

A new species of nocturnal gecko (*Paroedura*) from karstic limestone in northern Madagascar

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Abstract

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Paroedura hordiesi sp. n. is described from Montagne des Français, a karstic limestone massif in the far north of Madagascar recently established as nature reserve. The new species has the nostril in contact with the rostral scale and shares many characters with *P. karstophila* and especially with *P. homalorhina* which are also restricted to karstic habitats. *Paroedura hordiesi* differs from *P. karstophila* by a smoother skin on dorsum and legs, by original and regenerated tails being both entirely smooth, by colouration, and by larger snout-vent length. Morphologically the new species is most similar to *P. homalorhina* from the Ankarana reserve from which it can be distinguished by shorter limbs and a less slender habitus. Published molecular data place the new species as close relative of *P. homalorhina* and another undescribed species from Nosy Hara Island, while newly determined data of the *cox1* gene for *P. karstophila* confirm the distinctness of the new species from this taxon. Integrating the information from published and novel molecular data, the new species differs from all nominal *Paroedura* (except *P. vahiny* for which no molecular data are available to date) by strong genetic divergences. *P. hordiesi* might be another microendemic species of the Montagne des Français region. We suggest its IUCN Red List classification as “Critically Endangered” on the basis that it has an extent of occurrence of at most 50 km², it is known from a single location, and there is a continuing decline in the extent and quality of its habitat.

Introduction

The far north of Madagascar comprises a mosaic of heterogeneous landscapes ranging from rainforests on volcanic basement to deciduous dry forests in karstic massifs and littoral habitats on sandy ground (e. g. Lavranos et al. 2001, Vences et al. 2009, Crottini et al. 2012). The geological and climatic diversity of this area is reflected by a high species diversity and a high degree of microendemism (e. g. Andreone 2004, Wilmé et al. 2006, Ranaivoarisoa et al.

2013). Endemism is usually restricted to the species level but one monotypic family of blindnakes (Xenotyphlopidae) is also endemic to this area (Wegener et al. 2013). Many new species of amphibians and especially reptiles have been discovered and described from far northern Madagascar in recent years, both from humid rainforests of the Montagne d’Ambre massif (e. g. Raxworthy and Nussbaum 2006, Glaw et al. 2007, 2010, Köhler et al. 2008, D’Cruze et al. 2010, Ratsoavina et al. 2011) and from the region around the dry karst forest formation of

Montagne des Français and adjacent littoral habitats (Ramanamanjato et al. 1999, Raselimanana et al. 2000, Glaw et al. 2001, 2005, 2012, 2013, Köhler et al. 2010a, 2010b, Miralles et al. 2011). These major habitat types are separated from each other by rather steep ecotones in northern Madagascar and thus in part constitute “habitat islands” for several species, possibly allowing allopatric speciation. Several taxa including dwarf frogs (*Stumpffia*), dwarf chameleons (*Brookesia*), burrowing skinks (*Paracontias*), leaf-tail geckos (*Uroplatus*), and the nocturnal geckos of the genus *Paroedura* have undergone remarkable diversification in northern Madagascar (Jackman et al. 2008, Köhler et al. 2010a, 2010b, Ratsoavina et al. 2011).

The genus *Paroedura* is widely distributed throughout Madagascar’s biomes, including eastern rainforest, western dry forest, extremely arid thornbush savanna and high mountain habitats (Angel 1942, Guibé 1956, Dixon and Kroll 1974, Rösler and Krüger 1998, Nussbaum and Raxworthy 2000). Five of the 15 described species from Madagascar occur in the far north, and two additional species from the Comoro islands have close relationships to the northern *P. lohatsara* and *P. stumpffi* suggesting that they originated by two colonization events from the northern species (Hawltischek and Glaw 2013). Recent surveys indicate that the karstic limestone massifs in this region still harbour further undescribed reptile species (e. g. Jackman et al. 2008, Recknagel et al. 2013). Some of them might be microendemic and threatened by substantial habitat destruction. In the following we describe a new *Paroedura* species from Montagne des Français to contribute to the taxonomic inventory of this massif, and to highlight the threats affecting this microendemic species and other biota in the region.

Methods

Specimens were anesthetized by injection with chlorobutanol, fixed with 96% ethanol and stored in 70% ethanol. Terminology and abbreviations of characters partly follow Nussbaum and Raxworthy (2000). Abbreviations used: MNHN = Muséum national d’Histoire naturelle, Paris; UADBA = Université d’Antananarivo, Département de Biologie Animale; ZSM = Zoologische Staatssammlung, München; SVL = snout-vent length. All measurements were taken with a caliper to the nearest 0.1 mm.

To obtain molecular comparisons of the new species with previously unstudied nominal *Paroedura* species, we sequenced a fragment of the mitochondrial gene for cytochrome oxidase subunit I (cox1) with primers and protocols defined by Nagy et al. (2012) for several *Paroedura* samples from Tsingy de Namoroka (corresponding voucher specimens to be catalogued in MNHN). These samples have become available through a recent herpetological survey by one of us (II) and include topotypical *P. karstophila*, previously unstudied from a molecular perspective. The resulting sequences were combined with those of Nagy et al. (2012) and Koubová et al. (2014) in

MEGA version 5 (Tamura et al. 2011) to yield an alignment of 664 bp. We performed phylogenetic inference in MEGA under the Maximum Likelihood optimality criterion, with a general time-reversible substitution model with gamma-distributed rates and invariant sites, NNI branch swapping, and assessing robustness of nodes with 500 bootstrap replicates. Newly obtained sequences were submitted to GenBank (accession numbers: KM978078–KM978080).

Results

Molecular differentiation in the genus *Paroedura*

The multigene phylogenies of Jackman et al. (2008) and Hawltischek and Glaw (2013) as well as the combined cox1 sequences of Nagy et al. (2012), Koubová et al. (2014) and those newly obtained (Fig. 1) provide evidence of strong genetic divergence of *P. hordiesi* to all other described *Paroedura* species except *P. vahiny* for which DNA sequence data is not yet available.

The cox1 data place the new species sister to an undescribed candidate species from Nosy Hara (79% bootstrap support), and this clade forms part of a more inclusive clade with *P. oviceps* and the undescribed Ankarafantsika species (bootstrap support 69%; no cox1 sequences were available for *P. homalorhina* from Ankarana which in a previous study was the sister taxon of *P. hordiesi*, see Jackman et al. 2008). All studied species and candidate species of *Paroedura* included in the cox1 data set were differentiated by very high pairwise uncorrected distances. *P. hordiesi* differed from its Nosy Hara sister lineage by a p-distance of 16.3–16.5%, and from all other *Paroedura* including the relatively distantly related *P. karstophila* by >20%. Two samples sequenced from the Tsingy de Namoroka, the type locality of *P. karstophila*, were sister to each other but showed a substantial divergence of 15.9% cox1 p-distance, suggesting that possibly two cryptic species may be hiding under the name *P. karstophila* in this karstic massif. The sample from Ankarafantsika (*P. sp.* Ankarafantsika in Fig. 1), identified in Jackman et al. (2008) as *P. karstophila*, in fact belongs to yet another, undescribed species according to our subsequent comparisons and is only distantly related to *P. karstophila* (Fig. 1). The DNA barcoding voucher sequence for the karyotype of *P. karstophila* (Koubová et al. 2014) is identical to our sequences of *P. hordiesi*, suggesting that the karyotype description in this paper refers to our new species rather than to *P. karstophila*.

Description of a new species

Paroedura hordiesi sp. n.

<http://zoobank.org/8F5AA095-C68A-43E6-BCF8-4A02815A693F>

Figs 2–4, Table 1

Remarks. This species has been treated or figured under the name *Paroedura homalorhinus* (Henkel and Schmidt

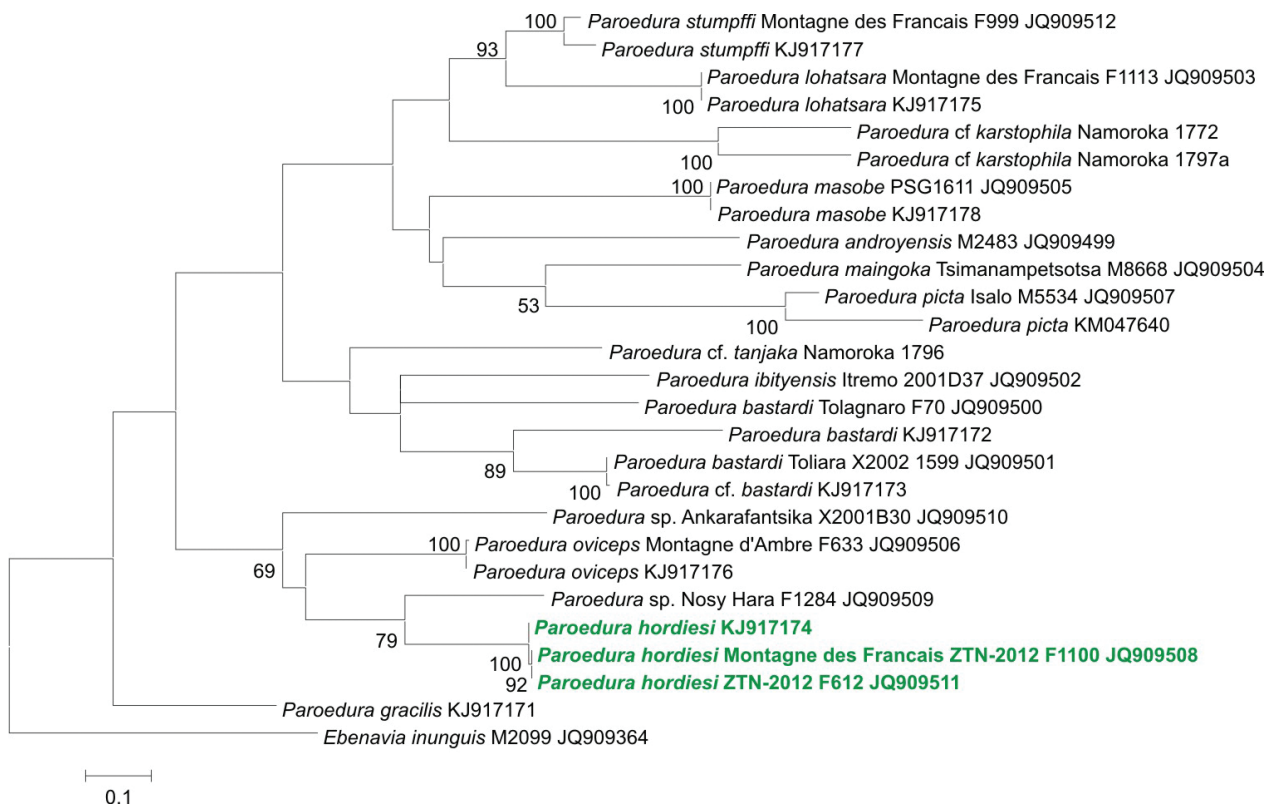


Figure 1. Maximum Likelihood tree inferred from 664 bp of the mitochondrial cytochrome oxidase subunit I (cox1) gene, showing the differentiation between *Paroedura* species. Note that this single-gene tree is not suitable to reconstruct the basal relationships of these geckos but is rather shown to document the large genetic divergences among all of them, and of *P. hordiesi* to its relatives. Numbers behind species names are sample numbers as given in Nagy et al. (2012) and Koubová et al. (2014), as well as GenBank accession numbers of the respective sequences.

1995), *Paroedura karstophila* (Glaw et al. 2001), *Paroedura* sp. “Montagne des Français” (Glaw and Vences 2007), *Paroedura* sp. (D’Cruze et al. 2007), *Paroedura* aff. *karstophila* (Schönecker 2008), *Paroedura* cf. *karstophila* (Megson et al. 2009), *Paroedura* sp. n. / sp. n. 1 (Jackman et al. 2008 and Nagy et al. 2012). Its karyotype ($2n = 36$) has been described under the names *Paroedura* sp. n. I ‘Montagne des Français’ (Aprea et al. 2013) and *Paroedura karstophila* (Koubová et al. 2014). DNA-sequences of this species have been published in Jackman et al. (2008), Aprea et al. (2013), and Koubová et al. (2014).

Holotype. ZSM 342/2004 (field number FGZC 639), adult male with (broken) original tail and everted hemipenes, collected at Montagne des Français (12°19’34”S, 49°20’09”E, 334 m above sea level), Antsiranana Province, north Madagascar, on 18 February 2004 by F. Glaw, M. Puente and R. Randrianiana. GenBank accession numbers for sequences of the holotype (Jackman et al. 2008): EF536213 (ND2), EF536239 (ND4), EF536165 (RAG1) and EF536189 (PDC).

Paratypes. All paratypes were collected in the “tsingy” limestone massif at Montagne des Français, Antsiranana province, north Madagascar. Specimens were collected on the tsingy outcrops along the way between the Hotel “Kings Lodge” (12°18’44,8”S, 49°20’22,6”E, 10 m

a.s.l.) and the remains of the French Fort (12°19’34”S, 49°20’09”E, 334 m), except where other locality information and coordinates are given in the following: UAD-BA uncatalogued (FG/MV 2000-317), sex unknown, and ZSM 531/2000 (FG/MV 2000-316), adult male with everted hemipenes, both collected on 14 March 2000 by F. Glaw, K. Glaw and M. Vences; ZSM 532/2000 (no field number), adult female, collected on 21 March 2000 by F. Glaw and K. Glaw; ZSM 1108/2003 (no field number), adult female, collected on ca. 20 February 2003 by F. Glaw and R. D. Randrianiana; ZSM 337/2004 (FGZC 634), subadult, and ZSM 338/2004 (FGZC 635), subadult, both collected at 12°19’34”S, 49°20’09”E, 334 m a.s.l., on 23 February 2004 by F. Glaw, M. Puente and R. D. Randrianiana; ZSM 339/2004 (FGZC 636), adult female, ZSM 340/2004 (FGZC 637), adult female, ZSM 341/2004 (FGZC 638), adult female [original tail broken], all three with same data as holotype; ZSM 343/2004 (FGZC 640), adult male without tail, and ZSM 350/2004 (FGZC 647), adult female, both without reliable locality and collection data, but most likely with same data as holotype; UADBA uncatalogued (FGZC 612), sex unknown, collected at 12°19’34”S, 49°20’09”E, 334 m a.s.l., on 20-28 February 2004 by F. Glaw, M. Puente and R. D. Randrianiana; ZSM 352/2004 (FGZC 649), adult, and ZSM 353/2004 (FGZC 650), adult female, both collected at 12°19’34”S, 49°20’09”E, 334 m a.s.l.,

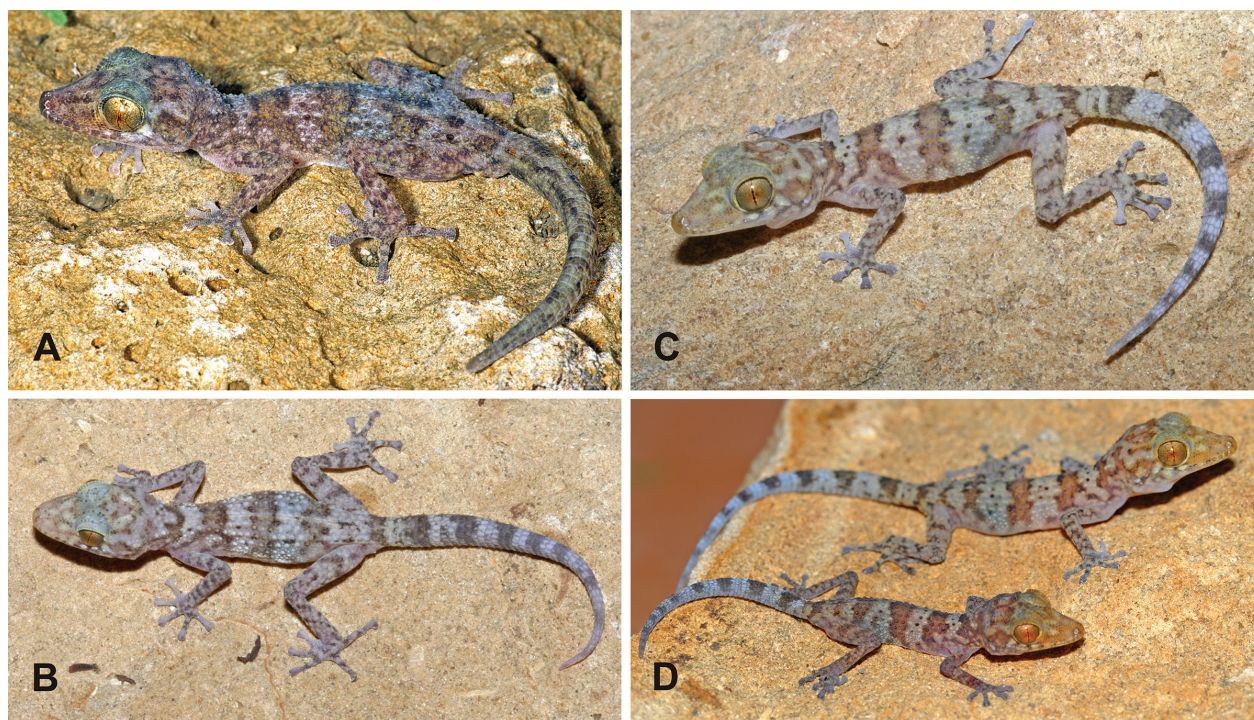


Figure 2. Paratypes of *Paroedura hordiesi*: (A) adult male ZSM 531/2000 (SVL 53.5 mm) in dorsolateral view; (B) adult female ZSM 2113/2007 (SVL 46.1 mm) in dorsal view; (C) subadult ZSM 2107/2007 in lateral view; (D) juvenile (ZSM 2106/2007, SVL 28.1 mm) and subadult (ZSM 2107/2007, SVL 35.2 mm) in dorsolateral view.

on 18–23 February 2004 by F. Glaw, M. Puente and R. D. Randrianiana; UADBA-R 70183 (FGZC 1109), adult male with everted hemipenes, UADBA-R 70185 (FGZC 1112), male, UADBA-R 70184 (FGZC 1114), adult female, ZSM 2106/2007 (FGZC 1099), juvenile, ZSM 2107/2007 (FGZC 1100), juvenile, ZSM 2113/2007 (FGZC 1115), adult female, all six collected around the remains of the French Fort (12°19'33"S, 49°20'17"E), collected on 27 February 2007 by P. Bora, H. Enting, F. Glaw, A. Knoll and J. Köhler; UADBA-R 70281 (FGZC 1659), sex unknown, ZSM 1530/2008 (FGZC 1660), adult female, both collected in the cave between Andavakoera and remains of French Fort, on 16 February 2008 by M. Franzen, F. Glaw, J. Köhler and Z. T. Nagy.

Diagnosis. *Paroedura hordiesi* sp. n. is a medium-sized species (SVL up to 58 mm, tail length up to 53 mm), having moderately prominent dorsal tubercles disposed into moderately distinct, and generally regular longitudinal rows and an original tail with no spines.

The new species can be easily attributed to the genus *Paroedura* based on its nested phylogenetic position within the genus (Jackman et al. 2008) and its morphological similarity to other *Paroedura* species, especially concerning the ventral structure of their fingers and toes which comprise a pair of squarish terminal adhesive pads. Among Malagasy geckos this terminal toe structure is only found in *Paroedura* and the related genus *Ebenavia* (Glaw & Vences, 2007). The latter genus can be easily distinguished from *Paroedura* by its much narrower and strongly pointed head, its elongated body, and smaller size.

Comparisons. The new species can be distinguished from the 17 other currently recognized *Paroedura* species (including the three available junior synonyms in the genus) as follows: From *P. androyensis*, *P. bastardi*, *P. ibityensis*, *P. lohatsara*, *P. maingoka*, *P. picta*, and *P. vahiny* by having the nostril in contact with the rostral scale; from *P. gracilis* by absence of a raised vertebral ridge on the body and shorter forelimbs which are not extending forward beyond tip of snout; from *P. masobe* by much smaller size (SVL up to 58 mm versus 107 mm), much smaller eyes with a pigmented iris (versus black iris) and absence of a dorsal row of paired spines on the tail; from the two Comoroan species *P. sancti-johannis* and *P. stellata* by slightly smaller size (SVL up to 58 mm versus 68 mm and 62 mm, respectively) and absence of whorls with distinct spiny tubercles of the original tail; from the syntopically distributed *P. stumpffi* by smaller size (SVL up to 58 mm versus 70 mm) and absence of whorls with distinct spiny tubercles of the original tail; from *P. tanjaka* by much smaller size (SVL up to 58 mm versus 102 mm) and absence of whorls with distinct spiny tubercles of the original tail; from *P. vazimba* by larger size (SVL up to 58 mm versus 49 mm) and absence of whorls with distinct spines of the original tail; from *P. oviceps* from its type locality Nosy Be by smaller size (SVL up to 58 mm versus 69 mm) and rather regularly arranged tubercle rows on the back (versus rather irregular rows of tubercles); from *P. karstophila* by the absence of whorls with distinct spiny tubercles of the original tail (and by a smoother regenerated tail, see Nussbaum and Raxworthy 2000) and by

Table 1. Morphometric and meristic variation of several type specimens of *Paroedura hordiesi* from the type locality Montagne des Français. Abbreviations for measurements and counts (see Materials and Methods for other abbreviations): ZSM = Zoologische Staatssammlung München; SVL = snout-vent length; TL = tail length; HL = maximum head length (from tip of snout to posterior margin of ear); HW = maximum head width, at widest point; HH = maximum head height; AGL = axilla-groin distance; ED = maximum eye diameter; EO = maximum ear opening diameter; FOL = forelimb length, from axilla to tip of longest finger; HIL = hindlimb length, from groin to tip of longest toe; SPL = number of supralabial scales; IFL = number of infralabial scales; NAS = number of nasals in direction from rostral to labial including nasorostrals, supranasals, postnasals; IN = number of internasals; IO = number of interorbitals; PM = number of postmentals; SLM4 = number of subdigital lamellae on fourth digit of manus; SLP4 = number of subdigital lamellae on fourth toe of pes; PCT = number of postcloacal tubercles; TLT = number of tubercle rows on tail. Counts are listed left-right. All measurements in Tables 1 and 2 were taken by H. Rösler with a caliper to the nearest 0.1 mm. HT = holotype, PT = paratype, F = female, M = male, SA = subadult.

ZSM	352/2004	353/2004	340/2004	350/2004	339/2004	341/2004	338/2004	337/2004	342/2004	343/2004
Type status	PT	PT	PT	PT	PT	PT	PT	PT	HT	PT
Sex	F	F	F	F	F	F	SA F	SA	M	M
SVL	56.0	55.0	56.0	54.5	58.0	57.3	43.5	43.0	52.6	51.8
TL		48.5				53.0			51.0	
HL	16.7	17.0	17.0	16.4	18.7	18.0	14.9	14.8	16.3	17.0
HW	12.8	12.1	12.3	10.8	12.5	12.4	9.6	9.1	10.9	11.2
HH	8.0	7.1	7.2	6.3	7.4	6.6	5.8	5.1	6.4	5.7
AGL	25.0	22.0	23.0	22.8	23.0	23.7	17.0	18.1	21.7	21.0
ED	3.1	3.4	3.5	3.3	4.6	4.7	4.1	4.4	3.5	4.5
EO	2.2	1.9	1.7	1.9	1.8	1.8	1.5	1.5	1.7	
FOL	20.0	19.8	20.2	20.0	20.6	21.2	16.2	17.4	18.6	18.7
HIL	27.0	25.1	28.8	28.7	28.6	30.0	24.5	24.4	27.5	26.4
SVL:HIL	2.07	2.19	1.94	1.90	2.03	1.91	1.78	1.76	1.91	1.96
SPL	15–15	15–14	15–15	14–15	16–15	15–14	15–15	15–14	14–14	15–14
IFL	13–13	13–13	12–13	14–13	13–13	14–13	14–13	n.a.–12	13–12	14–14
NAS	5–5	5–5	5–5	4	5–5	5–5	5–5	5–5	5–5	5–5
IN	1	1	1	1	1	1	1	1	1	1
IO	6	6	6	7	7	7	8	6	7	6
PM	2	2	2	2	2	2	2		2	2
SLM4	13–13	14–14	15–16	15	17–15	16–16	15–15		15–15	15
SLP4	16–18	17–18	19–19	18–18	20–20	18–18	18–17		17–18	19–19
PCT	1–1	1–1	1–1		1–1	1–1	1–1	1–1	1–1	1–1
TLT		7				6			7	

colouration (see Fig. 2 versus Fig. 5); and from its close relative *P. homalorhina* (Jackman et al. 2008) by shorter limbs (finger tips reach the anterior margin of eye versus snout tip when forelimbs are adpressed along the body), slightly smaller size (SVL up to 58 mm versus 65 mm, see Table 2), distinct and generally regularly arranged tubercles rows on the back (versus less distinct and less regular rows), and a more slender habitus (see Fig. 2 versus Fig. 5). In addition, *Paroedura hordiesi* can be easily distinguished from most other *Paroedura* species (*P. androyensis*, *P. bastardi*, *P. gracilis*, *P. ibityensis*, *P. lohatsara*, *P. maingoka*, *P. masobe*, *P. oviceps*, *P. picta*, *P. sanctijohannis*, *P. stellata*, *P. stumpffi*, *P. tanjaka*, *P. vahiny* and *P. vazimba*) by adult colouration in life (see colour photographs in Glaw and Vences 2007, Schönecker 2008, Hawlitschek and Glaw 2013) and from *P. androyensis*, *P. bastardi*, *P. gracilis*, *P. homalorhina*, *P. ibityensis*, *P. lohatsara*, *P. maingoka*, *P. masobe*, *P. picta*, *P. sanctijohannis*, *P. stellata*, *P. stumpffi*, *P. tanjaka*, and *P. vazimba* by juvenile colouration (Glaw and Vences 2007, Schönecker 2008, Hawlitschek and Glaw

2013, FG pers. obs.; juvenile colouration of the other species still unknown). Genetically, *P. hordiesi* can be distinguished from all other species in the genus by its molecular differentiation in mitochondrial and nuclear genes (Jackman et al. 2008, Nagy et al. 2012, Hawlitschek and Glaw 2013, Fig. 1) except for *P. vahiny* for which DNA sequences are not yet available.

Description of the holotype. SVL 52.6 mm, further measurements and counts are given in Table 1. Holotype in good condition, with complete but broken original tail and everted hemipenes. Head distinctly wider than neck and wider than body. Snout angled downward to tip, slight depression between poorly developed canthal ridges. Ear opening is a vertical slit. Original tail slightly shorter than snout-vent length, nearly round in cross section in its proximal part, laterally compressed in its distal half, with sharply pointed tip; ventral pygal section with pair of postcloacal sacs. Digits moderately expanded at tips. Rostral scale rectangular, much wider than tall and wider than mental. Nostril in contact with



Figure 3. Dorsal view of the male holotype of *Paroedura hordiesi* in preservative (ZSM 342/2004).

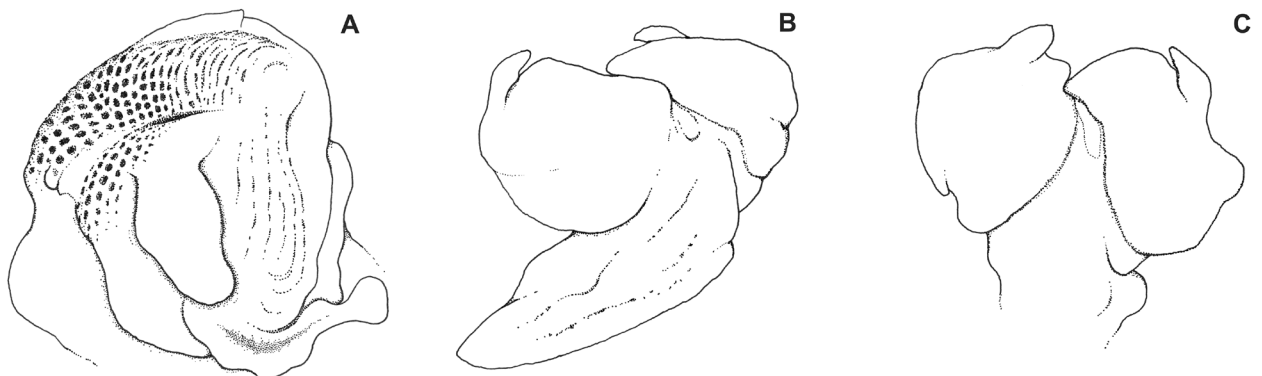


Figure 4. Drawings of hemipenis of *Paroedura hordiesi* (ZSM 343/2004): (A) asulcal view; (B) lateral view; (C) detailed view on cranial lobe.

rostral, first supralabial, and five further scales. First supralabial largest, labials smooth. Snout and interorbital scales juxtaposed, some raised, some scales in front of orbits tuberculate, as are some larger lateral occipital scales. Dorsolateral neck and body scales very heterogeneous with about eight partly poorly recognizable longitudinal rows at midbody of enlarged tubercles; enlarged tubercles separated partly by small flat scales and smaller tubercles. Dorsal scales of forelimbs mostly flat. Dorsal scales of hindlimbs large and tuberculate, much smaller above knee. Ventral scales of forelimbs slightly smaller than surrounding ventral scales of the body. Dorsal pygal scales like dorsal body scales; lateroventral pygals tuberculate. Tail scales flat, tail segments without any transverse row of spiny tubercles. Mental triangular, bordered posteriorly by a pair of elongate, irregular hexagonal postmentals. Postmentals contact mental, first and second infralabial, one enlarged lateral gular, one smaller posterolateral gular, and one larger central gular. First three infralabials not significantly larger than others. Gulars small, granular. Ventrals of chest and abdomen flat. Proximal subdigitals in rows

of 2–3. Pair of squarish, terminal pads. Claws curving downwards between terminal pads of digits.

Colour after 10 years in alcohol (Fig 3): head dorsally beige with almost no recognizable pattern except a whitish dorsolateral spot above each ear opening and a well-defined blackish area above each eye which represents, however, no pigmentation of the skin, but is due to the blackish eyeball shining through the skin. Dorsum greyish with four poorly defined beige spots on the back which are the remains of dorsal crossbands: one distinct spot between the forelimbs, two poorly recognizable spots on the back between forelimbs and hindlimbs, and a fourth poorly recognizable spot between the hindlimbs. Dorsal surfaces of forelimbs and hindlimbs marbled with beige and grey. Flanks with similar colour as dorsum, but without any recognizable traces of light crossbands. Tail dorsally with whitish-grey and brown alternating transverse bands which are poorly delimited in the distal portion of the tail. Throat, chest, venter, ventral parts of forelimbs and hindlimbs and ventral side of tail whitish. Iris dark grey, pupil white. Colour of holotype in life unknown (no colour photographs available).

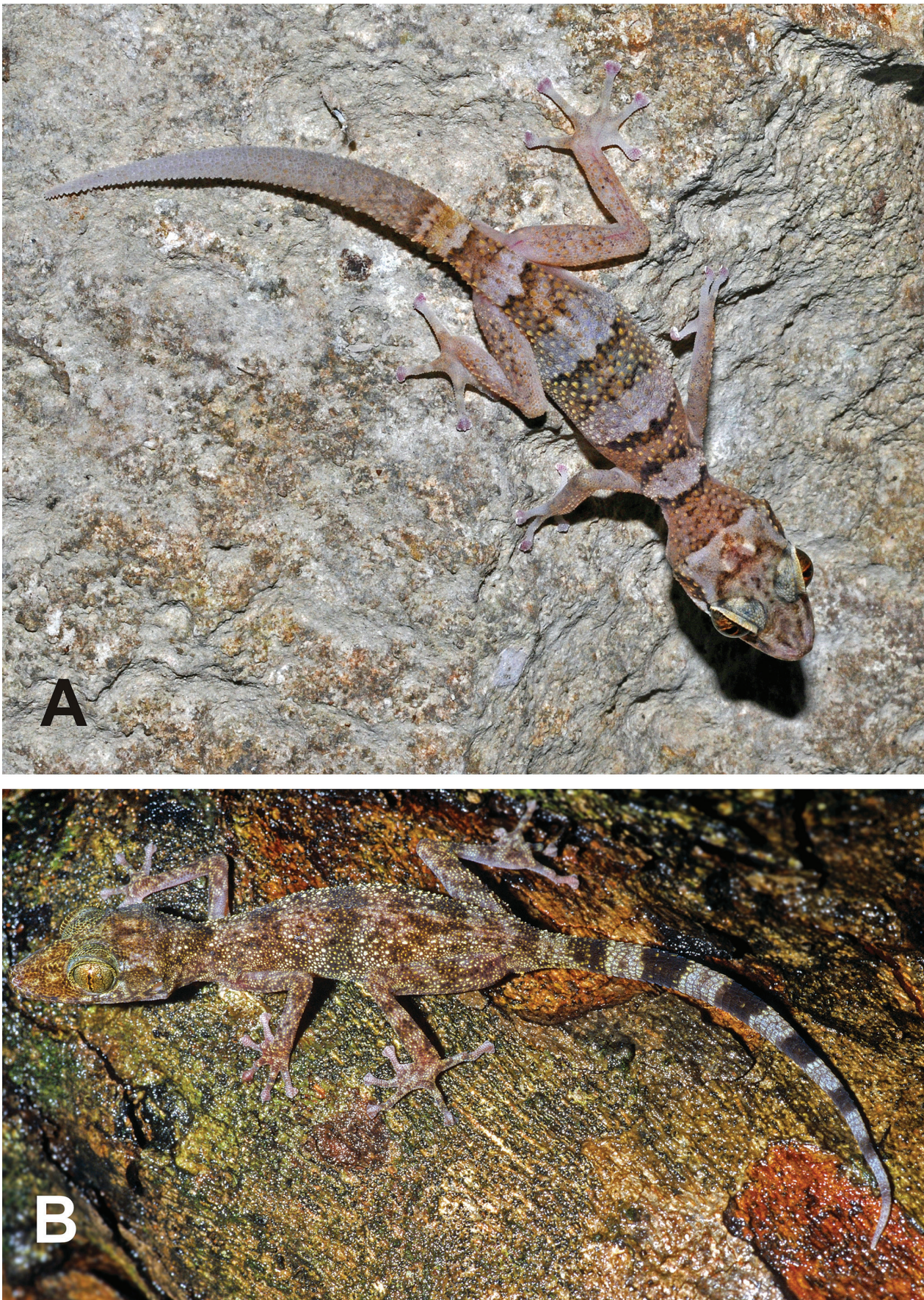


Figure 5. *Paroedura karstophila* from its type locality Tsingy de Namoroka (A), observed in the night of 10 September 2012 around 22:50 (not collected), and *P. homalorhina* from its type locality Ankarana (B).

Table 2. Morphometric and meristic variation of *Paroedura homalorhina* from the type locality Ankarana. See Table 1 for abbreviations and further details.

ZSM	345/2004	347/2004	348/2004	346/2004	349/2004	344/2004	768/2003	781/2003
Sex	M	F	F	M	F	F	F	M
SVL	64.8	58.6	58.8	61.5	61.3	61.7	60.4	62.8
TL	68.0	60.0					61.7	
HL	19.6	17.6	17.7	19.0	17.8	19.2	18.3	18.7
HW	12.6	12.0	11.4	12.9	12.2	12.6	11.3	12.9
HH	7.3	7.2	6.4	7.2	7.0	7.5	7.2	7.0
AGL	26.8	24.0	23.0	27.8	28.0	27.1	26.4	24.4
ED	3.8	3.5	4.3	4.3	3.8	4.0	4.7	4.4
EO	1.6	1.7	1.5	1.6	1.8	1.6	1.7	1.6
FOL	23.9	23.8	22.4	25.2	21.7	25.4	24.1	25.7
HIL	36.4	36.6	33.0	39.2	35.3	33.0	34.5	35.8
SVL:HIL	1.78	1.60	1.78	1.57	1.74	1.87	1.75	1.75
SPL	15–14	16–15	16–15	15–15	14–14	15–15	15–14	15–16
IFL	13–13	13–13	12–14	13–12	14–13	12–13	13–12	13–12
NAS	5–5	5–5	5–5	5–5	5–6	6–6	6–6	5–5
IN	1	1	1	1	1	1	1	1
IO	6	6	6	6	6	6		6
PM	2	2	2	2	2	2	2	2
SLM4	16–16	15–16	16–16	16–16	17–17	n.a.–17	16–16	15–14
SLP4	18–19	18–19	18–17	20–20	19–20	19–19	19–19	19–18
PCT	1–1	1–1	1–1	1–1	1–1	1–1	1–1	1–1
TLT	3	5					2	

Variation. Morphometric and meristic variation of ten specimens of the type series is summarized in Table 1, but there is also a remarkable individual variation in dorsal colouration and pattern (Fig. 2). Paratype ZSM 2106/2007, the smallest known juvenile (SVL 28.1 mm, tail length 25.2 mm), shows a moderately distinct juvenile colouration both in life (Fig. 2) and in preservative consisting of four light crossbands on the back between the insertion of forelimbs and the insertion of hindlimbs. A similarly distinct banding on body and original tail is still visible in the larger juvenile paratype ZSM 2107/2007 (Fig. 2, SVL 35.2 mm, tail length 34.7 mm). Although the juvenile colouration is distinct compared to most adults, it is less colourful and less contrasting in comparison with many other *Paroedura* species. The adult paratypes usually have a less distinct dorsal colour pattern than the juveniles, ranging from poorly recognizable (e. g. ZSM 532/2000) to distinct and well delimited (e. g. ZSM 531/2000) after 14 years in alcohol. Additional photographs of living individuals are provided in Henkel and Schmidt (1995), Glaw and Vences (2007), and Schönecker (2008). Most of the adult type specimens have a regenerated tail (without distinct transversal banding of dark and white), indicating a high pressure by predation or intraspecific aggression.

Hemipenis. The following description is based on the everted right organ of ZSM 343/2004 (Fig. 4). Hemipenis medium-sized (total length 6.4 mm, width at apex 4.5 mm), apex divided in two lobes. Sulcus spermaticus forms an S-shaped, narrow and deep groove, bordered by moderately distinct lips reaching the apex. On the

apex, the sulcus is becoming broader and divides in two branches. A horn-like apical cone is present in the center of each lobe. Calyces on the apex are only present at the border of the lobes. The hemipenes of the holotype (ZSM 342/2004) are virtually identical in every respect.

Habitat and habits. *Paroedura hordiesi* was observed multiple times at night in karstic dry forest in the rainy season, mainly climbing on karstic rocks and the ruins of an old fort. It was found in close syntopy with *P. lohatsara* in the karstic limestone areas, whereas *P. stumpffi* was only encountered on the slope between the massif and the sea, in areas without karstic formations.

Etymology. The specific name is dedicated to Freddy Hordies, in recognition of his support for biodiversity research and conservation through the BIOPAT initiative.

Distribution and conservation status. *Paroedura hordiesi* is reliably known only from the recently established nature reserve of Montagne des Français. The species possibly also occurs at Ampombofofo, ca. 25 km north of this massif (Megson et al. 2009: ZSM 1531/2008), but the identity of this population needs further study as molecular data are not available thus far. Surveys in other limestone areas of northern Madagascar revealed a superficially similar *Paroedura* at Nosy Hara (Metcalf et al. 2007) which is, however, strongly differentiated by colouration (see photo in Glaw and Vences 2007) and mitochondrial DNA sequences (Fig. 1 and Nagy et al. 2012), and is therefore considered a further undescribed candi-

date species. The Ankarana massif is known to harbour *P. homalorhina*, *P. karstophila*, and *P. stumpffi* (Nussbaum and Raxworthy 2000, Raselimanana 2008). Our own surveys in Ankarana revealed only *P. homalorhina* and *P. stumpffi* and we consider the occurrence of *P. hordiesi* unlikely in this massif. Rakotondravony (2006a) found *Paroedura* sp. at Binara in the Loky-Manambato region which potentially could refer to *P. hordiesi*, but the identity of this record remains to be studied. No unidentified *Paroedura* species was found at Analamera (Rakotondravony 2006b). Thus current evidence suggests that *P. hordiesi* is microendemic of Montagne des Français and perhaps the adjacent Ampombofofo region.

For consistency with the IUCN Red List Assessment for *Paroedura lohatsara* (Raxworthy et al. 2011) and other potential microendemic species of the Montagne des Français region, we suggest a classification as “Critically Endangered” on the basis that *P. hordiesi* has an extent of occurrence of at most 50 km², it is known from a single location, and there is a continuing decline in the extent and quality of its habitat.

Discussion

With the description of *Paroedura hordiesi* we add a further, probably microendemic new species to the herpetofauna of Montagne des Français. Although this population is already known for approximately 20 years, several factors have hampered the clarification of its identity, including the variability in colouration and in distinctiveness of longitudinal rows of dorsal tubercles of *P. hordiesi*, *P. homalorhina* and *P. karstophila*, the existence of several undescribed species with similar key characters, the rarity of individuals with an original tail, and the absence of genetic data and colour photographs reliably referable to *P. karstophila*. This situation has led to substantial uncertainty about the correct name for the species from Montagne des Français, as is reflected by the different preliminary names that have been used for this species in the literature (see above). DNA sequences are now available from two *P. karstophila*-like specimens from the type locality Namoroka (Fig. 1). These strongly differ from each other, suggesting that *P. karstophila* is possibly a composite taxon including two cryptic species which occur in syntopy at Namoroka. Although the identity of *P. karstophila* remains to be further studied, we have little doubts that one of the two Namoroka lineages will turn out to correspond to this taxon.

Due to PCR failure with universal reptile primers (Nagy et al. 2012), no *cox1* sequences are available for several species of *Paroedura*, including *P. homalorhina* which was sister to *P. hordiesi* in the study of Jackman et al. (2008; as *P. sp. n.*). On the other hand, the new species from Nosy Hara and *P. karstophila* have not yet been sequenced for the genes used by Jackman et al. (2008). This unfortunate lack of overlap of the two molecular data sets, to be remedied by future sequencing efforts, hampers our

ability to determine whether *P. hordiesi* is more closely related to *P. homalorhina*, or to the undescribed species from Nosy Hara. It does not, however, compromise our taxonomic conclusion of *P. hordiesi* being a valid species differentiated from both these close relatives by a substantial genetic divergence and morphological characters.

Paroedura hordiesi is a typical example of a microendemic karst specialist of an isolated habitat island that apparently has lost its ability to survive outside its special habitat and thus has lost the genetic exchange with populations from neighboured karstic massifs. Although the surrounding massifs are only separated by several kilometers of grassland or other non-karstic habitats, they are often populated by different species which might have evolved in isolation for millions of years. The *cox1* data presented in Fig. 1 suggest that the undescribed *Paroedura* species from the island Nosy Hara is a close relative of *P. hordiesi*. The two species differ by a substantial genetic distance, and distinctly by their colouration (see photographs in Glaw and Vences 2007), although the distance between this island and Montagne des Français is just about 35 km. The distance between Montagne des Français and Ankarana is approximately 50 km, yet the latter massif is populated by *P. homalorhina*, the second close relative of *P. hordiesi* (see discussion in previous paragraph). Similar patterns of microendemism and comparable phylogenetic relationships have been found in dwarf chameleons of the genus *Brookesia* (Glaw et al. 2012), in a clade of dwarf frogs of the genus *Stumpffia* (Köhler et al. 2010a), and in lizards of the genus *Zonosaurus* (Raselimanana et al. 2009, Recknagel et al. 2013), suggesting that similar vicariant processes among karstic habitat islands might have affected these groups of organisms in the far north of Madagascar. The karstic massifs might have provided sufficient resources and protection from desiccation during periods of drier climate to allow the long-term survival of these populations, finally leading to completed speciation. The evolution and long-term survival of these microendemic species suggests rather stable conditions without catastrophic events over very long time periods. The apparent lack of gene flow among the karstic habitat islands also suggests a limited dispersal capacity of karst specialists across the non-karstic interspersed matrix.

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