Zootaxa 2195: 61–68 (2009)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

A new species of cryptically coloured day gecko (*Phelsuma*) from the Tsingy de Bemaraha National Park in western Madagascar

FRANK GLAW[1,4], JÖRN KÖHLER[2] & MIGUEL VENCES[3]

[1]*Zoologische Staatssammlung München, Münchhausenstr. 21, 81247 München, Germany*
[2]*Department of Natural History - Zoology, Hessisches Landesmuseum Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany*
[3]*Division of Evolutionary Biology, Zoological Institute, Technical University of Braunschweig, Spielmannstr. 8, 38106 Braunschweig, Germany*
[4]*Corresponding author. E-mail: Frank.Glaw@zsm.mwn.de*

Abstract

Phelsuma borai **sp. nov.** (Squamata: Gekkonidae) is described from the Tsingy de Bemaraha National Park, a deciduous dry forest on a karstic limestone massif in western Madagascar. The new species, known from a single specimen only, has a greyish-brown ground colouration and the ability of remarkable colour change. In terms of colouration and morphology it most closely resembles *Phelsuma mutabilis*, which might occur in sympatry, but differs by scalation, colouration and strong genetic divergence.

Key words: Squamata, Gekkonidae, *Phelsuma*, new species, Madagascar, Tsingy de Bemaraha National Park

Introduction

Most of the 1250 species of currently recognized geckos (Uetz 2009) are nocturnal and cryptically coloured. The genus *Phelsuma* represents one of the most remarkable exceptions, comprising diurnal geckos of mostly bright green colouration, often with red and blue colour elements, that probably have evolved in Madagascar but subsequently colonized many other islands in the western Indian Ocean. The closest known relative of *Phelsuma* probably is *Rhoptropella ocellata*, a cryptically coloured gecko from dry habitats in South Africa and Namibia (Austin *et al*. 2004). Recent molecular phylogenetic studies (Rocha *et al*. 2007, 2009; Raxworthy *et al.* 2007) suggest that the few cryptically coloured *Phelsuma* species from Madagascar (*P. breviceps, P. mutabilis, P. standingi*) occupy rather basal positions and occur in dry habitats of the west and southwest. These data would suggest that the ancestor of *Phelsuma* was a dry-adapted gecko species from Africa that first colonized dry areas of western Madagascar by oversea dispersal before the genus spread into more humid habitats and radiated into the wealth of colourful species that today are considered typical for *Phelsuma*. To support or reject this hypothesis, a full species inventory of *Phelsuma*, and especially of greyish species from arid western Madagascar is essential.

In the following, we describe a new, cryptically coloured *Phelsuma* that resembles *P. mutabilis* and was captured during a survey in the Tsingy de Bemaraha massif in western Madagascar. This bizarre limestone massif with steep slopes and sharp needle-like peaks is largely covered by deciduous dry forest and has recently revealed a remarkable number of new species of amphibians and reptiles (e. g. Schimmenti & Jesu 1996; Jesu *et al.* 1999; Nussbaum & Raxworthy 2000; Vences *et al.* 2000; Glos *et al.* 2005; Köhler *et al.* 2007; Glaw *et al*. 2007, 2009; Andreone & Randrianirina 2008) and its herpetofauna is still far from being sufficiently known (Bora *et al.* in press).

Accepted by A. Bauer: 12 Jun. 2009; published: 12 Aug. 2009

Materials and methods

The holotype was anesthetized by injection with chlorobutanol, fixed with 96% ethanol and stored in 70% ethanol. Abbreviations used: MNHN, Museum national d'Histoire naturelle, Paris; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; UADBA, Université d'Antananarivo, Département de Biologie Animale; ZSM, Zoologische Staatssammlung, München. All measurements were done with a caliper to the nearest 0.1 mm by the first author.

Description of a new species

***Phelsuma borai* sp. nov.**
(Figs. 1–2)

Phelsuma sp. "Bemaraha" — Glaw & Vences 2007: 400–401
Phelsuma sp. (Bemaraha) — Hallmann et al. 2008: 220–221
Phelsuma sp. aff. *mutabilis* — Rocha et al. 2009: 533–536

Holotype. ZSM 103/2006, adult male, collected at Andafiabe, Beboka River, 18°47'03" S, 44°46'46" E, 177 m above sea level, Tsingy de Bemaraha National Park, western Madagascar, on 24 March 2006 by P. Bora, H. Enting, F. Glaw & J. Köhler.

Diagnosis. *Phelsuma borai* **sp. nov.** is a medium-sized day gecko with greyish-brown ground colouration and without any green or red colours. It differs from most other *Phelsuma* species by the combination of (1) absence of green and red colours on the dorsal surface in life and (2) a low number of lamellae below the fourth toe (11 in *P. borai* vs. 12–28 in most other species). It differs from *P. pronki* which has a smilar low number of lamellae by a very different life-colouration and smaller size (42 vs. 49–50 mm SVL). *P. borai* shares most characteristics with *P. breviceps* and *P. mutabilis*, but differs from both species by a higher number of supralabials (9–10 vs. 6–8), a higher number of internasals (3 vs. 1–2), a distinctly concave groove between the nasals (vs. not concave), a triangular mental scale (vs. mostly bell-shaped mental), and the configuration of the throat scalation (see Fig. 3). Furthermore, it differs from *P. mutabilis* by the absence of a dark stripe along the infralabials. In addition, *P. borai* is characterized by a very strong differentiation from all other *Phelsuma* species in the studied mitochondrial genes (16S rRNA and cytochrome *b*) and by a substantial divergence in the nuclear (C-mos, Rag-1 and Rag-2) gene fragments (see Rocha et al. 2009 and Discussion below).

Description of the holotype. Well preserved, with largely complete original tail with the terminal 13.8 mm regenerated. Fourth toe of left foot missing. Hemipenis not extruded. Body and head flattened dorsoventrally. Head slightly wider than neck, about as wide as body. Ear opening roundish. Tail longer than snout-vent length, dorsoventrally flattened in cross section. No distinct tail whorls recognizable. Digits strongly expanded at tips, first finger and first toe vestigal, comparative finger and toe length 1<2<5<3<4. Rostral scale wider than tall, less wide as mental. Distinct rostral cleft in dorsal process of rostral scale. Three internasals, the central one in a deep depression. Nostril in contact with four scales, the first supralabial, the nasal and two small postnasals, but no contact with rostral. Pupil round. Dorsal and lateral scales of head smooth, nearly flat, becoming increasingly rounded in profile on the posterior regions of the head. Dorsal and lateral scales of body semi-spherical, dorsal scales of tail flattened in profile. All ventral scales smooth. The median row of subcaudal scales distinctly enlarged transversely, more than twice as long as wide. Mental scale triangular, bordered posteriorly by a pair of elongate, irregular hexa- and pentagonal postmentals. Postmentals contact mental, first infralabial and two or three, relatively large gulars. Gulars decrease gradually in size posteriorly.

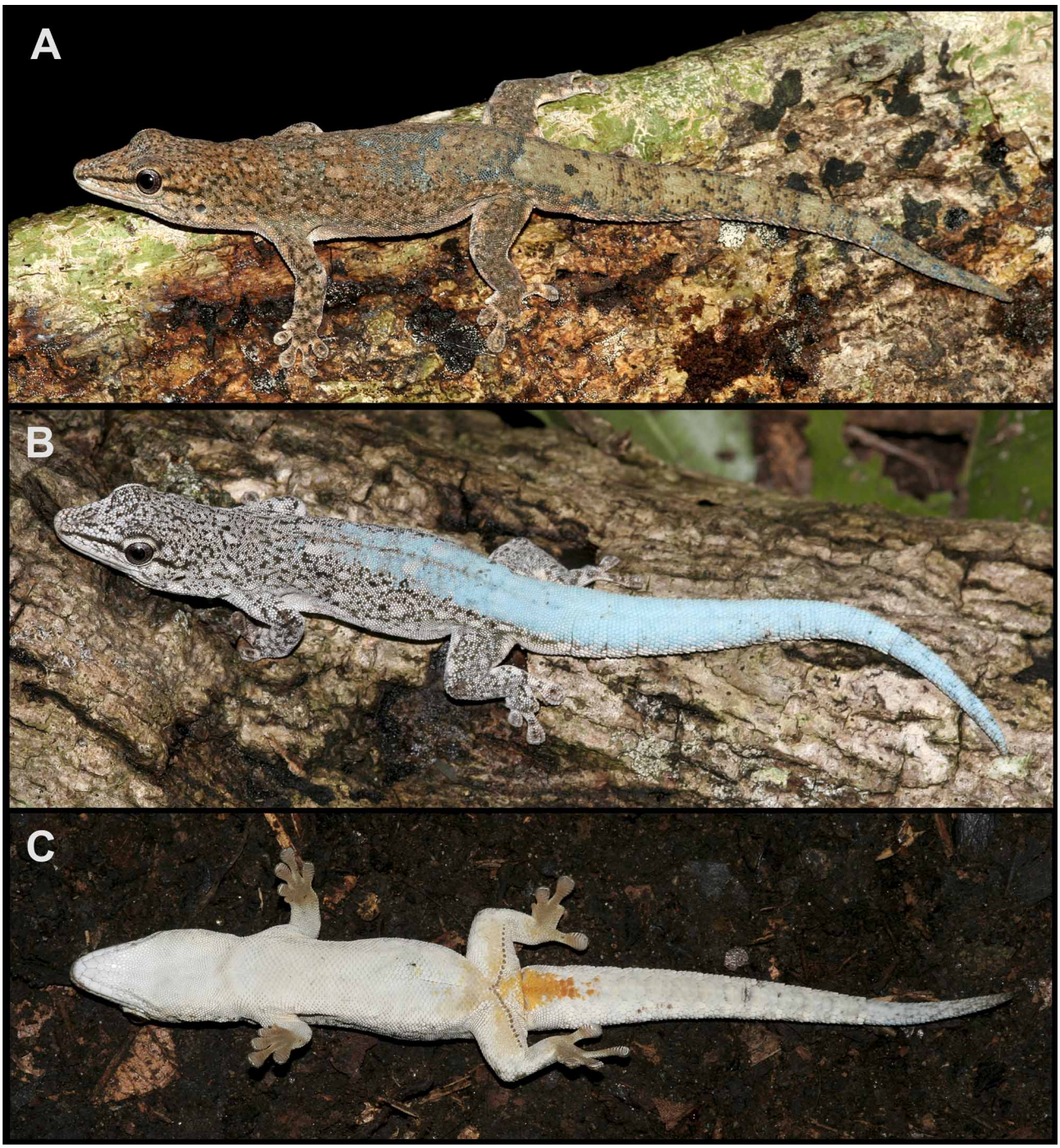

FIGURE 1. *Phelsuma borai* **sp. nov.**, male holotype (ZSM 103/2006) in life: dorsolateral views in (A) cryptic colour phase and (B) splendid colour phase; (C) ventral view.

Measurements: Snout-vent length 41.7 mm; tail length 46.4 mm; head length 14.5 mm; head width (at widest point) 9.6 mm; snout length (anterior edge of eye to tip of snout) 6.4 mm; horizontal eye diameter 2.6 mm; ear opening diameter 1.0 mm; eye-ear distance 3.3 mm; internarial distance 2.4 mm; nostril-eye distance 5.1 mm, axilla-groin length 15.4 mm; forelimb length (from axilla to tip of longest finger) 12.1 mm; hindlimb length (from groin to tip of longest toe) 15.6 mm. Several additional measurements and counts are given in table 1.

TABLE 1. Morphological variation in *Phelsuma borai* and the related species *P. breviceps* and *P. mutabilis* (*P. androyense* and *P. micropholis* being junior synonyms of *P. mutabilis*). Abbreviations: Status (HT, holotype; LT, lectotype; PLT, paralectotype; ST, syntype), Sex (M, male; F, female), SVL, snout-vent length (in mm); TL, total length (in mm), in parenthesis if tail regenerated; SL, number of supralabials (left/right); IL, number of infralabials (left/right); IN, number of internasals (c, concave groove between nasals; nc, no concave groove between nasals); NC, nostril contact (0, in contact with rostral and first supralabial; 1, in contact with first supralabial only); PFP, number of preanofemoral pores; RC, rostral cleft above (+, present; -, absent); ME, mental (1, bell-shaped; 2, triangle-shaped; 3, trapezoid); DO, dorsals (s, smooth; k, keeled), VE, ventrals (s, smooth; k, keeled); SC= subcaudals (s, smooth; k, keeled); SCE, subcaudals enlarged transversely +, present; -, absent), SL4, number of (transversely enlarged) subdigital lamellae under fourth toe; TS, dark throat stripe below infralabials (+, present; -, absent).

Catalogue number	Taxon	Status	Sex	SVL	TL	SL	IL	IN	NC	PFP	RC	ME	DO	VE	SC	SCE	SL4	TS
ZSM 103/2006	*P. borai*	HT	M	41.7	88.1	10/9	7/6	3 (c)	1/1	29	+	2	s	s	s	+	-/11	-
ZSM 585/2000	*P. breviceps*	—	M	52.1	116.4	7/8	6/6	1 (nc)	1/1	31	-	3	s	s	s	+	11/10	-
MNHN 1895.152	*P. mutabilis*	ST	M	46.9	(83.5)	7/8	7/7	1 (nc)	1/1	31	+	1	s	s	s	+	10/11	+
MNHN 1895.154	*P. mutabilis*	ST	W	39.5	(67.4)	7/8	7/6	1 (nc)	1/1	0	+	1	s	s	s	+	11/10	+
MNHN 1901.150	*(P. androyense)*	ST	M	44.5	(84.2)	7/7	7/6	1 (nc)	1/1	28	-	1	s	s	s	+	11/11	+
MNHN 1901.151	*(P. androyense)*	ST	M	38.3	79.1	7/7	7/6	1 (?)	1/1	32	+	1	s	s	s	+	10/11	+
SMF 9470	*(P. micropholis)*	PLT	M	44.1	95.7	7/7	7/5	1 (nc)	1/1	29	+	1	s	s	s	+	10/11	+
SMF 9471	*(P. micropholis)*	PLT	M	43.8	94.0	7/7	5/6	2 (nc)	1/1	29	+	1	s	s	s	+	11/10	+
SMF 9472	*(P. micropholis)*	PLT	M	36.3	77.5	7/7	6/7	1 (nc)	1/1	29	+	1	s	s	s	+	10/10	+
SMF 9473	*(P. micropholis)*	LT	M	43.3	89.6	7/7	6/5	1 (nc)	1/1	28	-	2	s	s	s	+	11/11	+
ZSM 587/2000	*P. mutabilis*	—	W	40.6	81.8	7/6	5/5	2 (nc)	1/0	0	+	1	s	s	s	+	11/11	(+)
ZSM 588/2000	*P. mutabilis*	—	M	43.9	92.4	7/7	5/6	2 (nc)	1/1	30	+	1	s	s	s	+	10/11	(+)
ZSM 945/2003	*P. mutabilis*	—	W	39.2	82.0	7/7	5/5	2 (nc)	1/1	0	+	1	s	s	s	+	11/11	+
ZSM 948/2003	*P. mutabilis*	—	W	39.4	(71.3)	7/7	5/5	1 (nc)	1/1	0	+	1	s	s	s	+	10/10	+
ZSM 186/2004	*P. mutabilis*	—	W	40.1	76.2	6/6	5/5	1 (nc)	1/1	0	+	1	s	s	s	+	10/9	+

Colour after more than two years in alcohol partly similar to that of the splendid colour-phase in life (Fig. 1B). Ground colour of head, body and dorsal parts of the limbs dorsally and laterally grey-brown with blackish spots and dots. A purplish middorsal band (largely without black spots) runs from the middle of the back to the tip of the tail. A black band from the nostril to anterior eye and from posterior eye to a point above the ear opening. Supralabials and infralabials white. Throat, chest, venter, and ventral parts of forelimbs and hindlimbs whitish; ventral side of tail whitish with a purplish shade, especially in the anterior part. No dark stripe on throat recognizable along the lower suture of infralabials, although scattered dark pigment is present. In life, colouration was extremely variable (Fig. 1), see also additional colour photographs of the holotype in Glaw & Vences (2007: 401) and Hallmann *et al.* (2008: 221). One cryptic colour phase resembled the bark of tree, with a beige or brownish-greyish ground colouration with irregular grey-blue and blackish pigment and with a series of three pairs of light spots (one pair in neck, one pair on anterior back, one pair on posterior back). The dorsal surface of the tail was olive-green with dark grey and bluish flecks, reminding to the colour of lichens (Fig. 1A). Labials were light. When exposed to sunlight the same individual changed colour to a whitish-greyish ground colour with black reticulations, a blue tail and a broad blue middorsal band, here called splendid colour phase (Fig. 1B). The ventral surfaces were white, with exception of the yellowish area of the preanofemoral pores and the anteriormost part of the tail which showed an orange spot (Fig. 1C). No dark stripe on throat was recognizable along the lower suture of infralabials, although scattered dark pigment is present when examined after preservation (Fig. 3).

FIGURE 2. *Phelsuma borai* **sp. nov.**, male holotype (ZSM 103/2006) in cryptic colour phase camouflaged on tree bark.

Distribution and conservation. *Phelsuma borai* is reliably known only from the Tsingy de Bemaraha National Park in western Madagascar. However, Mori *et al.* (2006) and Mori & Ikeuchi (2006), in publications on the herpetofauna of the Ankarafantsika National Park in northwestern Madagascar, provided a total of three different photographs of a *Phelsuma* species identified as *P. mutabilis* which—based on its life-colouration—is likely to represent *P. borai*. It is therefore reasonable to assume that *P. borai* might be distributed in the dry forests between the Tsingy de Bemaraha and Ankarafantsika. It is also possible that

other records of *P. mutabilis* from northwestern Madagascar, especially the localities Ankarafantsika, Namoroka, Andranomanintsy and Maevatanana (Hallmann *et al.* 2008, Ramanamanjato & Rabibisoa 2002, Raselimanana 2008) actually refer to *P. borai* or to both *P. mutabilis* and *P. borai*. The confirmed northernmost record of *P. mutabilis* is from Antsalova (UADBA uncatalogued [FGCZ 971]) where we observed this species abundantly on trees. All records of *P. mutabilis* from further north should be revised in order to determine the extent of occurrence of *P. borai* and the northern range limits of *P. mutabilis*. Due to the very limited current knowledge on this species we suggest to consider the conservation status of *P. borai* as "Data Deficient" according to the IUCN criteria as used for the Malagasy amphibians (see Andreone *et al.* 2005).

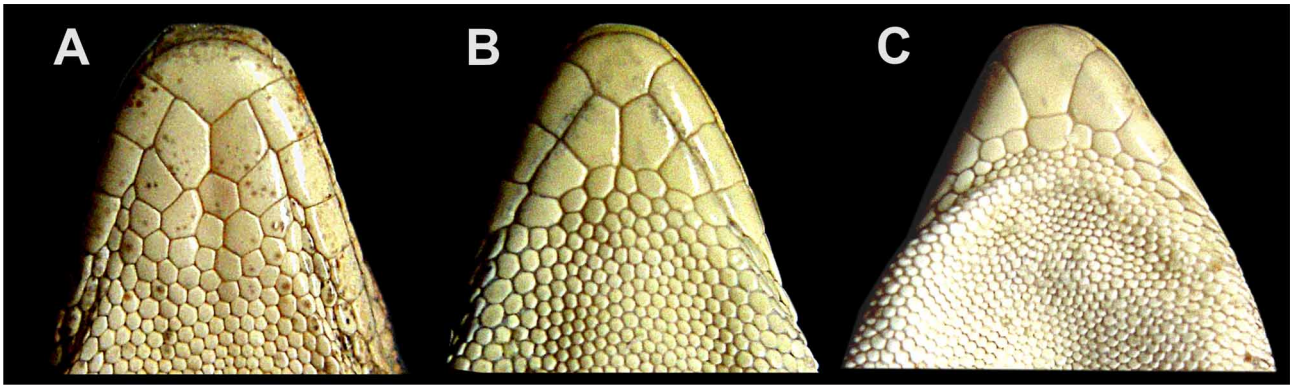

FIGURE 3. Close-up views of mental region of preserved specimens, showing differences in scalation: (A) *Phelsuma borai* **sp. nov.**, holotype (ZSM 103/2006); (B) *Phelsuma mutabilis* (ZSM 588/2000); (C) *Phelsuma breviceps* (ZSM 585/2000).

Habitat and habits. The holotype of *Phelsuma borai* was captured after dusk in karstic dry forest in the rainy season, roosting in the vegetation close to a cave entrance. The specimens from Ankarafantsika (Mori *et al*. 2006) considered by us to possibly represent *P. borai* were found on trees and in a pitfall. Before preserving the holotype we noticed its extraordinary ability to change the colouration (Fig. 1) and the unusual cryptic nature of one colour phase (Fig. 2). Two other *Phelsuma* species, *P. abbotti chekei* and *P. kochi* were found around the type locality and two additional species, *P. mutabilis* and *P.* cf. *dubia*, were found at Antsalova, just outside of the Tsingy de Bemaraha National Park. Sympatric occurrence of *P. borai* and *P. mutabilis* is, therefore, likely but still needs confirmation.

Etymology. We dedicate this new species to our student, colleague and friend Parfait Bora who captured the holotype and was of invaluable help during several expeditions in Madagascar.

Available names. Two available names are currently considered as junior synonyms of *Phelsuma mutabilis* (see Hallmann *et al.* 2008): The original description of *Phelsuma androyense* Mocquard, 1901 was based on two males from Androy Nord (Mocquard 1901), both studied by us (see table 1). In the original description of *Phelsumia micropholis*, Boettger (1913: 293–294) mentioned a total of 28 specimens (20 specimens from Tulear, one adult male from Andranohinaly, one adult male from Tsimanampetso and five males and one female from Menabe). He also stated that the original description was based on one male from Tsimanampetso (= Tsimanampetsotsa) as well as one male and one female from Menabe and provides measurements for these three specimens. Four paralectotypes, including the male from Tsimanampetso and three specimens from Menabe were identified by Bauer & Günther (1991) in the Zoological Museum at Berlin (ZMB). Boettger (1913) provides partial data of at least 18 specimens in his description and we consider the whole series of 28 specimens as type material. However, Mertens (1962), in a review of the genus *Phelsuma*, listed only five of these specimens, SMF 9470-9473 (studied in this paper) and the male from Andranohinaly, indicating that many paralectotypes were exchanged or lost. Although Mertens (1962) already considered the male SMF 9473 from Menabe as "Typus" and SMF 9470-9472 as "Paratypen" he later considered SMF 9473 as lectotype (Mertens 1967), indicating that SMF 9470-9472 are paralectotypes. Upon

examination these four specimens were morphologically homogeneous (Table 1). Based on the throat scalation and further morphological data (Table 1), it is evident that both *Phelsuma androyense* Mocquard, 1901 and *Phelsumia micropholis* Boettger, 1913 are indeed junior synonyms of *Phelsuma mutabilis* (see also table 1) and not conspecific with *Phelsuma borai*.

Discussion

The description of *P. borai* adds a distinctive new species to the genus *Phelsuma*. Based on the phenetic similarities *P. borai* appears to be most closely related to *P. mutabilis* and *P. breviceps*, which together form the *Phelsuma mutabilis* species group. This group is characterized by medium size, greyish-brownish ground colour, a relatively short head, a low number of subdigital lamellae below the fourth toe (10–12), relatively low numbers of supralabials (6–10) and infralabials (5–8), and its distribution in arid western Madagascar. Furthermore, this species group forms a well supported monophyletic lineage in molecular studies (Rocha *et al*. 2009) which, however, found a rather high genetic divergence between all three species (23.5% uncorrected pairwise sequence divergence in the cytochrome *b* gene and 11.2% divergence in the 16S rRNA gene between *P. borai* and *P. mutabilis*; cytochrome *b* distance 22.1% and 16S rRNA distance 11.6% between *P. borai* and *P. breviceps*). Interestingly, all three species of the *P. mutabilis* group show distinct differences in the scalation of the throat. In *P. breviceps*, only the mental and infralabial scales are distinctly enlarged whereas the next posterior row of throat scales, the postmentals, are already much smaller and the following row of scales already has the size of the small scales which cover most of the throat. In *P. mutabilis*, there are usually six enlarged throat scales in addition to the mental and infralabials: one pair of enlarged postmentals and two enlarged scales on each side, which touch the second and third infralabial. Finally, in *P. borai* the posterior size-reduction of throat scales is enlarged to several scale rows.

P. borai is apparently the only species in the genus *Phelsuma* showing an extremely cryptic colouration that might be a mimesis to the bark of tree, the obvious habitat of this species. In contrast to most other *Phelsuma* species *P. borai* is apparently rarely encountered within its habitat, which might suggest that it lives mainly high up in the canopy of trees and rarely close to the ground. The most remarkable characteristic of *P. borai* was its ability for quick colour change, which in this extent is unusual for *Phelsuma* and might allow the species to switch from cryptic to a relatively splendid courtship colouration.

Acknowledgements

We are grateful to Parfait Bora, Hildegard Enting and local guides for their help in the field, as well as to Ivan Ineich (MNHN) and Gunther Köhler (SMF) who allowed the loan of specimens under their care. Akira Mori shared information with us. The research in Madagascar was made possible by a cooperation accord between the UADBA and the ZSM. Malagasy authorities are acknowledged for collection and export permits. The field work was financially supported by the "Freunde der Zoologischen Staatssammlung München" and the "Hessisches Landesmuseum Darmstadt".

References

Andreone, F., Cadle, J.E., Cox, N., Glaw, F., Nussbaum, R.A., Raxworthy, C.J., Stuart, S., Vallan, D. & Vences, M. (2005) Species review of amphibian extinction risks in Madagascar: conclusions from the Global Amphibian Assessment. *Conservation Biology*, 19, 1790–1802.

Andreone, F. & Randrianirina, J.E. (2008) An unexpected *Rhombophryne* record at Tsingy de Bemaraha confirms the presence of cophyline frogs in western Madagascar. *Zootaxa*, 1812, 46–48.

Austin, J.J., Arnold, E.N. & Jones, C.G. (2004) Reconstructing an island radiation using ancient and recent DNA: the

extinct and living day geckos (*Phelsuma*) of the Mascarene islands. *Molecular Phylogenetics and Evolution*, 31, 102–109.

Bauer, A. & Günther, R. (1991) An annotated type catalogue of the geckos (Reptilia: Gekkonidae) of the Zoological Museum, Berlin. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Zoologische Reihe*, 67 (2), 279–310.

Boettger, O. (1913) Reptilien und Amphibien von Madagascar, den Inseln und dem Festland Ostafrikas, pp. 269–375, plates 23–30, in Voeltzkow, A.: Reise in Ostafrika in den Jahren 1903–1905, Wissenschaftliche Ergebnisse, dritter Band, systematische Arbeiten, Schweizerbartsche Verlagsbuchhandlung, Stuttgart.

Bora, P., Randrianantoandro, J.C., Randrianavelona, R., Hantalalaina, E.F., Andriantsimanarilafy, R.R., Rakotondravony, D., Ramilijaona, O.R., Vences, M., Jenkins, R.K.B., Glaw, F. & Köhler, J. (in press) Amphibians and reptiles of the Tsingy de Bemaraha plateau, western Madagascar: checklist, biogeography and conservation. *Herpetological Conservation and Biology.*

Glaw, F., Köhler, J., Bora, P., Rabibisoa, N.H.C., Ramilijaona, O. & Vences, M. (2007) Discovery of the genus *Plethodontohyla* (Anura: Microhylidae) in dry western Madagascar: description of a new species and biogeographic implications. *Zootaxa*, 1577, 61–68.

Glaw, F., Nagy, Z.T., Köhler, J., Franzen, M. & Vences, M. (2009) Phylogenetic relationships of a new species of pseudoxyrhophiine snake (Reptilia: Lamprophiidae: *Thamnosophis*) suggest a biogeographic link between western and northern Madagascar. *Organisms Diversity & Evolution*, 9 (1), 13–22.

Glaw, F. & Vences, M. (2007) A Field Guide to the Amphibians and Reptiles of Madagascar, third edition. Vences and Glaw Verlag, Köln (Cologne), 496 pp.

Glos, J., Glaw, F. & Vences, M. (2005) A new species of *Scaphiophryne* from western Madagascar. *Copeia*, 2005, 252–261.

Hallmann, G., Krüger, J. & Trautmann, G. (2008) Faszinierende Taggeckos. Die Gattung *Phelsuma* (2. Auflage). Natur und Tier-Verlag, Münster, 253 pp.

Jesu, R., Mattioli, F. & Schimmenti, G. (1999) On the discovery of a new large chameleon inhabiting the limestone outcrops of western Madagascar: *Furcifer nicosiai* sp. nov. (Reptilia, Chamaeleonidae). *Doriana*, 7, 1–14.

Köhler, J., Glaw, F. & Vences, M. (2007) A new green treefrog, genus *Boophis* Tschudi 1838 (Anura Mantellidae), from arid western Madagascar: phylogenetic relationships and biogeographic implications. *Tropical Zoology*, 20, 215–227.

Mertens, R. (1962) Die Arten und Unterarten der Geckonengattung *Phelsuma*. *Senckenbergiana biologica*, 43, 81–127.

Mertens, R. (1967) Die herpetologische Sektion des Naturmuseums und Forschungsinstitutes Senckenberg in Frankfurt a. M. nebst einem Verzeichnis ihrer Typen. *Senckenbergiana biologica*, 48 (special issue/Sonderheft A), 1–106.

Mocquard, M.F. (1901) Note préliminaire sur une collection de reptiles et de batraciens recueillis par M. Alluaud dans le sud de Madagascar. *Bulletin du Muséum national d'Histoire Naturelle, Paris*, 7, 251–256.

Mori, A. & Ikeuchi, I. (eds.) (2006) A photographic guide to the reptiles and amphibians of Ampijoroa. *Kyoto University, Japan*.

Mori, A., Ikeuchi, I. & Hasegawa, M. (2006) Herpetofauna of Ampijoroa, Ankarafantsika Strict Nature Reserve, a dry forest in northwestern Madagascar. *Herpetolgical Natural History*, 10, 31–60.

Nussbaum, R.A. & Raxworthy, C.J. (2000) Systematic revision of the genus *Paroedura* Günther (Reptilia: Squamata: Gekkonidae), with description of five new species. *Miscellaneous Publications, Museum of Zoology, University of Michigan*, 189, 1–26.

Ramanamanjato, J.B. & Rabibisoa, N. (2002) Evaluation rapide de la diversité biologique des reptiles et amphibiens de la Réserve Naturelle Intégrale d'Ankarafantsika, in: Alonso, L.E., Schulenberg, T.S., Radilofe, S., Missa O. (Eds.), Une evaluation biologique de la Réserve Naturelle Intégrale d'Ankarafantsika, Madagascar. Bull. RAP eval. rapide 23, Conservation International, Washington, DC., pp. 98–103 and 135–138.

Raselimanana, A.P. (2008) Herpétofaune des forêts sèches malgaches. *Malagasy Nature*, 1, 46–75.

Raxworthy, C.J., Ingram, C.M., Rabibisoa, N. & Pearson, R.G. (2007) Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using Day Geckos (*Phelsuma*) from Madagascar. *Systematic Biology*, 56, 907–923.

Rocha, S., Posada, D., Carretero, M.A. & Harris, D.J. (2007) Phylogenetic affinities of Comoroan and East African day geckos (genus *Phelsuma*): multiple natural colonisations, introductions and island radiations. *Molecular Phylogenetics and Evolution*, 43, 685–692.

Rocha, S., Vences, M., Glaw, F., Posada, D. & Harris, D.J. (2009) Multigene phylogeny of Malagasy day geckos of the genus *Phelsuma*. *Molecular Phylogenetics and Evolution*, 52, 530–537.

Schimmenti, G. & Jesu, R. (1996) *Brookesia exarmata* sp. nov. (Reptilia, Chamaeleonidae): a new dwarf chameleon from the limestone outcrops of western Madagascar. *Italian Journal of Zoology*, 63, 193–197.

Uetz, P. (2009) The TIGR Reptile database (http://www.reptile-database.org/)

Vences, M., Glaw, F., Jesu, R. & Schimmenti, G. (2000) A new species of *Heterixalus* (Amphibia: Hyperoliidae) from western Madagascar. *African Zoolgy*, 35, 269–276.