

A new dwarf species of day gecko, genus *Phelsuma*, from the Ankarana pinnacle karst in northern Madagascar

FRANK GLAW¹, PHILIP-SEBASTIAN GEHRING², JÖRN KÖHLER³, MICHAEL FRANZEN¹ & MIGUEL VENCES²

¹) Zoologische Staatssammlung München, Münchhausenstr. 21, 81247 München, Germany

²) Division of Evolutionary Biology, Zoological Institute, Technical University of Braunschweig, Spielmannstr. 8, 38106 Braunschweig, Germany

³) Department of Natural History – Zoology, Hessisches Landesmuseum Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany

Corresponding author: FRANK GLAW, e-mail: Frank.Glaw@zsm.mwn.de

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Abstract. We describe a new day gecko, *Phelsuma roesleri* sp. n. (Squamata: Gekkonidae) from Ankarana, a karstic limestone massif in northern Madagascar. The new species is characterized by a comparatively very small body size (snout–vent length about 33–36 mm, total length 69–72 mm) and by its colouration, and was found exclusively on *Pandanus* screw pines in the Tsingy karst formation outside the Ankarana nature reserve. Sequences of the 16S rRNA gene suggest that it is the sister species to the allopatric *Phelsuma laticauda* rather than to *P. lineata bombetokensis* from the northwest of Madagascar, albeit with low support from the short DNA fragments studied. This latter taxon instead was genetically similar to other *P. lineata* populations from the northern central east. We consider the new species as “Critically Endangered” according to the IUCN criteria, mainly due to its assumed very small and patchy area of occupancy.

Key words. Squamata, Gekkonidae, *Phelsuma*, *P. roesleri* new species, *P. lineata bombetokensis*, *Pandanus*, Madagascar, Ankarana.

Introduction

Day geckos of the genus *Phelsuma* represent one of the most successful reptile radiations in Madagascar and on most other islands and archipelagos in the western Indian Ocean. Due to their splendid colouration and diurnal activity, *Phelsuma* are very conspicuous lizards, but despite intensive research efforts, the taxonomy and phylogenetic relationships of several taxa are still unclear and new species are regularly discovered and described (NUSSBAUM et al. 2000, RÖSLER et al. 2001, SCHÖNECKER et al. 2004, LERNER 2004, RAXWORTHY et al. 2007, BERGHOF & TRAUTMANN 2009, GLAW et al. 2009). The genus probably originated in Madagascar and subsequently dispersed and radiated in the other island archipelagos (AUSTIN et al. 2004, HARMON et al. 2008). Recent phylogenetic studies have shown that the colonization history of each island group is different (e.g. ROCHA et al. 2009). The species of the Mascarene Islands form an old monophyletic group of which the closest Malagasy relatives still remain to be identified (e.g. HARMON et al. 2008). The Malagasy sister group of the smaller radiation of the continental Seychelles Islands is possibly *Phelsuma vanheygeni* (ROCHA et al. 2009), a species that has been described only recently from the Sambirano region in northwestern Madagascar (LERNER 2004). The Comoro Islands have the most complex colonization history and were colonized by three different endemic *Phelsuma* lineages, (1) the ancestor of *P. comorensis*, (2) the ancestor of *P. nigristriata* and (3) a lineage that radiated into *P. pasteuri*, *P. robertmertensi*, *P. v-nigra* and two

further subspecies; the sister group of the latter lineage is probably *Phelsuma laticauda* from northern Madagascar (ROCHA et al. 2009), a region that served as the source for the colonization of the Comoro Islands.

Here we describe a new *Phelsuma* species from the Ankarana Massif in northern Madagascar. The new species is probably the sister species of *P. laticauda* and therefore of special interest to understand the colonization history of the *Phelsuma laticauda* group in the Comoros.

Materials and methods

The type specimens were euthanized by injection with chlorobutanol, fixed with 90% ethanol and stored in 70% ethanol. Locality information was recorded with GPS receivers. Acronyms and institutional abbreviations used are: SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; UADBA, Université d’Antananarivo, Département de Biologie Animale; ZMA, Zoologisch Museum Amsterdam; ZSM, Zoologische Staatssammlung München. SG, FGZC, and ZCMV refer to field numbers of S. Gehring, F. Glaw and M. Vences, respectively.

All measurements were taken with digital callipers to the nearest 0.1 mm by the first author.

After salt extraction of total genomic DNA, fragments of the mitochondrial 16S rRNA gene were PCR-amplified using the primers 16SAL and 16SBH (PALUMBI et al. 1991) or the newly designed primers 16S-Phel-L1 (5' AACCGT-GCAAAGGTAGCATAA 3') and 16S-Phel-H1 (5' GAG-

GTCGTAAACCCCCTTG 3') as per standard protocols. Sequences were resolved on an ABI 3130XL automated sequencer (Applied Biosystems). All sequences were checked for their quality by eye and aligned manually. Hypervariable regions that could not be reliably aligned were excluded from analysis (positions 115–148 and 245–247 of the alignment).

The obtained sequences were combined with those from ROCHA et al. (2009): *Lygodactylus luteopicturatus* (FJ829971), *Phelsuma standingi* (FJ829961), *Phelsuma antanosy* (FJ829895), *Phelsuma grandis* (FJ270569), *Phelsuma laticauda laticauda* (FJ8289924, FJ8929925), *Phelsuma serraticauda* (FJ829960); ROCHA et al. (2010): *Phelsuma lineata elanethana* (ZMA 19302), *Phelsuma dorsivittata* (UADBA 24777); and SOUND et al. (2006): *Phelsuma lineata lineata* (DQ270570).

We deposited the newly resolved DNA sequences in Genbank. Accession numbers are HMO30810 for *Phelsuma laticauda angularis* (ZCMV 11434, from Antsohihy), HMO30811 for *P. serraticauda* (SG 300, from Manompana), HMO30812 for *P. serraticauda* (SG 304, from Manompana), HMO30808 for *P. lineata bombetokensis* (ZCMV 3643, from Ankarafantsika) and HMO30807 and HMO30809 for *P. roesleri* (ZSM 1517/2008 and ZSM 1516/2008 from Ankarana).

In the data set including the outgroup, 84 of 328 characters were parsimony informative. MrModeltest version 2.3 (NYLANDER 2004) was used to select the best-fitting nucleotide model of evolution by the Akaike Information Criterion (AIC). A phylogenetic tree based on Bayesian inference was computed with MrBayes v3.ob4 (RONQUIST & HUELSENBECK 2003), using Markov Chain Monte Carlo (MCMC) sets for 5×10^6 generations and sampled every 100 generations. The trees corresponding to the first 2×10^6 generations were discarded as burn-in after empirically assessing the log-likelihood values of the sampled trees.

As a further measure of node support, we performed a bootstrap analysis under the Maximum Parsimony optimality criterion with 2000 replicates, using PAUP* 4.ob10 software (SWOFFORD 2002).

Systematics

Phelsuma roesleri sp. n.

(Figs. 1–4)

Holotype: ZSM 1517/2008 (FGZC 1828), adult male, hemipenes everted, collected in the Ankarana Massif approximately 2 km NE Mahamasina (aerial distance), 12°57'42" S, 49°08'59" E, 128 m above sea level, Antsiranana Province, north Madagascar, on 24 February 2008 by F. GLAW & Z. T. NAGY.

Paratypes: UADBA uncatalogued (FGZC 1645–1646), two specimens (most probably adult) of unknown sex, ZSM 1516/2008 (FGZC 1667), male, all collected at the type locality, on 14 February 2008 by F. GLAW, M. FRANZEN, J. KÖHLER, A. G. RAKOTOVAO & K. ZAFINASOLO.

Diagnosis: A comparatively very small, green *Phelsuma* (snout–vent length 33–36 mm, total length 69–72 mm) with a characteristic colour pattern in life, consisting of four red transverse bands or markings on snout and head, followed by three parallel red stripes along the anterior back that run from neck to forelimb insertion, and a distinct H-, II-, or V-shaped red marking on the lower back. In life, this unique colour pattern alone allows an easy and immediate distinction from all other valid *Phelsuma* species. In addition, *Phelsuma roesleri* differs from all other *Phelsuma* species except *P. borai*, *P. hoeschi*, *P. kely*, *P. parva*, *P. pusilla*, and *P. vanheygeni*, by its distinctly smaller size (snout–vent length 33–36 vs. 43–135 mm; total length 69–72 vs. 90–300 mm). Beside its life colouration, it differs from *P. borai* by having only one internasal scale (versus three), from the four small species of the *P. lineata* group (*P. hoeschi*, *P. kely*, *P. parva*, and *P. pusilla*) by unkeeled ventrals and subcaudals and almost unkeeled dorsals (vs. keeled), and from *P. vanheygeni* by having the nostril not in contact with the rostral (vs. nostril in contact with rostral according to ROCHA et al. 2010). It differs from the similar subspecies *P. lineata bombetokensis* from northwestern Madagascar by



Figure 1. *Phelsuma roesleri* sp. nov., male holotype from Ankarana (ZSM 1517/2008) in life.



Figure 2. Portrait of *Phelsuma roesleri* sp. nov., male holotype from Ankarana (ZSM 1517/2008) in life. Note the position of the nostril placed above the suture between the rostral and first upper labial.

unkeeled ventrals and subcaudals (vs. keeled), less distinctly keeled dorsals, by smaller size (maximum total length 72 vs. 110 mm), the absence of a distinct dark lateral spot behind the forelimb, and by the absence of a dark spot in front of the hindlimb (vs. presence of these spots). *Phelsuma roesleri* differs from the phylogenetically related *P. laticauda* by its much smaller size (total length up to 72 vs. 130 mm), absence of distinctly broadened median subcaudals (vs. presence), and a less broadened tail. In addition, *P. roesleri* differs from all *Phelsuma* species and subspecies for which DNA sequence data are available by a strong genetic differentiation in the studied fragment of the mitochondrial 16S rRNA gene (see ROCHA et al. 2009, 2010; Fig. 6).

Description of the holotype: Well-preserved, with complete original tail and everted hemipenes. Right hand and lower arm of left forelimb removed as tissue sample. Body and head flattened dorsoventrally. Head slightly wider than neck, about as wide as body. Ear opening rounded. Tail longer than snout–vent length, dorsoventrally flattened in cross section. Distinct tail whorls with 7 scale rows recognizable from above. Digits strongly expanded at tips, first finger and first toe vestigial, comparative finger and toe lengths $1 < 2 < 5 < 3 < 4$. Number of transversely enlarged subdigital lamellae under fourth toe 14/14 (left/right). Rostral scale wider than tall, less wide than mental. No rostral

cleft in dorsal process of rostral scale. One internasal scale. Centre of nostril placed almost above, only slightly behind the suture between rostral and first supralabial. Nostril in contact with four scales (first supralabial, nasal, two small postnasals), but not in contact with rostral. Pupil round. Dorsal and lateral scales of head smooth, nearly flat, becoming increasingly smaller in the posterior regions of the head. Dorsal and lateral scales of body hemispherical, some of them, especially towards the flanks, slightly keeled. Dorsal scales of tail mostly conical and unkeeled, but with few keeled scales on the tail base. All ventral and subcaudal scales smooth. Median row of subcaudal scales only slightly and irregularly enlarged transversely. Mental scale largely triangular, bordered posteriorly by a pair of elongate, irregular hexa- and pentagonal postmentals. Postmentals contact mental, first infralabial and two or three gulars. Gulars decrease gradually in size posteriorly. Number of supralabials (left/right) 8/9; number of infralabials (left/right) 6/7, number of well-developed preanofemoral pores 12, with 11 additional distinctly smaller and poorly developed pores. Hemipenes relatively slender, with two terminal lobes.

Measurements: Snout–vent length 32.6 mm; tail length 36.4 mm; head width (at widest point) 6.4 mm; snout length (anterior edge of eye to tip of snout) 4.5 mm; horizontal eye diameter 2.1 mm; ear opening diameter 0.7 mm; eye–ear distance 2.9 mm; internarial distance 1.5 mm; nos-

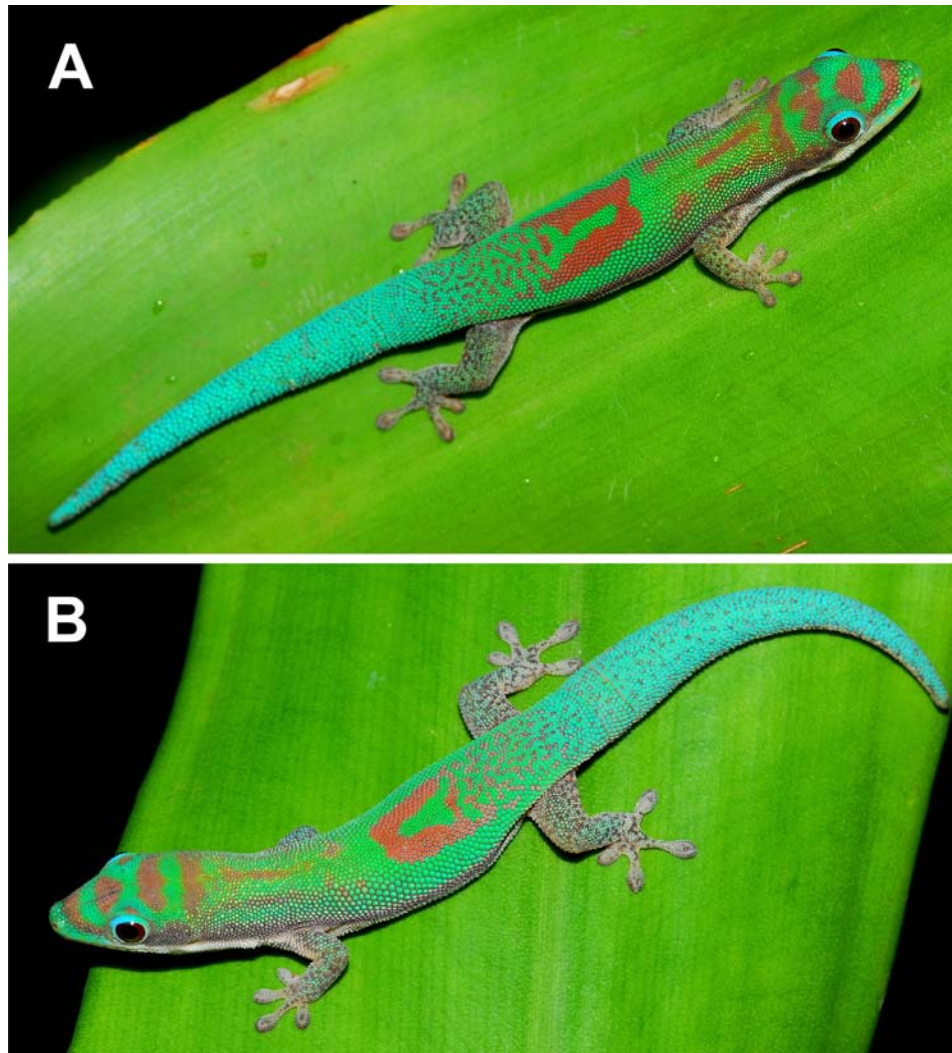


Figure 3. Male paratypes of *Phelsuma roesleri* sp. nov. in life, (A) ZSM 1516/2008 and (B) UADBA uncatologued.

tril-eye distance 3.9 mm, axilla-groin length 13.5 mm; forelimb length (from axilla to tip of longest finger) 9.3 mm; hindlimb length (from groin to tip of longest toe) 12.5 mm.

In life, the holotype was bright green dorsally with four symmetrical red transverse bands or markings on the snout and head (Fig. 1): The anteriormost band extended from the anterior edge of the eye to a point behind the nostrils where the bands of both sides fuse. The second band formed a trapezoidal transverse patch between the eyes without reaching them. The third transverse band extended from behind the eyes and ran farther dorsolaterally than the second one. It had a central process directed anteriorly and another one posteriorly. The posteriormost transverse band was a regular narrow stripe extending even farther towards the flanks than the preceding marking. This posteriormost stripe was followed by three parallel red stripes along the anterior dorsum running from the neck to forelimb insertion, and a distinct angular H-shaped red marking on the lower back that disintegrated posteriorly into a reddish reticulated pattern at the level of the hindlimbs. The tail was green with a bluish turquoise tint (Fig. 1). The limbs were scattered with fine dark pigment and all ventral surfaces

were creamy whitish. The supralabials anterior to the eyes were green. A blackish lateral band ran from the eye to the cloacal region. The iris was reddish-brown, and the eye was surrounded dorsally by an incomplete blue ring (Fig. 2).

After 20 months in alcohol, the colouration has faded greatly. Dorsal ground colour of body grey-brown, dorsal side of tail purplish. The four red crossbands on the snout and head have faded to brown but are still recognizable and the space between them appears bluish-grey. A distinct black spot on the head behind the eyes. The red stripes and markings on the back have almost entirely disappeared and do not allow a re-identification of the pattern photographed in life. The dark lateral band from the eye to the cloacal region is still recognizable. Ventral surfaces uniformly whitish except for the greyish tail tip.

Variation: All three paratypes and a few additional specimens, which were observed at the type locality, but not collected, were similar to the holotype in their small size, indicating that all specimens were adult rather than immature. The paratypes were similar to the holotype in life colouration and general pattern, but also showed distinct varia-



Figure 4. Paratype of *Phelsuma roesleri* sp. nov. (UADBA uncatalogued) in life, showing stress colours.

bility in the shape of the red marking on the lower back, which can be shaped like a posteriorly open rectangle (Fig. 3A), V-shaped (Fig. 3B), or even be split into two parallel streaks (Fig. 4). ZSM 1516/2008 is shown in Fig. 3A, whereas Fig. 3B and 4 show the two UADBA paratypes that were not available for detailed studies. Measurements of these UADBA paratypes (FGZC 1645, 1646) are as follows: snout–vent lengths 35 and 38 mm, respectively; total lengths 67 and 83 mm, respectively. The tail of FGZC 1645 is regenerated.

Description of paratype ZSM 1516/2008 (FGZC 1667): Specimen well preserved. Left arm removed as tissue sample. Hemipenes not everted. General morphology similar to that of the holotype. Tail complete but largely regenerated, with only one whorl with 7 scale rows (seen from above) at the tail base, its length slightly less than snout–vent length, dorsoventrally flattened in cross section. Number of transversely enlarged subdigital lamellae under fourth toe (left/right) 13/14. Rostral scale wider than tall, narrower than mental. No rostral cleft in dorsal process of rostral scale. One internasal scale. Centre of nostril placed behind the suture between rostral and first supralabial. Nostril in contact with four scales (first supralabial, nasal, two small postnasals), but no contact with rostral. Pupil round. Dorsal and lateral scales of head smooth, dorsal and lateral scales of body hemispherical, some of them slightly keeled. Dorsal scales of tail mostly conical, unkeeled and larger than in the holotype, and with few keeled scales on the tail base. All ventral and subcaudal scales smooth. The median row of subcaudal scales only partially and irregularly enlarged transversally. Mental scale largely triangular, bordered posteriorly by a pair of elongate, pentagonal postmentals. Postmentals contact mental, first infralabial and two gulars. Gulars decrease gradually in size posteriorly. Number of supralabials (left/right) 8/8; number of infralabials (left/right) 7/7, number of preanofemoral pores 23. Measurements: Snout–vent length 36.6 mm; tail length 35.0 mm; head width (at widest point) 7.0 mm; snout length (anterior edge of eye to tip of snout) 5.0 mm; horizontal eye diameter 2.2 mm; ear opening diameter 0.5 mm; eye–ear distance 3.1 mm; internarial distance 1.7 mm; nostril–eye distance 4.0 mm; axilla–groin length 13.6 mm; forelimb length (from axilla to tip of longest finger) 10.5 mm; hindlimb length (from groin to tip of longest toe) 13.9 mm.

Distribution: Reliably known only from the type locality, but see discussion below.

Habitat and habits: The holotype and all paratypes of *Phelsuma roesleri* were captured in larger stands of *Pandanus* screw pines within a disturbed, semi-open deciduous dry forest on loose limestone blocks (Fig. 5). We observed an additional specimen within the same karstic forest fragment, but under more humid conditions, within a more or less closed canopy forest near a small intermittent brook. In contrast, the species was not observed within stands of taller and more humid dry forests on fine-grained, loamy soil of the nearby Ankarana Reserve. The climate of Ankarana is seasonal, with rainfall being moderately high for the western region with approximately 1890 mm of precipitation per annum (HAWKINS et al. 1990). The principal rains fall mainly during the months of December to April, leaving a seven-month dry season (FOWLER et al. 1989, CARDIFF & BEFOUROUACK 2003), and suggesting that we might have encountered the species in the period of its highest activity. Since no eggs were found, it is unclear if *P. roesleri* attaches its eggs to the substrate or not. However, its phylogenetic relationships suggest that its eggs are probably not attached since all other species of the *Phelsuma laticauda* group are “non-gluers”. As can be seen in Fig. 3B, one paratype had two small red mites, one on the anterior back above the right forelimb and one on the inner toe of the left forelimb. The two other *Phelsuma* species known from the Ankarana Massif (*P. grandis* and *P. abbotti*) were not found in the *Pandanus* habitat of *P. roesleri*.

Etymology: We dedicate this new species to our colleague and friend HERBERT RÖSLER, in recognition of his contributions to the knowledge of geckos in general and of the genus *Phelsuma* in particular.

Available names: Most species-level nomina of *Phelsuma* are either valid species or subspecies, or unambiguously assignable as synonyms to valid species, but two exceptions are evident. *Phelsuma minuthi* was described by BÖRNER (1980), based on a single specimen without locality data. It is currently considered as synonym of *P. lineata* (RAXWORTHY & NUSSBAUM 1994). *Phelsuma roesleri* can be easily



Figure 5. *Pandanus* screw pines in Ankarana, the typical habitat of *P. roesleri* at the type locality.

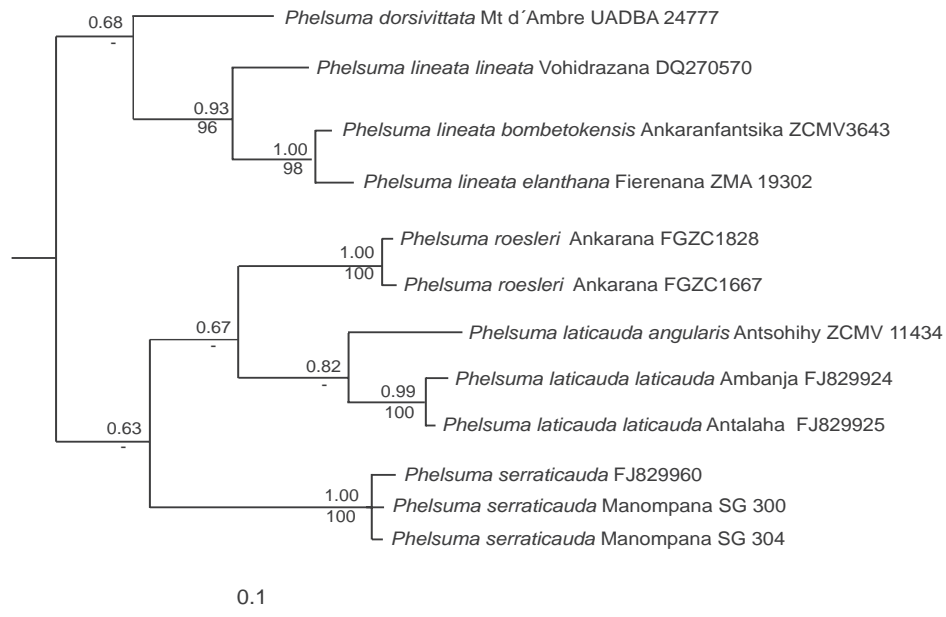


Figure 6. Bayesian 50%-majority-rule consensus phylogram based on sequences of the mitochondrial 16S rRNA gene of species of *Phelsuma* (328 bp aligned length). Posterior probabilities are shown above branches, parsimony bootstrap values (2000 replicates) below branches. *Lygodactylus luteopicturatus* was used as outgroup, *Phelsuma standingi*, *Phelsuma grandis* and *Phelsuma antanosy* were chosen as hierarchical outgroups (not shown).

distinguished from the holotype of *P. minuthi* by its smaller size (snout–vent length 33–36 mm vs. 48 mm, total length 69–72 mm vs. 105 mm) and unkeeled ventrals (vs. strongly keeled).

Phelsuma trilineata was described by GRAY (1842) and also based on a single, today greatly faded specimen (Fig. 7) without locality data. With just four lines this description is very short and difficult to interpret. BOULENGER (1885) stated that *P. trilineata* “agrees in every respect with *P. cepedianum*, but the ventral scales are keeled, though less strongly than in *P. lineatum*, and the segments of the tail are composed of seven transverse rows of scales above and five or six on the side.” He also gave the locality of the holotype as “Madagascar”, although the source of this information is unknown and there appears to be no supportive evidence (RAXWORTHY & NUSSBAUM 1993). MERTENS (1962) also discussed the relationships between *P. cepedianana* and *P. trilineata*, and the uncertain origin of the latter taxon. RAXWORTHY & NUSSBAUM (1993), after studying the available specimens including the holotype, synonymized *P. trilineata* with *P. cepedianana*. These authors also demonstrated for *P. antanosy* that the position of the nostril can be a variable character as is the case in *P. roesleri*. Furthermore, this subtle character is difficult to interpret. For example, A. G. C. GRANDISON verified the nostril position of two further specimens assigned to *P. trilineata* in the British Museum and found it to be placed above the suture of rostral and first supralabial in both specimens (MERTENS 1962), whereas RAXWORTHY & NUSSBAUM (1993) found one of these specimens to be a misidentified *P. pusilla* with the nostril positioned well behind the suture between rostral and first supralabial. One differ-

ence between *P. trilineata* and *P. cepedianana* mentioned by BOULENGER (1885) is the number of scale rows in each tail whorl (7 vs. 8–9) although RÖSLER (pers. comm.) found that *P. cepedianana* has 7–8 scale rows and that most *Phelsuma* species exhibit a range of 6–8 scale rows. Another difference refers to the ventral scales, which are moderately (BOULENGER 1885) or weakly (RAXWORTHY & NUSSBAUM 1993) keeled in *P. trilineata* and considered entirely unkeeled in *P. cepedianana*. However, RAXWORTHY & NUSSBAUM (1993) found that some specimens from Mauritius also have weakly keeled ventrals, suggesting that this is no reliable character that would allow the two taxa to be distinguished. A third, hitherto undiscussed potential difference is the contact of the nostril with the rostral, which is clearly recognizable in at least some specimens of *P. cepedianana* (from ZSM), but absent in the holotype of *P. trilineata*, although this character might vary among individuals. Summarizing, we confirm the synonymy of *P. trilineata* with *P. cepedianana*. Independent from this synonymy, *Phelsuma roesleri* differs from the holotype of *Phelsuma trilineata* by smaller size (33–36 mm vs. 44 mm SVL, 69–72 mm vs. 98 mm total length), unkeeled ventral scales (vs. moderately or weakly keeled), fewer infralabials (6–7 vs. 8), and more preanofemoral pores (23 vs. 19). In addition, *P. roesleri* seems to be restricted to a small geographical area and appears to be not very common within its range. This area (Ankarana and its surroundings) is not known as an early historical collecting locality, which makes an origin of the holotype of *P. trilineata* from this geographic area very unlikely. Thus, we are convinced that *P. trilineata* can be excluded as an available name for the new species described herein, *P. roesleri*.



Figure 7. Head of the preserved holotype of *Phelsuma trilineata* (BM 1946.8.26.32). Note the position of the nostril above the suture between the rostral and first upper labial.

Molecular differentiation and relationships: The 16S rRNA gene sequences of *P. roesleri* showed a high divergence to all recognized extant *Phelsuma* species (sequences available from the work of ROCHA et al. 2009). The lowest divergences were found to *P. l. laticauda* (9.5% uncorrected pairwise sequence divergence) and *P. l. angularis* (9.8%). It needs to be noted, however, that these percentages are comparatively higher than those previously reported among *Phelsuma* species (e.g. ROCHA et al. 2009, GLAW et al. 2009) because the fragment used was very short and contained a high proportion of hypervariable segments (corresponding to loops in the secondary structure of the 16S rRNA molecule).

The phylogenetic tree presented in Figure 6 is based on a short fragment (328 bp) of the mitochondrial 16S rRNA gene only and therefore has limited phylogenetic resolution. The main purpose of this tree is thus not to reliably resolve relationships, but visualize the molecular differentiation among taxa. *Phelsuma roesleri* is recovered, albeit without statistical support, as sister species to *P. laticauda*. The three representatives of *P. laticauda* form a monophyletic group: the two samples from the northeast coast (Antalaha) and the Sambirano region (Ambanja) are closely related and genetically very similar, whereas *P. l. angularis* from Antsohihy in the northwest is more strongly differentiated, supporting its subspecific status and indicating that the east coast populations may have originated from a more recent immigration from the Sambirano region.

Phelsuma lineata bombetokensis, which shows some morphological similarities to *P. roesleri* and has possibly been confused with this species in a previous survey of the Ankarana reserve (see discussion below), was recovered as deeply nested within the *P. lineata* clade and genetically strongly divergent from *P. roesleri*. It surprisingly formed with strong support the sister group of a *P. lineata* specimen from an eastern rainforest site (Fierenana) bordering the high plateau, which corresponds to *P. lineata elanthana* (see ROCHA et al. 2010).

Discussion

The description of *P. roesleri* adds a distinctive new species to the genus *Phelsuma*. Based on morphological similarities and colouration, *P. roesleri* is similar to *P. laticauda* on the one hand and to *P. lineata bombetokensis* on the other. According to ROCHA et al. (2009, 2010) the *P. laticauda* group (including *P. laticauda*, *P. pasteuri*, *P. robertmertensi*, and *P. v-nigra*) is a well-defined clade that is characterized by being “non-gluers” with smooth ventral and subcaudal scales, three nasals and without nostril-rostral contact. They are mostly bright green in colour and have no lateral or dorsal pattern of stripes. *Phelsuma roesleri* largely fits this definition, but has a distinct dark lateral band that is easily recognizable both in life and in preservative, and that is otherwise typical for the *Phelsuma lineata* species group. A closer look reveals that the morphology of *P. roesleri* is relatively similar to *P. l. bombetokensis*. Although the latter form is known to have keeled dorsal and ventral scales, these keels are relatively poorly developed (in the three comparative specimens used for this study: ZSM 324/0, ZSM 473/2001, and SMF 59379, the holotype of *bombetokensis*) compared with other taxa of the *P. lineata* group. The median subcaudals are not broadened in *P. l. bombetokensis* and only slightly and partly broadened in *P. roesleri* (versus distinctly broadened in *P. laticauda*), and *P. roesleri* (total length up to 72 mm) is closer in size to *P. l. bombetokensis* (total length up to 110 mm) than to *P. laticauda* (total length up to 130 mm).

Phelsuma roesleri is known only from a single locality in the Ankarana Massif in northern Madagascar. Although we found this species only outside of the protected area, it is very likely that it occurs inside the reserve as well. BLOXAM & BARLOW (1987) and HAWKINS et al. (1990) recorded – besides *P. madagascariensis* and *P. abbotti* – the presence of an unidentified *Phelsuma* sp. from the area around the “Grand Canyon” on the western side of the Ankarana Massif. This species was classified as uncommon but, unfortunately, no

specimens were collected and no further data were provided. RASELIMANANA (2008), in his work on the herpetofauna of the dry forests of western Madagascar, recorded "*Phelsuma bombetokensis*" from Ankarana, a taxon hitherto known only from much farther south (around Mahajanga and Ankarafantsika) but superficially similar to *P. roesleri* in its relatively small size, morphology and colouration. Examination of the voucher specimens in the UADBA collection is necessary to clarify if this record refers to *P. lineata bombetokensis* or to the new species described herein. However, given that *P. l. bombetokensis* is similar to *roesleri* in some respects, it is likely that RASELIMANANA (2008) indeed observed *P. roesleri*. During intensive surveys in dry and mostly karstic forests of northern Madagascar at Montagne des Français (D'CRUZE et al. 2007), Forêt d'Ambre (D'CRUZE et al. 2008), Ampombofofo (MEGSON et al. 2009), Nosy Hara and surrounding islands (METCALF et al. 2007), and Daraina (RAKOTONDRAVONY 2009), *P. roesleri* was not recorded, indicating that it is probably endemic to the Ankarana Massif, although herpetological survey data are still missing or insufficient for several karstic regions (e. g., for Analamera). Even in Ankarana, *P. roesleri* was not unambiguously recorded by published reptile surveys (BLOXAM & BARLOW 1987, HAWKINS et al. 1990, RASELIMANANA 2008), nor by amateur researchers interested in day geckos (e.g. BERGHOF 2004), nor by ecotourists or others who sent us photographs of amphibians and reptiles from this massif. Our own fieldwork between 1995 and 2007 also failed to find the species, probably because of its patchy distribution and the fact that regular trails do not pass through many *Pandanus* stands, which are probably the species' preferred or exclusive habitat. If *P. roesleri* is really restricted to these screw pines, its area of occupancy might be extremely small and patchy, but in this case mapping the *Pandanus* stands would allow a rough estimate of possible population densities of this gecko as a first important conservation measure. The main threats to Ankarana's biodiversity stem from anthropogenically induced habitat loss and degradation, including clearing of forest, burning, sapphire mining and free-ranging grazing of livestock (FOWLER et al. 1989, HAWKINS et al. 1990, CARDIFF & BEFOUROUACK 2003). According to our observations, *Pandanus* screw pines are often logged and used by local people throughout Madagascar. Further potential threats of the splendidly-coloured new species include its attractiveness for the international pet trade. According to the IUCN criteria as used for the Malagasy amphibians (see ANDREONE et al. 2005) we tentatively consider this species to be "Critically Endangered" because its known extent of occurrence is less than 100 km², its area of occupancy is less than 10 km², all positively identified individuals are from a single location, and there is an ongoing decline in the extent and quality of its habitat along the borders of the Ankarana Massif.

The Ankarana Massif harbours numerous extraordinary species and recent surveys have revealed new endemics, including a snake (*Heteroliodon lava*), a deeply divergent new lineage of mantellid frog (*Tsingymantis antitra*), and a new dwarf frog of the genus *Stumpffia* (NUSSBAUM & RAXWORTHY 2000, GLAW et al. 2006, KÖHLER et al. in press). Beside *P. roesleri*, at least two other *Phelsuma* species, *P. abbotti chekei* and *P. grandis* occur in Ankarana (BLOXAM &

BARLOW 1987, RASELIMANANA 2008, pers. obs.), whereas *P. laticauda*, the apparent sister species of *P. roesleri*, has not been recorded from this massif and has its northernmost known locality at Ambilobe, ca. 29 km south of the type locality of *P. roesleri* on the northern border of a more humid climatic zone, called the Sambirano region. Allopatric speciation across this climatic and ecological border, comparable to the ecogeographic constraint hypothesis for divergence by specialization to the eastern and western biomes of Madagascar (see VENCES et al. 2009), might be a plausible scenario to explain the split of these two species. Similar examples of allopatric sister species distributed in the humid Sambirano region versus the northern karstic dry forests can be found in many biotic groups (e.g., the mouse lemurs *Microcebus sambiranensis* [Sambirano] and *M. tavaratra* [north]) and allow a northern biogeographic region to be distinguished from the Sambirano region (e.g. WILMÉ et al. 2006, BOUMANS et al. 2007) with a border just south of Ankarana. Additional examples from the herpetofauna include the geckos *Uroplatus henkeli* (Sambirano) and *Uroplatus* sp. nov. aff. *henkeli* (Ankarana and far north, GREENBAUM et al. 2007), and the frogs *Mantidactylus ulcerosus* (Sambirano) and *M. bellyi* (Ankarana and far north; VIEITES et al. 2009). However, the perhaps most intriguing example, the gerrhosaurid species pair *Zonosaurus subunicolor* (Sambirano and Marojejy) and *Z. tsingy* (Ankarana and north) turned out not to be a species pair (RASELIMANANA et al. 2009), which emphasizes the need for robust phylogenetic data to reconstruct the biogeographic diversification of Madagascar's biota reliably (TOWNSEND et al. 2009).

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References

- ANDREONE, F., J. E. CADLE, N. COX, F. GLAW, R. A. NUSSBAUM, C. J. RAXWORTHY, S. STUART, D. VALLAN. & M. VENCES (2005): Species review of amphibian extinction risks in Madagascar: conclusions from the Global Amphibian Assessment. – *Conservation Biology*, **19**: 1790–1802.

- AUSTIN, J. J., E. N. ARNOLD & C. G. JONES (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.
- BERGHOF, H.-P. (2004): Unterwegs im “Reserve Speciale” von Ankarana. – *Draco*, **5**(19): 44–49.
- BERGHOF, H.-P. (2005): Taggeckos. Die Gattung *Phelsuma*. Pflege und Vermehrung. – Natur und Tier-Verlag, Münster, 142 pp.
- BERGHOF, H.-P. & G. TRAUTMANN (2009): Eine neue Art der Gattung *Phelsuma* GRAY, 1825 (Sauria: Gekkonidae) von der Ostküste Madagaskars. – *Sauria*, **31**: 5–14.
- BLOXAM, Q. M. C. & S. C. BARLOW (1987): A summary of the reptile field survey in the Ankarana massif, Madagascar. – *Dodo*, **24**: 61–67.
- BÖRNER, A.-R. (1980): A new species of the *Phelsuma lineata* group. – *Miscellaneous Articles in Saurology*, **6**, published by the author.
- BOULENGER, G. A. (1885): Catalogue of the lizards in the British Museum (Natural History) Vol. 1, 2nd ed., London.
- BOUMANS, L., D. R. VIEITES, F. GLAW & M. VENCES (2007): Geographical patterns of deep mitochondrial differentiation in widespread Malagasy reptiles. – *Molecular Phylogenetics and Evolution*, **45**: 822–839.
- CARDIFF, S. & J. BEFOUROUACK (2003): The Reserve Speciale d'Ankarana. – pp. 1501–1507 in GOODMAN, S. M. & J. P. BENSTEAD (eds.): *The Natural History of Madagascar*. – Chicago, USA: University of Chicago Press.
- D'CRUZE, N., J. SABEL, K. GREEN, J. DAWSON, C. GARDNER, J. ROBINSON, G. STARKIE, M. VENCES & F. GLAW (2007): The first comprehensive survey of amphibians and reptiles at Montagne des Français, Madagascar. – *Herpetological Conservation and Biology*, **2**: 87–99.
- D'CRUZE, N., J. KÖHLER, M. FRANZEN & F. GLAW (2008): A conservation assessment of the amphibians and reptiles of the Forêt d'Ambre Special Reserve, north Madagascar. – *Madagascar Conservation and Development*, **3**: 44–54.
- FOWLER, S. V., P. CHAPMAN, D. CHECKLEY, S. HURD, M. MCHALE, G.-S. RAMANGASON, J.-E. RANDRIAMASY, P. STEWART, R. WALTERS & J. M. WILSON (1989): Survey and management proposals for a tropical deciduous forest reserve at Ankarana in northern Madagascar. – *Biological Conservation*, **47**: 297–313.
- GLAW, F., S. HOEGG & M. VENCES (2006): Discovery of a new basal relic lineage of Madagascar frogs and its implications for mantellid evolution. – *Zootaxa*, **1334**: 27–43.
- GLAW, F. & M. VENCES (2007): *A Field Guide to the Amphibians and Reptiles of Madagascar*, third edition. Vences and Glaw Verlag, Köln (Cologne), 496 pp.
- GLAW, F., J. KÖHLER & M. VENCES (2009): A new species of cryptically coloured day gecko (*Phelsuma*) from the Tsingy de Bemaraha National Park in western Madagascar. – *Zootaxa*, **2195**: 61–68.
- GRAY, J. E. (1842): Description of some new species of reptiles, chiefly from the British Museum collection. – *The Zoological Miscellany*: 57–59.
- GREENBAUM, E., A. M. BAUER, T. R. JACKMAN, M. VENCES & F. GLAW (2007): A phylogeny of the enigmatic Madagascar geckos of the genus *Uroplatus* (Squamata: Gekkonidae). – *Zootaxa*, **1493**: 41–51.
- HALLMANN, G., J. KRÜGER & G. TRAUTMANN (2008): Faszinierende Taggeckos. Die Gattung *Phelsuma* (2. Auflage). – Natur und Tier-Verlag, Münster, 253 pp.
- HARMON, L. J., J. MELVILLE, A. LARSON & J. B. LOSOS (2008): The role of geography and ecological opportunity in the diversification of day geckos (*Phelsuma*). – *Systematic Biology*, **57**: 562–573.
- HAWKINS, A. F. A., P. CHAPMAN, J. U. GANZHORN, Q. M. C. BLOXAM, S. C. BARLOW & S. J. TONGE (1990): Vertebrate conservation in Ankarana Special Reserve, northern Madagascar. – *Biological Conservation*, **54**: 83–110.
- KÖHLER, J., M. VENCES, N. D'CRUZE & F. GLAW (in press): Giant dwarfs: discovery of a radiation of large-bodied ‘Stump-toed Frogs’ from karstic cave environments of northern Madagascar. – *Journal of Zoology*.
- LERNER, A. (2004): A new taxonomically isolated species of the genus *Phelsuma* GRAY, 1825 from the Ampasindava peninsula, Madagascar. – *Phelsuma*, **12**: 91–98.
- MEGSON, S., P. MITCHELL, J. KÖHLER, C. MARSH, M. FRANZEN, F. GLAW & N. D'CRUZE (2009): A comprehensive survey of amphibians and reptiles in the extreme north of Madagascar. – *Herpetology Notes*, **2**: 31–44.
- MERTENS, R. (1962): Die Arten und Unterarten der Geckonengattung *Phelsuma*. – *Senckenbergiana biologica*, **43**: 81–127.
- METCALF, C. J. E., K. HAMPSON, A. GRAY, & R. ANDRIANIRINA (2007): Herpetofaunal assemblages on seven offshore islands of northwestern Madagascar. – *Tropical Zoology*, **20**(2): 151–161.
- NUSSBAUM, R. A. & C. J. RAXWORTHY (2000): Revision of the Madagascar snake genus *Heteroliodon* Boettger (Reptilia: Squamata: Colubridae). – *Herpetologica*, **56**: 489–499.
- NUSSBAUM, R. A., C. J. RAXWORTHY, A. P. RASELIMANANA & J. B. RAMANAMANJATO (2000): New species of day gecko, *Phelsuma* GRAY (Reptilia: Squamata: Gekkonidae), from the Réserve Naturelle Intégrale d'Andohahela, Southern Madagascar. – *Copeia*, **2000**: 763–770.
- NYLANDER, J. A. A. (2004): MrModeltest v2.3. – Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
- PALUMBI, S., A. MARTIN, S. RAMANO, W. O. McMILLAN, L. STICE & G. GRABOWSKI (1991): *The Simple Fool's Guide to PCR*, version 2. – University of Hawaii Zoology Department, Honolulu, Hawaii, 46 pp.
- RAKOTONDRAVONY, H. A. (2009): Reptiles, amphibiens et gradient altitudinal dans la région de Daraina, extrême nord-est de Madagascar. – *Malagasy Nature*, **2**: 52–65.
- RASELIMANANA, A. P. (2008): Herpétofaune des forêts sèches malgaches. – *Malagasy Nature*, **1**: 46–75.
- RASELIMANANA, A. P., B. NOONAN, K. P. KARANTH, J. GAUTHIER & A. D. YODER (2009): Phylogeny and evolution of Malagasy plated lizards. – *Molecular Phylogenetics and Evolution*, **50**: 336–344.
- RAXWORTHY, C. J. & R. A. NUSSBAUM (1993): A new Madagascar *Phelsuma*, with a review of *Phelsuma trilineata* and comments on *Phelsuma cepedianana* in Madagascar (Squamata: Gekkonidae). – *Herpetologica*, **49**: 342–349.
- RAXWORTHY, C. J. & R. A. NUSSBAUM (1994): A partial systematic revision of the day geckos, *Phelsuma* GRAY, of Madagascar (Reptilia: Squamata: Gekkonidae). – *Zoological Journal of the Linnean Society*, **112**: 321–335.
- RAXWORTHY, C. J., C. M. INGRAM, N. RABIBISOA. & R. G. PEARSON (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., D. POSADA, M. A. CARRETERO & D. J. HARRIS (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., M. VENCES, F. GLAW, D. POSADA & J. D. HARRIS (2009): Multigene phylogeny of Malagasy day geckos of the genus *Phelsuma*. – *Molecular Phylogenetics and Evolution*, **52**: 530–537.
- ROCHA, S., H. RÖSLER, P. S. GEHRING, F. GLAW, D. POSADA, D. J. HARRIS & M. VENCES (2010): Phylogenetic systematics of day geckos, genus *Phelsuma*, based on molecular and morphological data (Squamata: Gekkonidae). – *Zootaxa*, **2429**: 1–28.
- RÖSLER, H., F. J. OBST & R. SEIPP (2001): Eine neue Taggecko-Art von Westmadagaskar: *Phelsuma hielscheri* sp. n. (Reptilia: Sauria: Gekkonidae). – *Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden*, **51**: 51–60.
- RONQUIST, F. & J. P. HUELSENBECK (2003): MRBAYES 3: Bayesian phylogenetic inference under mixed models. – *Bioinformatics*, **19**: 1572–1574.
- SCHÖNECKER, P., S. BACH & F. GLAW (2004): Eine neue Taggecko-Art der Gattung *Phelsuma* aus Ost-Madagaskar (Reptilia: Squamata: Gekkonidae). – *Salamandra*, **40**: 105–112.
- SOUND, P., J. KOSUCH, M. VENCES, A. SEITZ & M. VEITH (2006): Preliminary molecular relationships of Comoroan day geckos (*Phelsuma*). – pp. 175–179 in VENCES, M., J. KÖHLER, T. ZIEGLER & W. BÖHME (eds.): *Herpetologia Bonnensis II*. – Proceedings of the 13th Congress of the Societas Europaea Herpetologica. Bonn, Zoologisches Forschungsmuseum A. Koenig and Societas Europaea Herpetologica.
- SWOFFORD, D. L. (2002): PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b5. Sinauer Associates, Sunderland, Massachusetts
- TOWNSEND, T. M., D. R. VIEITES, F. GLAW & M. VENCES (2009): Testing species-level diversification hypotheses in Madagascar: the case of microendemic *Brookesia* leaf chameleons. – *Systematic Biology*, **58**: 641–656.
- VENCES, M., K. C. WOLLENBERG, D. R. VIEITES & D. C. LEES (2009): Madagascar as a model region of species diversification. – *Trends in Ecology and Evolution*, **24**: 456–465.
- VIEITES, D. R., K. C. WOLLENBERG, F. ANDREONE, J. KÖHLER, F. GLAW & M. VENCES (2009): Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. – *Proceedings of the National Academy of Sciences of the United States of America*, **106**: 8267–8272.
- WILMÉ, L., S. M. GOODMAN & J. U. GANZHORN (2006): Biogeographic evolution of Madagascar's microendemic biota. – *Science*, **312**: 1063–1065.