SALAMANDRA **55**(2) | 73–81 | 15 May 2019 | ISSN 0036–3375

A new species of nocturnal gecko, genus *Paroedura*, from the karstic Tsingy de Bemaraha formation in western Madagascar

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Manuscript received: 1 February 2019
Accepted: 1 March 2019 by Stefan Lötters

Abstract. We describe the new gecko species *Paroedura neglecta* sp. n. from the Tsingy de Bemaraha National Park in western Madagascar, belonging to the *P. bastardi/tanjaka* clade. The species in this clade are characterized by three light dorsal crossbands on the dorsum of juveniles and subadults whereas all other *Paroedura* species have four such bands. The new species differs from all species in the *P. bastardi* complex in having the nostril in contact with the rostral scale. It is most similar to the sympatric *P. tanjaka*, from which it differs by the presence of prominent dorsal tubercles arranged in regular longitudinal rows (versus rather irregular rows of dorsal tubercles), smaller size, details of the dorsal colour pattern and strong genetic divergence.

Key words. Squamata, Gekkonidae, *Paroedura neglecta* sp. n., systematics, taxonomy, morphology, molecular genetics.

Introduction

The Tsingy de Bemaraha National Park in western Madagascar not only represents spectacular limestone landscape (Goodman & Benstead 2003), but also is a hotspot of karst-adapted herpetofauna in the arid west of the island, including 19 species of amphibians and 60 species of reptiles (Schimmenti & Jesu 1997, Raselimanana 2008, Bora et al. 2010). Expeditions in the past decades have revealed several new squamate species from this protected area (e.g., Domergue 1995, Schimmenti & Jesu 1996, Jesu et al. 1999, Nussbaum et al. 1999, Nussbaum & Raxworthy 2000, Glaw et al. 2009a, b). During our field work in this area in March and April 2006, we discovered three new gecko species, two of which were already described (Glaw et al. 2009a, 2018), whereas the third species, belonging to the genus *Paroedura*, still awaits taxonomic treatment.

The gecko genus *Paroedura* is endemic to Madagascar and the Comoro archipelago (Nussbaum & Raxworthy 2000, Hawlitschek & Glaw 2013) and currently comprises 21 species (Glaw et al. 2018). In the genus, two phenetic groups are traditionally distinguished (e.g., Nussbaum & Raxworthy 2000): (1) one group (*P. sanctijohannis* group) having the nostril in contact with the rostral scale, and (2) another group (*P. picta* group) having the nostril separated from it. The position of the nostril and the scale configuration around the nostril are important and largely reliable characters to distinguish between closely related species in different gecko groups including the genus *Phelsuma* (Rocha et al. 2010). However, the molecular phylogeny of *Paroedura* of Jackman et al. (2008) revealed that this character does not define monophyletic groups in *Paroedura*. For example, *Paroedura lohatsara* is sister to *P. sanctijohannis* (in the *P. sanctijohannis* group), but has the nostril condition of the *P. picta* group (Glaw et al. 2018).

The analyses of Jackman et al. (2008) revealed one well-supported phylogenetic clade that contained *Paroedura bastardi*, *P. ibityensis*, *P. tanjaka*, and an unnamed lineage from Bemaraha (as *Paroedura* sp. n.). This clade can be easily distinguished from all other *Paroedura* species by a differing colouration of juveniles and subadults, which show three light dorsal crossbands only, the anteriormost between the forelimbs, one at midbody and the posteriormost between the hindlimb insertions. All other known *Paroedura* species have four crossbands (one between forelimbs, two on dorsum and one between the hindlimbs). In this *P. bastardi/tanjaka* clade, the species have the nostril either separated from the rostral (*P. bastardi*, *P. ibityensis*; here treated as the *P. bastardi* complex due to the existence of multiple unnamed lineages belonging to this clade), or in contact with the rostral (*P. tanjaka*, *P.* sp. n.).

Given the strong genetic differentiation of the unnamed Bemaraha lineage from all other *Paroedura* species, including those of the *P. bastardi* complex, together with clear morphological differences that we have identified, we here describe it as a new species.

Materials and methods

Specimens were collected at night by opportunistic searching in potential habitats. Specimens were fixed in 90% ethanol and transferred to 70% ethanol for long-term storage. Tissue samples were stored in 99% ethanol. Field numbers refer to the collections of Frank Glaw (FGZC). Specimens were deposited in the Zoologische Staatssammlung München (ZSM) and collections of the Mention Zoologie et Biodiversité Animale of the Université d'Antananarivo (UADBA), Madagascar.

Measurements were taken using a digital vernier calliper to the nearest 0.1 mm by FG, following the measurement scheme of Glaw et al. (2018), which we here reiterate verbatim for practicality: 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 (toe pad, excluding claw); HIL = hindlimb length, from groin to tip of longest toe pad (excluding claw).

Our molecular analysis is based on the dataset of partial cytochrome oxidase subunit I (cox1) sequences in Glaw et al. (2018) expanded with sequences from previous publications and from Cocca et al. (2018). Additional sequences of this gene were obtained for six *Paroedura* samples from Tsingy de Bemaraha, the type locality of the new species herein. A stretch of the cox1 gene was amplified alternatively with primer pairs: repCOI-F and repCOI-R (Nagy et al. 2012), Vert-F1 and Vert-R1 (Ward et al. 2005, Perl et al. 2014), and dgLCO1490 and dgHCO2198 (Meyer et al. 2005). For primer sequences and details of laboratory protocols, see Nagy et al. (2012) and Perl et al. (2014). PCR products were purified with ExoSAPIT (Thermo Fisher Scientific, Waltham, MA, USA), directly sequenced on an ABI 3130 capillary sequencer. New sequences were checked, corrected and trimmed with the software CodonCode Aligner (CodonCode Corporation), and submitted to GenBank (accession numbers: MK473869–MK473874).

We aligned sequences using the Clustal algorithm in MEGA7 (Kumar et al. 2016) and determined in MEGA7 the best fitting substitution model based on the Bayesian Information Criterion (a GTR+I+G model). Phylogenetic inference under the Maximum Likelihood optimality criterion was carried out in MEGA7, with SPR branch swapping, and assessing robustness of nodes with 500 bootstrap replicates.

Nomenclatural act

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: urn:lsid:zoobank.org:pub: A88F6033-E230-431A-8938-080E5859FE56. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: www.salamandra-journal.com, zenodo.org.

Results

Molecular phylogeny

Maximum Likelihood analysis of a 599 bp fragment of the cox1 gene yielded a tree (Fig. 1) which resolved several main groups in *Paroedura* in agreement with the results of the multi-gene tree of Jackman et al. (2008). The focal lineage from Bemaraha clustered with *P. tanjaka*, and the clade of these two species was in a clade together with several lineages of the *P. bastardi* complex and *P. ibityensis*.

Node support for these and many other nodes in the tree was very low or absent, as revealed by low bootstrap proportions, confirming that the cox1 gene alone is not suitable to reliably resolve deep phylogenetic relationships in this group, as in other Malagasy reptiles (Nagy et al. 2012, Glaw et al. 2018). For the purely taxonomic purpose of this study, our DNA barcoding tree however illustrates adequately that the new lineage from Bemaraha shows a high genetic distance from all other morphologically similar species, and from all other undescribed lineages in the *bastardi* complex. The sister-group relationship between the focal lineage and *P. tanjaka*, although unsupported by the bootstrap analysis in the present study, has also been recovered (with high support) in the multi-gene analysis of Jackman et al. (2008) for two specimens included in our tree: a paratype of the focal lineage (ZSM 163/2006 = FGZC 991) as *Paroedura* sp. n. 2, and a specimen of *P. tanjaka* (ZSM 40/2006 = FGZC 750).

Uncorrected pairwise distances (p-distances) of the focal lineage to its probable sister species *P. tanjaka* in the cox1 gene are 18.9–19.6%. Distances to all other species and undescribed lineages of *Paroedura* included in Fig. 1 range from 17.5–25.4%.

***Paroedura neglecta* sp. n.**

(Figs. 2–3)

LSID: urn:lsid:zoobank.org:act:5E5B7DD2-D277-47A0-9159-0329E4F3F1E4

Remarks: This species was previously treated as *Paroedura* sp. n. (Bemaraha-Andafiabe) by Jackman et al. (2008), as *Paroedura* sp. (aff. *tanjaka*) by Bora et al. (2010), and as *Paroedura* sp. (Bemaraha) by Glaw et al. (2018).

Holotype: ZSM 128/2006 (FGZC 992), adult (?) male, from Andafiabe at the Beboka River ("Camp 2"), 18°47'03" S, 44°46'46" E, 177 m above sea level, Tsingy de Bemaraha, Melaky region (former Mahajanga province), western Madagascar, collected on 1 April 2006 by Parfait Bora, Hildegard Enting, Frank Glaw and Jörn Köhler.

Paratypes: ZSM 163/2006 (FGZC 991), subadult male, same data as holotype; ZSM 18/2006 (field number FGZC 704; Fig. 3A, B), subadult of unknown sex, from Andranopasazy ("Camp 1"), 18°42'31" S, 44°43'08" E, 146 m above sea level), Tsingy de Bemaraha, Melaky region (former Mahajanga province), western Madagascar, collected on 19 March 2006 by Parfait Bora, Hildegard Enting, Frank Glaw and Jörn Köhler.

Potential additional non-type material: Specimens deposited at UADBA may potentially belong to this new species, but were not available for examination.

Diagnosis: The new species can be distinguished from most other currently recognized *Paroedura* species by the

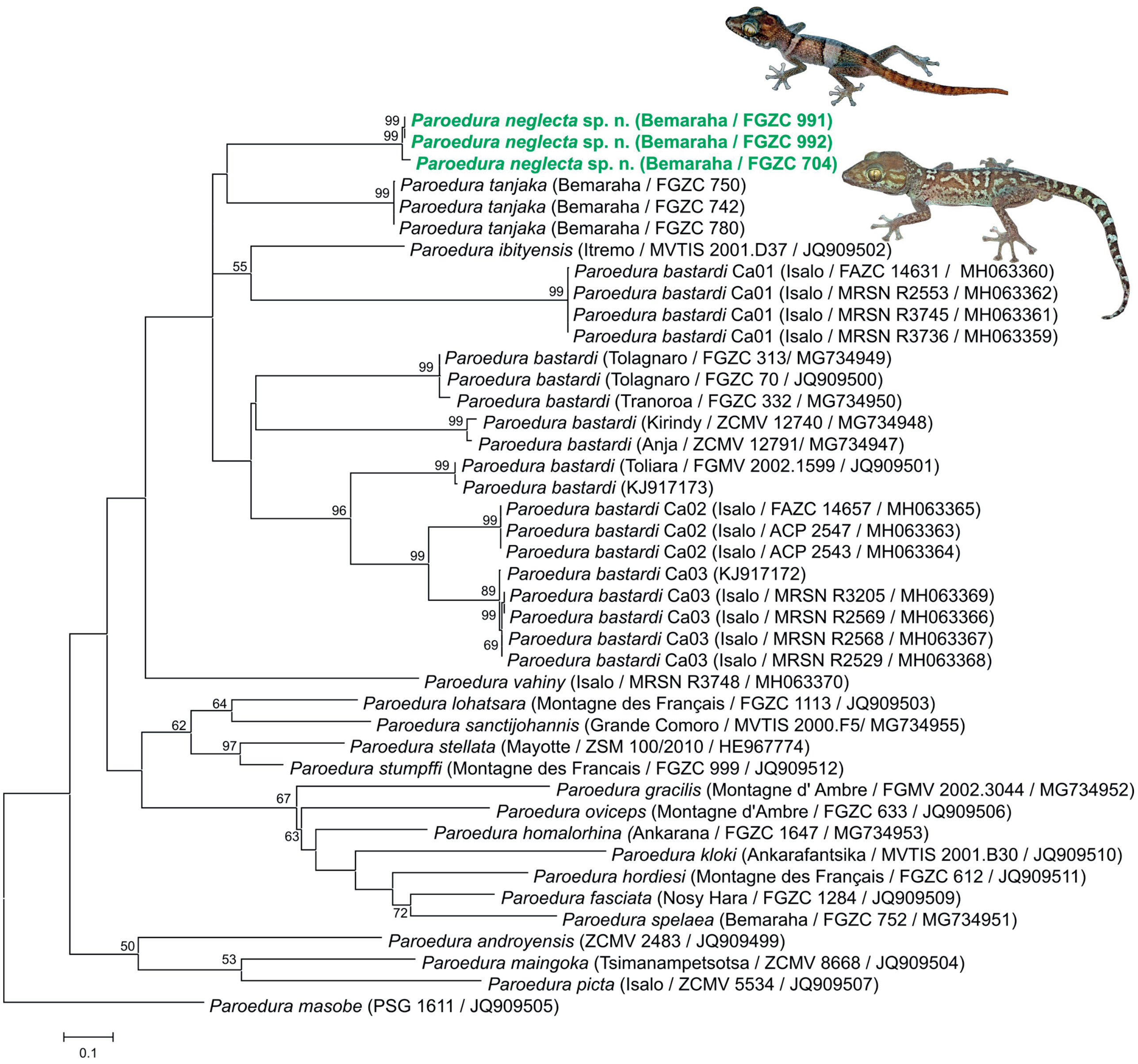

Figure 1. Maximum Likelihood phylogenetic tree of *Paroedura* based on a fragment of the mitochondrial cox1 gene (599 bp). Numbers at nodes are support values in percent from a bootstrap analysis (1000 pseudoreplicates; not shown if < 50%). *Paroedura masobe* was used as the outgroup, relying on the multi-gene analysis of Jackman et al. (2008) where this species was resolved as sister group of all other *Paroedura*.

presence of only three broad light crossbands on the dorsum (between forelimbs and hindlimbs) in juveniles and subadults versus four light crossbands in all other species except for *P. bastardi*, *P. ibityensis*, *P. tanjaka* (which all have only three crossbands) and *P. oviceps* and *P. vahiny* (in which the juvenile colouration is still unknown). In addition it can be distinguished 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 dorsum and shorter forelimbs which do not extend forward beyond tip of snout; from *P. masobe* by much smaller eyes and absence of a dorsal row of paired spines on the tail; from *P. fasciata, P. homalorhina*, *P. hordiesi*, *P. vahiny*, and *P. spelaea* by presence of spines on the original tail (versus absence); from *P. gracilis*, *P. homalorhina*, *P. kloki*, *P. maingoka*, *P. masobe*, *P. oviceps* from its type locality (Nosy Be), *P. picta*, *P. spelaea*, and *P. vahiny* by the presence of prominent dorsal tubercles arranged in regular longitudinal rows (versus rather irregular rows of dorsal tubercles). *Paroedura neglecta* is most similar to *P. tanjaka*, with which it occurs in syntopy in the Tsingy de Bemaraha. Both species share the character of nostril in contact with the rostral scale, presence of only three broad light crossbands on dorsum of juveniles, and similar general colouration. The new species differs from *P. tanjaka* by the presence of prominent dorsal tubercles arranged in regular longitudinal rows (versus rather irregular rows of dorsal tubercles; Fig. 3), more clearly outlined dorsal crossbands in adults (versus crossbands in adults mostly resolved into irregular blotches and flecks; Fig. 3), smaller size (maximum SVL 61 mm versus 102 mm; see Nussbaum & Raxworthy 2000), and strong genetic divergence (see phylogenetic tree in Jackman et al. 2008). *Paroedura neglecta* differs genetically from all species in the genus (note: *P. vahiny* sequences are not available) by pronounced differences in the DNA sequence of the mitochondrial cox1 gene (see Table 1 in Glaw et al. 2018; 18.9–19.6% uncorrected pairwise distance to its sister species, *P. tanjaka*).

Figure 2. Preserved male holotype of *Paroedura neglecta* sp. n. (ZSM 128/2006) from Andafiabe, Tsingy de Bemaraha, Madagascar, in dorsal view.

Available names: The types of the three available junior synonyms in the genus, *Diplodactylus porogaster* Boulenger, 1896 (synonym of *P. androyensis*); *Diplodactylus robustus* Boulenger, 1896 (synonym of *P. picta*); *Phyllodactylus madagascariensis* Mocquard, 1895 (synonym of *P. picta*), were not studied, but are obviously very different from *P. neglecta* described herein according to their original descriptions (Mocquard 1895, Boulenger 1896). The paratypes of *Paroedura guibeae* Dixon & Kroll, 1974 (synonym of *P. bastardi*) studied by us differ from *P. neglecta* by having the nostril separated from the rostral scale and the same is apparently true for all specimens in the type series (see Nussbaum & Raxworthy 2000).

Description of the holotype: Adult (?) male in reasonable condition, slightly desiccated with incomplete broken tail. Head distinctly wider than neck, wider than body. Snout angled downward to tip, slight depression between poorly developed canthal ridges. Ear opening is a vertical slit. Tail nearly round in cross section in its proximal part; ventral pygal section of tail with a pair of postcloacal sacs. Digits distinctly expanded at tips. Rostral scale rectangular, much wider than tall and wider than mental. Nostril in contact with rostral, first supralabial, and four (right) to five (left) further scales. 15/16 (left/right) smooth supralabials. Eyes desiccated. Snout and interorbital scales juxtaposed, some

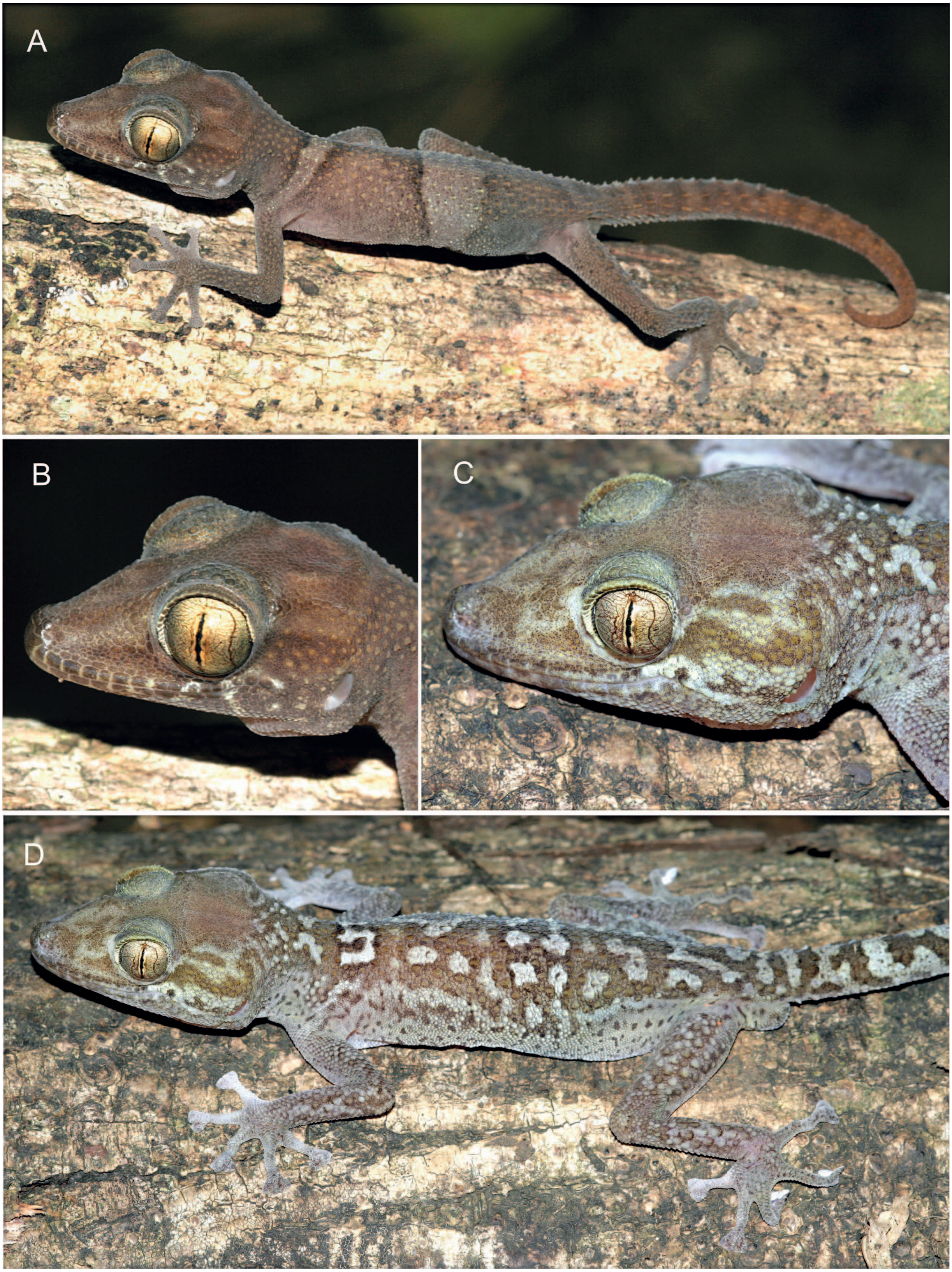

Figure 3. *Paroedura* specimens from Tsingy de Bemaraha, Madagascar, in life: (A) Paratype specimen (subadult male) of *Paroedura neglecta* sp. n. (ZSM 18/2006; SVL 50.4 mm) from Andranopasazy in dorsolateral view, and (B) in portrait; (C) *Paroedura tanjaka* from 'Grotte Crystal', 18°42'31" S, 44°43'08" E (ZSM 40/2006; SVL 98.5 mm) in portrait, and (D) in dorsolateral view.

raised, few occipital scales distinctly enlarged and tuberculate. Dorsolateral neck and body scales heterogeneous; dorsum and flanks with regularly separated enlarged tuberculate scales, those on dorsum arranged in four distinct longitudinal rows; enlarged tubercles separated by small flat scales and smaller tubercles. Dorsal scales of forelimbs mostly flat and unkeeled. Dorsal scales of hindlimbs mostly tuberculate and keeled. Ventral scales of forelimbs slightly smaller than surrounding ventral scales of the body. Dorsal pygal scales similar to dorsal body scales; lateroventral pygals smaller and unkeeled. Tail scales mostly tuberculate, tail segments without any transverse row of spiny tubercles. Mental triangular, bordered posteriorly by a pair of elongate, irregular hexagonal postmentals. Each postmental in contact with six scales: other postmental, mental, first infralabial, one enlarged lateral gular, one smaller posterolateral gular, and one larger central gular. First three infralabials slightly larger than others. Gulars small, slightly granular. Ventrals of chest and abdomen flat. Proximal subdigitals in rows of mostly 2. One pair of squarish terminal pads. Claws curving downwards between terminal pads of digits.

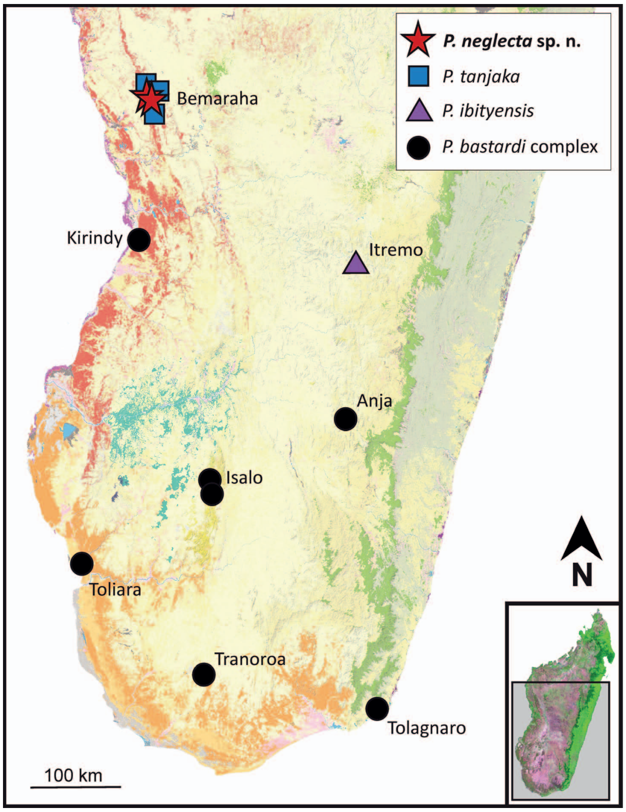

Figure 4. Map of central and southern Madagascar showing the known localities of *Paroedura neglecta* sp. n. and its closest relatives as included in our molecular analysis (see Fig. 1). Note that shown localities for *P. tanjaka* only refer to sequenced specimens that morphologically are in agreement with the original description (Nussbaum & Raxworthy 2000). Red (dry forest) and green (rainforest) show remaining primary vegetation in 2003–2006, modified from the Madagascar Vegetation Mapping Project (http://www.vegmad.org); see the project for a key to the other colours and the vegetation types they indicate.

Measurements of the holotype (in mm): SVL 61.3; TL not measurable, tail incomplete (separated tail fragment of 25.7 mm length, partly regenerated, with non-regenerated portion of 3.5 mm length; 2.1 to 4.1 mm width); HL 20.8; HW 14.6; HH 9.2; AGL 26.8; ED 6.8; EO 1.0; FOL 16.1; HIL 35.7.

After 12 years in alcohol (Fig. 2), head dorsally beige with a poorly recognizable dark dorsolateral band from eye to neck and dark area on the posterior head. Area along the upper lip reticulated brown and beige. Body dorsally brown to greyish with three distinct, regularly spaced light (darkly bordered) crossbands fading at the flanks: one narrow band on the neck (diameter at midbody 3.1 mm), pointing laterally and ending slightly anteriorly of the insertion of forelimbs, one distinctly broader crossband on midbody (diameter at midbody 7.4 mm), and one slightly less distinct band between the hindlimbs (2.5 mm). Dorsal surfaces of forelimbs and hindlimbs slightly marbled with beige and grey (hindlimbs not darker than forelimbs). Pygal region coloured similar to posterior body and hindlimbs. Flank colouration dorsally similar to dorsum, fading gradually towards the ventral surface. Ventral colouration (throat, chest, abdomen, ventral parts of forelimbs and hindlimbs) whitish (unpigmented) with a fine grey shade, especially on the thighs. The colour of the holotype in life is unknown due to the lack of respective field notes and photographs, but was probably similar to that in preservative.

Variation: The colouration of the paratype ZSM 18/2006 in life (Fig. 3) was generally similar to its colouration in preservative. However, the dorsal ground colour has slightly faded and is now (in preservative) more greyish than brown, but on the other hand the dark borders of the light crossbands, several small dark spots on the dorsum, especially around the keeled tubercles, and the light area running from the posterior eye margin over the neck to the other head side, are more distinct than they were in life. The iris was golden with a reddish area around the pupil and a red-brown vessel running through the posterior iris (Fig. 3). The original tail (which was lost) was reddish brown with distinct whorls and spiny tubercles until the tail tip (Fig. 3). Measurements (in mm) are as follows: SVL 49.7; TL not available, entire tail lost; HL 16.4; HW 10.6; HH 7.0; AGL 20.5; ED 4.4; EO 0.9; FOL 18.2; HIL 28.2.

The colouration of ZSM 163/2006 is similar to ZSM 18/2006, but more contrasting. Its measurements (in mm) are: SVL 52.4; TL ca. 43 mm (tail separated from body); HL 17.4; HW 11.9; HH 7.7; AGL 22.5; ED 4.7; EO 0.7; FOL 10.9; HIL 28.6.

Habitat and habits: The three specimens were collected at night in karstic dry forest in the rainy season. ZSM 128/2006 and 163/2006 were found close to the bed of the Beboka river and ZSM 18/2006 close to a small river of unknown name.

Distribution and conservation status: This species is known only from two localities in the central western part of Tsingy de Bemaraha National Park, with a straight-line distance of ca. 12 km between them (Fig. 4). Both localities were only slightly disturbed, but other surveyed areas of the park were severely affected by logging and cattle browsing (Bora et al. 2010). Due to the very limited data available we tentatively suggest assessing this species as Data Deficient according to the IUCN criteria, although Jenkins et al. (2011) classified *Brookesia exarmata*, which also is only known from Bemaraha as Endangered due to the fact that its habitat is undergoing a continuing decline due to fire, overgrazing, agriculture and selective logging.

Etymology: The species epithet is derived from the Latin adjective 'neglectus' meaning neglected. It refers to the fact that although identified as an unnamed species shortly after its collection (see Jackman et al. 2008), we refrained from describing it earlier for sentimental reasons only, due to the somewhat imperfect condition of the voucher specimens.

Discussion

Paroedura has experienced an enormous increase in species diversity and with the description of *Paroedura neglecta*, we add the 22nd species to the genus. Only nine species were distinguished by Dixon & Kroll (1974) and 14 species by Nussbaum & Raxworthy (2000). In the last 50 years (since 1969) only five reptile genera from Madagascar have increased by more than ten species (Uetz et al. 2018): the chameleon genera *Calumma* (23 new species) and *Brookesia* (20 valid new species), and the gecko genera *Phelsuma* (18 new species and subspecies from Madagascar), *Paroedura* (14 new valid species from Madagascar) and *Uroplatus* (11 new species). In contrast to *Paroedura*, the four other genera are mostly distributed in the humid eastern Madagascar, whereas *Paroedura* has its center of diversity in arid western and northern Madagascar. Similar to *P. neglecta*, many of the new *Paroedura* species have been described from karstic environments (Nussbaum & Raxworthy 2000, Glaw et al. 2014, 2018). In this respect, *Paroedura* is comparable to the Asian gecko genus *Cyrtodactylus* Gray, 1827 in which an enormous number of new species have been described in the last two decades, especially from karstic habitat (e.g., Bauer 2003, Heidrich et al. 2007, Grismer et al. 2017). Also in other gecko genera, new potentially microendemic species from karst environments have been regularly reported (e.g., Jono et al. 2015, Ineich et al. 2016, Scherz et al. 2017).

Our preliminary data indicate that the species diversity in *Paroedura* will continue increasing, and will do so even more as the species complexes of *P. bastardi/tanjaka* and *P. gracilis* are resolved (Glaw et al. 2018, Mohan et al. submitted). Including the sequences of Cocca et al. (2018), our tree (Fig. 1) reveals the existence of 5–7 lineages within *P. bastardi* that might represent distinct species, and according to our unpublished observations, also *P. tanjaka* might contain further, currently unrecognized diversity. Beside morphological and genetic studies, karyological data (Main et al. 2012, Aprea et al. 2013, Koubová et al. 2014) might also contribute significantly to elucidate the taxonomy of this genus in an integrative approach (Padial et al. 2010). The recently published genome of *Paroedura picta* (Hara et al. 2018) will be a valuable resource in our understanding of the evolution in the genus.

Paroedura neglecta is known from two localities in the Tsingy de Bemaraha massif, suggesting that the species might be widespread throughout this National Park. Although its distribution is poorly known, the species might be endemic to this massif as is also assumed for numerous other reptile species of the region (e.g., Bora et al. 2010). In any case, this massif is clearly a hotspot of *Paroedura* diversity. Raselimanana (2008) listed as many as five species (*Paroedura bastardi*, *P. homalorhina*, *P. karstophila*, *P. stumpffi* and *P. tanjaka*) and in a subsequent publication (Raselimanana 2013) even one additional species (*P.* aff. *tanjaka*). In the meantime, the population initially assigned to *P. homalorhina* has been described as *P. spelaea*, a species likely endemic to the Bemaraha massif (Glaw et al. 2018). One of the two species that were assigned by Raselimanana (2013) to *P. bastardi* and *P.* aff. *tanjaka* might actually belong to the morphologically similar species *P. neglecta* described herein, but further studies are necessary to proof this assumption. During our surveys we were unable to confirm *P. bastardi*, *P. karstophila* and *P. stumpffi* (Bora et al. 2010), but this might be due to our limited sampling of the massif.

Acknowledgements

We thank Parfait Bora and Hildegard Enting for company and assistance in the field, Alan Resatar from the Field Museum of Natural History for the loan of type specimens of *Paroedura guibeae*, and Ivan Ineich from the Muséum National d'Histoire Naturelle for the loan of type specimens of *P. bastardi* and valuable comments on the manuscript. We are grateful to the Malagasy Ministère de l'Environnement, des Eaux et des Forêts (Direction des Eaux et Forêts, DEF) for approving all field research, collecting and export of specimens under the permit 272-MINENV.EF/SG/DGEF/DPB/SCBLF/RECH dated 8 November 2005. Export of specimens was approved by the DEF under permits: 122N-EA04/MG06, dated 6 April 2006. Research was carried out in the framework of established collaborations with the UADBA.

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