girardi* Bocage, 1893, endemic to Annobon, and *Philothamnus dorsalis* (Bocage, 1866) from northern Angola and the Congo Basin (Engelbrecht et al. 2017). The phylogenetic relationship of the Gulf of Guinea *Panaspis* with *P. cabindae*, a Central African species complex extending from the Democratic Republic of Congo to northwest Angola, also presents noteworthy similarities to the case of two lineages of reed frogs of the genus *Hyperolius*. The *Hyperolius molleri* group occurs on both São Tomé and Príncipe Islands, and are sister taxa to the *H. cinnanomeoventris* species complex (Bell et al. 2015; Bell 2016), a Central African group, sympatric with the *P. cabindae* complex through a considerable part of its distribution. It has already been suggested by Measey et al. (2007) that the outflow of the major river basins along the western coast of Africa, in combination with regional sea currents, could be the major drivers of colonisation of terrestrial taxa across these islands. In the present case, it can be hypothesised that rafting material from the Congo River might have been “directed” to the islands by the strong south-to-north flowing Benguela Current.

Recognizing the true diversity of the terrestrial vertebrate fauna of these islands is of crucial importance for both our understanding of the evolutionary forces and colonisation patterns that acted on these islands in the past, and to inform management and

conservation strategies for the future of the islands. Despite their small area and the considerable number of surveys and studies across the islands over the past two centuries, the biodiversity of the Gulf of Guinea Islands are still suffering from a “Linnean shortfall” (Lomolino, 2004), because there are currently no solid or concrete numbers regarding the number of species that occur there.

The recent taxonomic history of the Gulf of Guinea leaf-litter skinks is also an example of the current reality of taxonomy as a discipline. Although in the past taxonomy (i.e. the correct identification of faunas and description of new species) was an objective in itself, now it is usually a secondary outcome of phylogenetic and phylogeographic studies, more focused on the evolutionary patterns that shape diversity in a given taxonomic group or geographic context, than in the species identification itself. This leads to the discovery of unknown and often unnamed lineages that have been neglected in the past. However, although it is important to quickly and properly taxonomically settle these divergent lineages after their discovery through phylogenetic/phylogeographic studies, this does not usually happen in a rapid fashion. In the present case, the time between the discovery of the genetic divergence between the island populations (Jesus et al. 2007) and the present species description was a decade. Many causes, not discussed in the present paper, may contribute to this “taxonomic delay”, but an immediate consequence is the impossibility of applying any needed conservation measures, because most legislative texts, red lists, custom documents, etc., only recognise such units if these bear Latin taxonomic *nomina* (Dubois & Raffaelli 2009). Also, when a species is not yet formally described, despite the published evidence that a given population is taxonomically distinct, it becomes harder for local authorities or conservation agencies, sometimes unaware of the given publication or untrained in taxonomy and consequently incapable to interpret taxonomic and nomenclatural implications of those results, to transport those findings to the more practical usages and needs. This is especially important in fragile and unique habitats and the oceanic islands of the Gulf of Guinea, and reinforces the importance and the need for taxonomic and natural history studies for conservation.

With the description of this long-known (but yet unnamed) new species from São Tomé Island, we raise the number of the reptile endemics of the island. Although the newly described species appear to be abundant in the primary and secondary forests of São Tomé Island, very little is known regarding its current population status, distribution and basic natural history. This is also true for the Príncipe endemic, *P. africana*, and for the Annobon endemic, *P. annobonensis*. Both *P. africana* and *P. thomensis* known distribution area appears to be covered by protected areas in their respective islands, however, rapid land use and agricultural changes, especially on São Tomé, could potentially affect the species. More detailed and focused studies are needed to address these questions and highlight the natural history of the Gulf of Guinea oceanic islands leaf-litter skinks.

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ORCID

Luis M. P. Ceriaco  <http://orcid.org/0000-0002-0591-9978>

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Appendix 1. Material examined

This includes specimens used in morphological and molecular analyses, as well as additional specimens with confirmed identity. The specimens used for the morphological analyses are denoted with an *, whereas those in the molecular analyses are listed in [Table 1](#).

Panaspis africana

“West Africa”: *British Museum of Natural History*: BMNH 1946.8.18.05 (holotype) [“West Africa”].

Príncipe Island: *Museu Nacional de História Natural e da Ciência*: MUHNAC/MB03-000936*, MUHNAC/MB03-000937*, MUHNAC/MB03-000938*, MUHNAC/MB03-000939*, MUHNAC/MB03-000940, MUHNAC/MB03-000941, MUHNAC/MB03-00942*, MUHNAC/MB03-00943* [Campo Político; N: 1.6446833, E: 7.395833, WGS-84]; MUHNAC/MB03-000910*, MUHNAC/MB03-000911*, MUHNAC/MB03-000933* [Porto Real; N: 1.62417, E: 7.40502, WGS-84]; MUHNAC/MB03-000912*, MUHNAC/MB03-000913 [Pincaté; N: 1.63205, E: 7.39869, WGS-84]; MUHNAC/MB03-000934, MUHNAC/MB03-000935* [road near to Pedreira; N: 1.62940, E: 7.40312, WGS-84]; MUHNAC/MB03-000944 [Praia Caixa; N: 1.62088, E: 7.37440, WGS-84]; MUHNAC/MB03-000945* [Maria Correia; N: 1.583333, E: 7.35, WGS-84] MUHNAC/MB03-000946 [climb to S^{to} Cristo; N: 1.63427, E: 7.42802, WGS-84]; MUHNAC/MB03-000914*, MUHNAC/MB03-000915*, MUHNAC/MB03-000916*, MUHNAC/MB03-000917*, MUHNAC/MB03-000918, MUHNAC/MB03-000919, MUHNAC/MB03-000920 [road from Pincaté to Oque Nazaré; impossible to geolocate]; MUHNAC/MB03-001120 to 001126 [Terreiro Velho; N: 1.610223, E: 7.420524, WGS-84]; MUHNAC/MB03-001127 to 001132 [Ponta do Sol; N: 1.654429, E: 7.37807, WGS-84]; MUHNAC/MB03-001133 to 001135 [Montalegre; N: 1.6333, E: 7.3833, WGS-84]; Instituto de Investigação Ciência Tropical: IICT 2-1954*, IICT 48-1954* [Roça Nova Moca; N: 0.283333, E: 6.633333, WGS-84]; IICT 71-1955*, IICT 81-1955*, IICT 82-1955*, IICT 83-1955*, IICT 84-1955*, IICT 85-1955*, IICT 88-1955*, IICT 89-1955*, IICT 90-1955*, IICT 91-1955*, IICT 92-1955*, IICT 93-1955*, IICT 95-1955*, IICT 97-1955*, IICT 98-1955* [Aeroporto; N: 1.66508, E: 7.41178, WGS-84]. *California Academy of Sciences*: CAS 219154 [Cerracao Sur Pina; next to Aeroporto; N: 1.66528, E: 7.41439, WGS-84]; CAS 219157, CAS 219158 [Cerracao Sur Pina; N: 1.66661, E: 7.41797, WGS-84]; CAS 219159 [Cerracao Sur Pina; N: 1.67461, E: 7.42486, WGS-84]; CAS 219166, CAS 219167, CAS 219168 [Cerracao Sur Pina; N: 1.67725, E: 7.42700, WGS-84]; CAS 219169 [Cerracao Sur Pina; N: 1.67731, E: 7.42594, WGS-84]; CAS 219191 (next to S^{to} Antonio; N: 1.66078, E: 7.39439, WGS-84); CAS 219209 [Baie das Agulhas; N: 1.60089, E: 7.35306, WGS-84]; CAS 219210 [plantation above Baie das Agulhas; N: 1.59864, E: 7.35306, WGS-84]; CAS 219215 [beach below Jouquim; N: 1.61392, E: 7.40431, WGS-84]; CAS 219395 [Pico de Príncipe; N: 1.58322, E: 7.38297, WGS-84]; CAS 219396 [tributary of Ribeira das Agulhas for Agua Agrião; N: 1.58908, E: 7.37953, WGS-84]; CAS 233417, CAS 233418 [near to Aeroporto; N: 1.65931, E: 7.39539, WGS-84]; CAS 233426 [road between Santo Antonio and São Joaquim; N: 1.62447, E: 7.39325, WGS-84]; CAS 233445, CAS 233446, CAS 233447, CAS 233448, CAS 233449, CAS 233450 [base camp of Pico de Príncipe; N: 1.58805, E: 7.38077, WGS-84]; CAS 233521, CAS 233522, CAS 233523 [road to radio tower; N: 1.62303, E: 7.39550, WGS-84]; CAS 233568 [Pico de Príncipe; N: 1.57992, E: 7.38363, WGS-84]; CAS 234525, CAS 234526, CAS 234527, CAS 234528 [St António; N: 1.63736, E: 7.41383, WGS-84]; CAS 238878, CAS 238879 [Nova Cuba, abandoned Roça; N: 1.63786, E: 7.40986, WGS-84]; CAS 238897 [road to Bom Bom; N: 1.69817, E: 7.40267, WGS-84]; CAS 244054 [East side of Island; N: 1.60067, E: 7.41578, WGS-84]; CAS 244055 [Bela Vista; N: 1.61967, E: 7.41381, WGS-84]; CAS 251571 [base of Pico Papagaio; N: 1.61678, E: 7.39083, WGS-84]; CAS 258959 [along path west of dirt road from Ponta do Sol to Monte Alegre; N: 1.63808, E: 7.38097, WGS-84]; CAS 258965, CAS 258966 [along path west of dirt road from Ponta do Sol to Monte Alegre; N: 1.63539, E: 7.38033, WGS-84].

Panaspis thomensis

São Tomé Island: *Museu Nacional de História Natural e da Ciência:* MUHNAC/MB03-000948*, MUHNAC/MB03-000949*, MUHNAC/MB03-000950* [Jardim Botânico, N: 0.27427, E: 6.58581, WGS-84]; MUHNAC/MB03-000947* [trail to lagoon Amélia; N: 0.26800, E: 6.59131, WGS-84]. *Instituto de Investigação Ciência Tropical:* IICT 50-1954* [Nova Moka; N: 0.28736, E: 6.3342, WGS-84]. *Muséum d'histoire Naturelle de la ville de Genève:* MHNG 2462.1*, MHNG 2462.2*, MHNG 2462.3*, MHNG 2462.4*, MHNG 2462.5*, MHNG 2462.6*, MHNG 2462.7*, MHNG 2462.8*, MHNG 2462.9* [Trindade; N: 0.29638, E: 6.68119, WGS-84]; MHNG 2496.11* [Roca Monte Café; N: 0.25282, E: 6.68320, WGS-84]; MHNG 2522.14* [Almeirim; impossible to geolocate, WGS-84]; MHNG 2540.63* [São Tomé; without precise location]. *California Academy of Sciences:* CAS 84206 [Makambreira; N: 0.26800, E: 6.63500, WGS-84]; CAS 218730 [Java; N: 0.26108, E: 6.65089, WGS-84]; CAS 218920 [slope on west side of Rio Contador; N: 0.30239, E: 6.55247, WGS-84]; CAS 218924 [slope on west side of Rio Contador; N: 0.31619, E: 6.55069, WGS-84]; CAS 218963, CAS 218964, CAS 218965, CAS 218966, CAS 218967, CAS 218968, CAS 218969, CAS 218970, CAS 218971, CAS 218972 [base of Muquiqui; N: 0.38119, E: 6.64878; WGS-84]; CAS 219035, CAS 219036, CAS 219037, CAS 219038, CAS 219039, CAS 219040, CAS 219041, CAS 219042, CAS 219043 [Rio do Ouro below Augustinho Neto; N: 0.36547, E: 6.64492, WGS-84]; CAS 219046* [along trail between Bom Sucesso and Lagoa Amélia; N: 0.26800, E: 6.59131, WGS-84]; CAS 219060 [slope on west side of Rio Contador; N: 0.31619, E: 6.55069, WGS-84]; CAS 219072, CAS 219073 [Canavial; N: 0.38403, E: 6.65397, WGS-84]; CAS 233693*, CAS 233694, CAS 233695, CAS 233969, CAS 233697 [near of Abade; N: 0.25411, E: 6.64458, WGS-84]; CAS 233702 [trail between Bom Sucesso and Lagoa Amélia; N: 0.26800, E: 6.59131, WGS-84]; CAS 238875 [on road to Bombain; N: 0.24555, E: 6.63263, WGS-84]; CAS 252820 [Bom Sucesso, Jardim Botânico; N: 0.28873, E: 6.61247, WGS-84]; CAS 258773 [Contador Valley; N: 0.31811, E: 6.54861, WGS-84]. *Zoologische Staatssammlung München:* ZSM 138/1992 [São Tomé island]. *Zoologisches Museum der Universität Hamburg:* ZMH R10918 ["St. Thomé"; without precise location]; ZMH R10898-901, R10910-917 [l. das Rolas; N: 0, E: 6.521732, WGS-84]. *Museum für Naturkunde der Humboldt- Universität zu Berlin:* ZMB 9708 [Rolas; N: 0, E: 6.521732, WGS-84], ZMB 83350 [São Tomé Town; N: 0.334602, E: 6.734507, WGS-84].

Panaspis annobonensis

Annobon Island: *Museu Nacional de História Natural e da Ciência:* MUHNAC/MB03-001104 to 001115*, MUHNAC/MB03-001116 to 001117 [Annobon; N: -1.414739, E: 5.632355, WGS-84]. *Zoologisches Museum der Universität Hamburg:* ZMH R10819, R10820 [Anno-bon; N: -1.414739, E: 5.632355, WGS-84].