Rediscovery, conservation status and genetic relationships of the Malagasy chameleon *Furcifer voeltzkowi*

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Abstract. The chameleon *Furcifer voeltzkowi* (Boettger, 1893) from northwestern Madagascar was considered to be a synonym of *Furcifer rhinoceratus* for many decades and was resurrected only recently based on studies of the morphology and osteology of a few male specimens, which were collected more than 100 years ago. However, basic data on this species remain unavailable, including its conservation status, life history, colouration in life, morphology of the female, genital morphology of the male, phylogenetic affinities, and genetic differentiation from *F. labordi* and other congeners. During a targeted expedition, we rediscovered *F. voeltzkowi* in its natural habitat close to its type locality, allowing us to fill some gaps of knowledge. *Furcifer voeltzkowi* is a sexually dimorphic species. The life colouration of males is largely green, whereas that of females is highly variable and can be extremely colourful. Both, morphology and life colouration of males and females show close similarities to *F. labordi* from west and southwest Madagascar, but also a number of distinct differences (e.g. a larger size of *F. voeltzkowi* and a smaller rostral appendage in both sexes), enabling a clear distinction of the two species in both sexes. DNA sequences of the nuclear CMOS gene and two mitochondrial markers (16S rRNA and ND4) also confirm that *F. voeltzkowi* is a distinct species and sister to *F. labordi* (pairwise differences in the 16S gene 3.5–3.6%). We estimate the distribution range (extent of occurrence) of *F. voeltzkowi* to comprise ca. 1.000 km² and suggest that it qualifies as Endangered B1ab(iii) under the IUCN Red List Criteria as its populations are expected to be severely fragmented, and there is continuing decline in the extent and quality of its habitat. Similar to *F. labordi*, *F. voeltzkowi* might be an extremely short-living chameleon with a post hatching life span of only several months in the rainy season. The assumed short life might also partly explain why this splendid species got "lost" for many decades, since most roads in its habitat are not accessible in the wet season.

Key words. Squamata, Chamaeleonidae, morphology, molecular genetics, rediscovery, conservation.

Introduction

Our planet is probably facing the beginning of an enormous extinction of species, often referred to as the "sixth mass extinction", the "Holocene extinction" or the "Anthropocene extinction". In contrast to the five earlier catastrophic extinction periods in the Earth's history the current loss of biodiversity is caused by human activity (Wake & Vredenburg 2008, Kolbert 2014, Ceballos et al. 2017). According to the IUCN Red List (2020) 878 species (755 animals and 123 plants) have been officially classified as Extinct since the beginning of modern times about 500 years ago. However, the number of recent extinctions documented by

the Extinct category on the IUCN Red List is likely to be a significant underestimate (IUCN 2020). The recently introduced IUCN category Possibly Extinct is already applied to more species (935) than the category Extinct (IUCN 2020), demonstrating the poor state of knowledge and the risk of "silent" (unrecognized) extinctions for many species. Numerous researchers and conservationists are convinced that these official figures do not appropriately mirror the dramatic extent of the present biodiversity loss, and if current estimates of extinction rates (e.g., Pimm et al. 2014) are correct, they would translate into hundreds of species being driven to extinction every year. There is widespread agreement that our knowledge on the total species number on

Earth is very rudimentary, and that the taxonomy of most organism groups is in urgent need of revision (Larsen et al. 2017). The lack of reliable knowledge is not restricted to microorganisms and insects – the continued existence of numerous vertebrate species is uncertain as well.

Rediscoveries of "lost" species are very important as they provide crucial data for conservation measures and also bring some hope amidst the biodiversity crisis. In 2017 the NGO Global Wildlife Conservation initiated a program to rediscover poorly known species, which had not been recorded for many decades or even centuries. For this program a list of "25 most wanted lost species" was produced. As of March 2020 four of them were successfully rediscovered: Jackson's climbing salamander (*Bolitoglossa jacksoni*), the silver-backed chevrotain (*Tragulus versicolor*), Wallace's giant bee (*Megachile pluto*), and the velvet pitcher plant (*Nepenthes mollis*), see https://www.globalwildlife.org/search-for-lost-species/. The chameleon species *Furcifer voeltzkowi*, which had not been recorded for more than 100 years, was also a target species of this program.

Furcifer voeltzkowi has a convoluted taxonomic history. The original description as *Chamaeleon voeltzkowi* by Boettger (1893) was based on a single male and complemented by data and photographs of additional specimens 20 years later (Boettger 1913). Based on the distribution of 12 morphological characters in a limited number of specimens Hillenius (1959) synonymized *C. labordi* and *C. voeltzkowi* with *Chamaeleo rhinoceratus* and insisted on this conclusion in a subsequent paper (Hillenius 1963). Mertens (1966) listed *labordi* and *voeltzkowi* as subspecies of *rhinoceratus* in his taxonomic checklist, though without providing a justification for this change. In their revision of the species group Brygoo & Domergue (1968) resurrected *C. labordi*, but left *C. voeltzkowi* in the synonymy of *C. rhinoceratus*. Klaver & Böhme (1986) split the genus *Chamaeleo* into four genera and placed several species in the resurrected genus *Furcifer*, including *F. rhinoceratus* and *F. labordi*. Glaw (2015) noted that the synonymy of *voeltzkowi* with *F. rhinoceratus* was in need of revision and finally Sentís et al. (2018) resurrected *F. voeltzkowi* based on comparisons of external morphology and micro-CT data with *F. labordi*, but the continued existence of this species remained uncertain.

In this paper, we report on the rediscovery of *Furcifer voeltzkowi* in northwestern Madagascar and aim to fill some of the major gaps in the knowledge of this species. We analyze its molecular phylogenetic relationships and the divergences from its sister species, describe the first known female and provide basic data on its habitat, life-history and conservation status.

Materials and methods

Our rediscovery expedition was conducted at the end of the rainy season from 25 March to 3 April 2018 in the Mahajanga region in northwestern Madagascar. We searched at and around the following localities for chameleons and other reptiles and amphibians: (1) unprotected dry forests near the Antsanitia hotel and the adjacent river (-15.567710°, 46.423104°, 10 m a.s.l.; 25–30 March), (2) a secondary forest near the river (-15.601593°, 46.436094°, 10 m a.s.l., 29 March), (3) around Betsako, the type locality of *Furcifer monoceras* (-15.65438, 46.51374, ca. 30 m a.s.l., coordinates according to Rakotoarison et al. 2015; 27 March), (4) Katsepy, mostly in the garden of Hotel Madame Chabaud (-15.762405°, 46.243561°, 10 m a.s.l.; 30 March to 2 April), (5) unprotected dry forest around the lighthouse near Antrema reserve (-15.716604°, 46.216802°, 90 m a.s.l.; 31 March), the approximate type locality of *Furcifer voeltzkowi*, and (6) area around limestone caves east of Mahajanga (-15.698694°, 46.403861°, ca. 30 m a.s.l.; 2–3 April). Specimens used for morphological comparisons are deposited in the Zoologische Staatssammlung München (ZSM), the Senckenberg Museum, Frankfurt am Main (SMF), and the Museum national d'Histoire naturelle Paris (MNHN). We examined one adult male (ZSM 223/2018) and one adult female (ZSM 222/2018) of *F. voeltzkowi* and compared them with several specimens of *Furcifer labordi*, which were found dead during a study in the Kirindy forest near Morondava (ZSM 210–215/2018). The terminology and description scheme of the hemipenes follows Prötzel et al. (2020). Morphological terminology and abbreviations of diagnostically relevant characters are given according to Sentís et al. (2018): (SVL) Snout–vent length, from the snout tip to the cloaca; (TaL) tail length, from cloaca to tail tip; (TL) total length, as the sum of TaL and SVL; (HW) head width, width between the posterior part of the two orbital crests in dorsal view; (LCL) lateral crest length, from the back of the eye ring to the back bone where the angle changes; (TCL) temporal crest length, from the end of lateral crest to the top of casque; (PCL) parietal crest length; (LRA) length of rostral appendage, from snout tip to tip of rostral appendage; (WRA), widest width of rostral appendage; (CH) casque height, vertical line from the end of lateral crest; (CN) casque to neck, from the casque tip vertically to the neck skin; (DC) dorsal crest presence (+) or absence (–); (DCc) dorsal crest continuous to tail crest presence (+) or absence (–); (NSL) number of supralabial scales, counted from the mouth slit to the snout tip. The following measurements were size-corrected using the ratios: (RTaL) TaL to SVL; (RHW) HW to HL; (RLCL) LCL to SVL; (RTCL) TCL to SVL; (RPCL) PCL to SVL; (RLRA) LRA to SVL; (RWRA) WRA to SVL; (RCH) CH to SVL; (RCN) CN to SVL.

Total genomic DNA was extracted following a standard salt extraction protocol using proteinase K digestion in a concentration of 10 mg/ml (Bruford et al. 1992). For molecular analysis, we complemented DNA sequences from GenBank obtained in previous studies (Raxworthy et al. 2002, Tolley et al. 2013) with new sequences for *Furcifer voeltzkowi*. Primers and PCR protocols were as employed in previous studies (Tolley et al. 2013). PCR products were sequenced directly using an automated DNA sequencer (ABI 3130 XL, Applied Biosystems) and quality-checked in CodonCode Aligner (Codon Code Corporation). Our analysis is based on DNA sequences of fragments of the

two mitochondrial genes NADH dehydrogenase subunit 4 (ND4) and 16S ribosomal RNA (16S), and of the nuclear locus oocyte maturation factor Mos (CMOS). Newly generated sequences were deposited in GenBank with the following accession numbers: MT663747–MT663763 and MT659380–MT659387. We used MEGA7 (Kumar et al. 2016) for sequence alignment, for calculating uncorrected p-distances between sequences, and for phylogenetic analysis. Because for several species (*F. antimena, F. belalandaensis*) sequences from reliably identified individuals were only available for ND4, and exploratory analyses of the available 16S sequences yielded poor phylogenetic support, we relied on ND4 only to reconstruct the mitochondrial phylogenetic relationships among the target taxa. Model testing based on the Bayesian Information Criterion in MEGA7 suggested a HKY+G model best fitting the data. We performed maximum likelihood (ML) analyses in MEGA7 with SPR3 branch swapping and 1000 bootstrap pseudoreplicates. For CMOS, sequences were aligned in MEGA7 and analyzed manually. Because two sequences were of poor quality in the beginning, a total of 195 bp were discarded given that these were completely invariable in six sequences for which they were fully represented; consequently only 234 bp were analyzed and since only two substitutions were found in the gene fragment, we drew a CMOS haplotype network manually to represent allelic variation.

Results
Molecular differentiation and genetic divergences

The newly obtained 16S sequences of the three *F. voeltzkowi* specimens from Katsepy (total alignment length 429 bp) were identical to each other, but differed from previously published and newly obtained 16S sequences of *F. labordi* by 14–15 substitutions (3.5–3.6% uncorrected pairwise distance).

The newly obtained ND4 sequences (of five individuals of *F. labordi* from Kirindy and three *F. voeltzkowi* from Katsepy) were aligned with sequences of the related species *F. labordi, F. antimena, F. viridis, F. major* and *F. belalandaensis* from GenBank. A sample of *F. verrucosus* was used as the outgroup. In the ND4 fragment, *F. voeltzkowi* and *F. labordi* differed by 37–39 substitutions (5.3–5.6% uncorrected pairwise distance). The inferred phylogenetic tree (Fig. 1) based on a total of 695 bp of ND4 reconstructed *F. voeltzkowi* as sister species to *F. labordi*. The tree also suggests that the ND4 sequence HF570573 of *F. antimena* in Tolley et al. (2013) most likely represents a sample confusion with *F. labordi*. On the other hand, the identical ND4 sequences of *F. antimena* (KX259939) and *F. belalandaensi*s (FJ981760) probably represent mitochondrial introgression of *F. antimena* into *F. belalandaensis* according to own, unpublished data.

In the nuclear CMOS gene, three alleles (haplotypes) were identified in the 234 bp analyzed, differing by 1–2 mutations from each other. No haplotype sharing between *F. voeltzkowi* and *F. labordi* was detected (Fig. 1).

New data on males of *Furcifer voeltzkowi*

Morphology: With 122.1 mm snout–vent length and 264 mm total length, the recently collected male (ZSM 223/2018) is larger than the studied *F. labordi* and all previously known males of *F. voeltzkowi*, which had a maximum total length of 244 mm (see Sentís et al. 2018 and Table 1). Although *F. voeltzkowi* males are larger than *F. labordi*, their rostral appendage length is consistently smaller (absolutely and relatively, see Table 1).

Colouration in life (based on photographs of two males, as shown in Figure 2, and observations in the natural habitat): Basic colouration of body, extremities and tail bright green; a white lateral stripe on enlarged tubercle scales that are in a line can occur from the neck across ¾ of the length of the body; the black interstitial skin can create a net-like pattern, especially on the head; if stressed, dark green vertical stripes appear on the body and the tail, also on the casque and radially on the eyelids; further bright green/yellowish dots contrast to the darker stripes; a black "C" occurs in the neck region and another mirrored "C" laterally on the body; throat can be speckled with black spots and the stripes on the casque and the anterior part of the body can intensify to black; eyelids can be crossed by a black stripe; supra- and infralabial scales can be brown/black coloured giving the mouth a " dirty-smeared" look; rostral appendage is of the same colour as the head. According to our limited observations, the display colouration is moderate and not as conspicuous as in males of other chameleon species.

Hemipenis morphology (based on ZSM 223/2018): Both hemipenes are fully everted (length 21.2 mm), the general form of the hemipenis is subcylindrical and symmetrical with a slightly bilobed apex; calyces on the truncus are distinct and clearly reduced on the sulcal side and towards the upper truncus and pedicel, size of calyces rather small; calyx ridges are smooth and not serrated; one pair of large rotulae that are finely denticulated, tips of the rotulae getting larger towards sulcal side; papillary field of medium sized, unpaired papillae on the sulcal side basal to the rotulae; no other ornaments (e.g. fleshy papillae, horns, pedunculi) were observed. Since the hemipenis morphology of *F. labordi* is unknown, a comparison of both species in this respect is currently not possible.

Description of the first known female of *Furcifer voeltzkowi*

Snout–vent length 75.9 mm, tail length 73.9 mm, total length 149.8 mm; rostral appendage very rudimentary and hardly recognizable, tip of snout rounded; small and rounded casque, elevated 1.0 mm from neck; lateral crest well developed, slightly curved; temporal crest indistinct, not meeting highest point of casque; parietal crest present, length 8.3 mm; occipital lobe absent; obvious axillary pits; gular crest and ventral crest present, consisting of small conical scales – still of white colour in preservation; dorsal crest and

tail crest absent; tail length shorter than body length; pholidosis homogeneous except for a few larger, circular scales on body. Overall colouration of the preserved specimen is a dark purple without any patterning except for the white ventral stripe, continuing on the ventral side of the tail and the inner surface of the extremities. The female contained
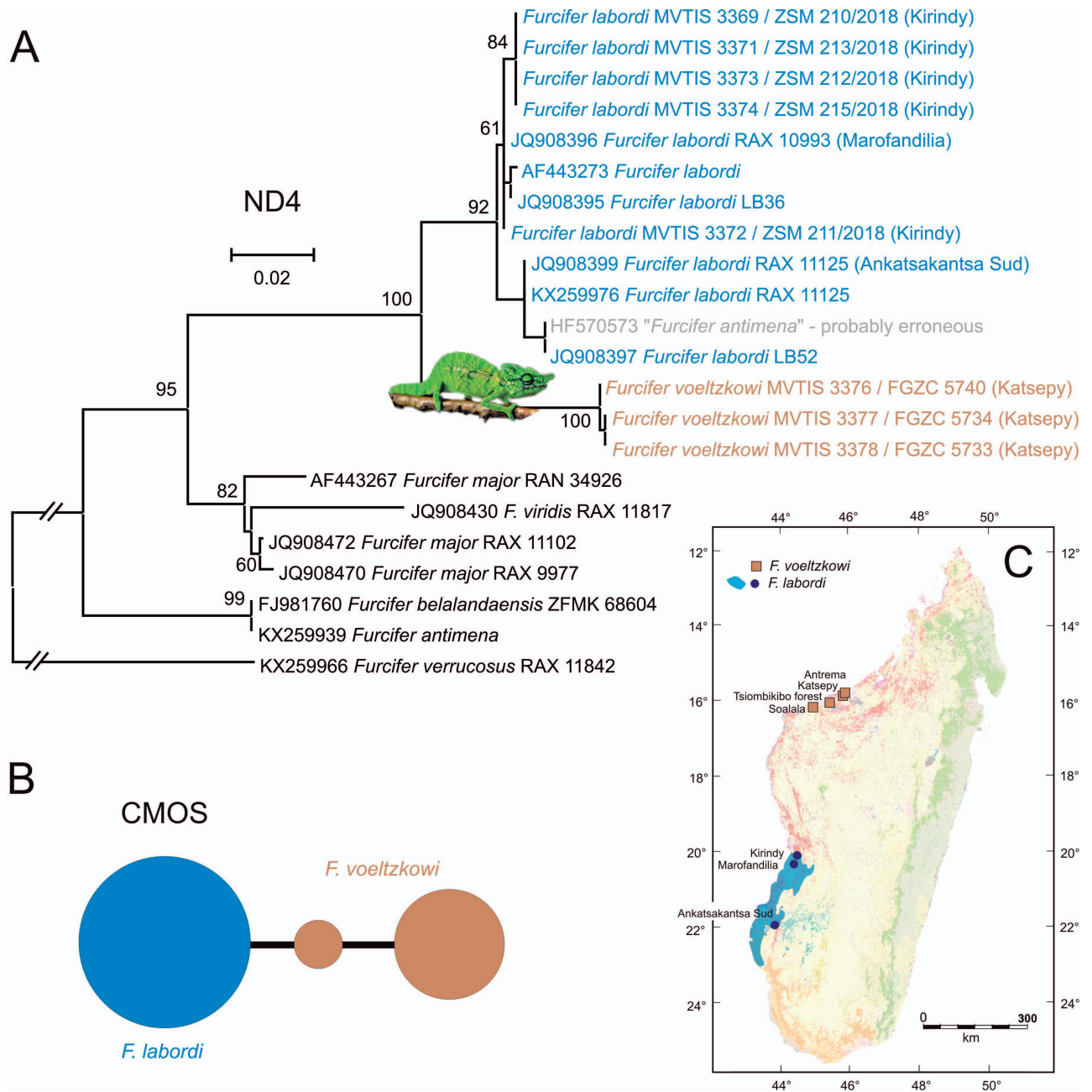

Figure 1. A) Maximum Likelihood phylogenetic tree of *Furcifer voeltzkowi, F. labordi,* and several related species, based on DNA sequences (695 bp) of the mitochondrial gene for ND4. *Furcifer verrucosus* was used as outgroup. Numbers at nodes are bootstrap support values in percent from an analysis with 1000 pseudoreplicates. The grey-shaded GenBank sequence originally assigned to *F. antimena* probably is based on a misidentified *F. labordi*, whereas the sequence identity between *F. antimena* and *F. belalandaensis* is probably due to mitochondrial introgression. B) Haplotype network constructed from DNA sequences of the nuclear CMOS gene (234 bp) of three *F. voeltzkowi* and six *F. labordi*. C) Map with the four known locality records of *F. voeltzkowi* of which only Katsepy is confirmed by DNA sequences, three locality records of *F. labordi* confirmed by DNA sequences, and the range map from the IUCN Red List assessment for *F. labordi* (DOI: 10.2305/IUCN.UK.2011-2.RLTS.T8765A12929754.en) modified by Sentís et al. (2018) to exclude records referred to *F. voeltzkowi*. The base map follows the Madagascar Vegetation Mapping Project carried out from 2003–2006 (Moat & Smith 2007); green is humid forest (rainforest), reddish tones are deciduous forest and spiny forest-thicket.

Table 1. Morphological characters of *Furcifer labordi* and *F. voeltzkowi* (combined data from Sentis et al. 2018 and new measurements presented herein). All measurements in mm. Abbreviations of variables are indicated in the Materials and methods; additional abbreviations: M = male, F = female, sa = subadult.

Collection n°	Species	Sex	SVL	TaL	RTaL	TL	HW	RHW	LCL	RLCL	TCL	RTCL	PCL	RPCL	LRA	RLRA	WRA	RWRA	CH	RCH	CN	RCN	DC	DCc	NSL
ZSM 223/2018	*F. voeltzkowi*	M	122.1	142.0	1.16	264.1	14.6	0.120	11.3	0.093	13.5	0.111	21.4	0.175	7.4	0.061	5.7	0.047	14.9	0.122	7.9	0.065	+	+	14
SMF 16375	*F. voeltzkowi*	M	101.3	133.5	1.32	234.8	11.4	0.113	10.5	0.104	12.2	0.120	20	0.197	7.2	0.071	4.6	0.045	10.3	0.102	7.4	0.073	+	+	13
SMF 16377	*F. voeltzkowi*	M	116.1	128.6	1.11	244.7	14.5	0.125	12.8	0.110	12.6	0.109	20.2	0.174	6.5	0.056	5.6	0.048	13.9	0.120	8.1	0.070	+	+	14
SMF 16378	*F. voeltzkowi*	sa M	88.4	100.3	1.13	188.7	10.4	0.118	9.8	0.111	5.7	0.064	13	0.147	6.7	0.076	4.3	0.049	8.9	0.101	5.6	0.063	+	+	13
ZSM 213/2018	*F. labordi*	M	90.4	94.9	1.05	185.3	14.1	0.156	8.1	0.090	11.4	0.126	16.1	0.178	8.2	0.091	4.3	0.048	12.2	0.135	9.8	0.108	+	+	20
ZSM 210/2018	*F. labordi*	M	97.5	103.2	1.06	200.7	12.9	0.132	9.6	0.098	12.4	0.127	17.1	0.175	9.7	0.099	4.9	0.050	18.5	0.190	7.9	0.081	+	+	17
ZSM 211/2018	*F. labordi*	M	90.5	112.5	1.24	203.0	13.2	0.146	8.9	0.098	13.4	0.148	19.5	0.215	10.8	0.119	5.4	0.060	21.3	0.235	9.4	0.104	+	+	15
MNHN 5469	*F. labordi*	M	103.2	118.0	1.14	221.2	12.0	0.116	10.6	0.103	13.8	0.134	19.4	0.188	9.3	0.090	6.2	0.060	15.2	0.147	9.1	0.088	+	+	17
ZSM 875/2000	*F. labordi*	sa M	86.7	89.4	1.03	176.1	10.0	0.115	6.0	0.069	10.4	0.120	14.5	0.167	5.8	0.067	3.8	0.044	11.5	0.133	7.8	0.090	+	+	13
ZSM 782/2000	*F. labordi*	sa M	71.9	73.7	1.03	145.6	8.0	0.111	5.9	0.082	5.8	0.081	10.6	0.147	4.0	0.056	3.1	0.043	6.8	0.095	3.6	0.050	+	+	14
ZSM 222/2018	*F. voeltzkowi*	F	75.9	73.9	0.97	149.8	9.2	0.121	6.1	0.080	5.1	0.067	8.3	0.109	–	–	–	–	9.2	0.121	1.0	0.013	–	–	14
ZSM 214/2018	*F. labordi*	F	60.5	65.1	1.08	125.6	8.8	0.145	5.3	0.088	5.4	0.089	7.8	0.129	0.8	0.013	1.4	0.023	9.1	0.150	1.2	0.020	–	–	14
ZSM 215/2018	*F. labordi*	F	58.0	cut	–	–	8.9	0.153	4.6	0.079	5.4	0.093	7.3	0.126	1.2	0.021	1.8	0.031	9.0	0.155	1.3	0.022	–	–	14
ZSM 25/1921	*F. 'voeltzkowi'*	sa M	81.9	101.1	1.23	183.0	9.4	0.115	8.7	0.106	7.8	0.095	13.7	0.167	4.7	0.057	4.6	0.056	6.4	0.078	5.3	0.065	+	+	14

seven well-developed cream-whitish eggs (size given as maximum length x maximum width in mm), four in the right oviduct (13.3 × 7.5, 12.8 × 8.0, 12.5 × 7.5, 13.8 × 7.4), and three in the left oviduct (13.2 × 7.3, 11.9 × 7.1, 13.5 × 7.2).

Colouration in life (based on photographs, e.g. in Figure 3 and observations of several females in the natural habitat): Distinct sexual dichromatism, displaying colouration of females is more colourful and more conspicuous than in males; in a relaxed state body with bright green ground colouration with dark green vertical stripes across the body and tail, extremities and tail of same colour as the body; dorsal part of the body and the casque can be reddish-brown, also the supra- and infralabial scales; a row of two or three dark to bright red spots is present dorsolaterally along the anterior body; when stressed, females radically change their colouration (Fig. 2): the dark green vertical stripes change to black; a broad lateral stripe occurs running from the cheek to the basis of the tail and develops a distinct violet colouration, contrasting well the two or three red spots; the remaining body colouration, extremities and dorsal part of the tail and head are speckled in black and white; throat with a red interstitial skin that is shown when hissing with the mouth open.

Morphological differences between female *Furcifer voeltzkowi* and *F. labordi*

Due to the general similarities between the females of *F. voeltzkowi* (Fig. 3) and its sister species *F. labordi* (Fig. 4) their differences are described in the following, based on the adult specimens ZSM 222/2018 of *F. voeltzkowi* and ZSM 214/2018 and ZSM 215/2018 of *F. labordi*.

Just like the males, the single studied female of *F. voeltzkowi* is distinctly larger than *F. labordi* with SVL of 75.9 mm and TL of 149.8 vs. SVL of 58.0–60.5 mm and TL of 125.6 mm, and observations of additional females (not measured) in their habitat confirm the larger size of *F. voeltzkowi*. Although *F. voeltzkowi* is the larger species, it appears to be more slender as can be seen in the relative head width (RHW) with 12.1% vs. 14.5–15.3% in *F. labordi*. Also, the casque height is lower in *F. voeltzkowi* with 1.3% (RCN) vs. 2.0–2.2%. Female *F. labordi* show a small rostral appendage of 0.8–1.2 mm (RLRA 1.3–2.1%), whereas it consists of only two scales in the studied female *F. voeltzkowi* (not quantifiable). However, photographs of additional *F. voeltzkowi* females show that the rostral appendage can also be of similar size as in *F. labordi*. The temporal and parietal crest is shorter in *F. voeltzkowi* with 6.7% (RTCL) vs. 8.9–9.3% and 10.9% (RPCL) vs. 12.6–12.9%. No differences could be found in pholidosis, but the colouration in life differs between females. In a relaxed state both species have a green body colouration with green or light brown vertical stripes (Figs 3B, 4C). In *F. labordi*, there is a series of ca. 5–8 orange-brown spots along the vertebral column inbetween these stripes and the upper side of the head is orange-brown as well; further there is only one red spot laterally on the neck. In *F. voeltzkowi* there are two or even three distinct
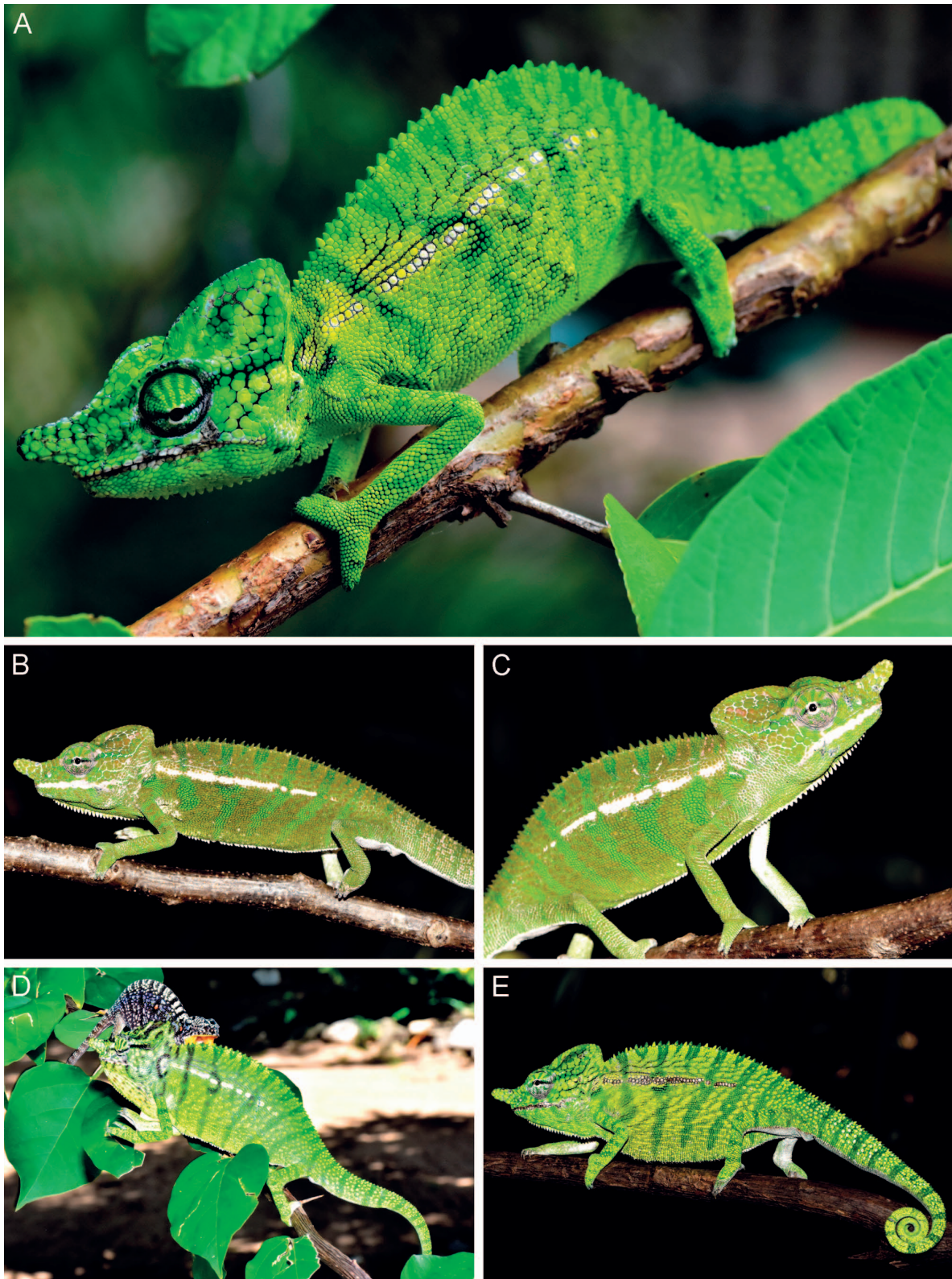
Figure 2. Males of *Furcifer voeltzkowi* from Katsepy near Mahajanga in different colour states: A) slightly stressed; B, C) relaxed (sub-adult); D, E) displaying. Note in (A) the injuries on the head probably resulting from intraspecific conflicts. Males differ from those of the sister species *F. labordi* by larger size, a lower casque, a shorter rostral appendage, darker skin around the scales and a row of white and distinctly enlarged tubercles along the flanks.

Figure 3. Females of *Furcifer voeltzkowi* from Katsepy near Mahajanga in different colour states: A) stressed/gravidity colouration; B, C) rather relaxed; D, E) stressed. The females differ from those of the sister species *F. labordi* by larger size, often by a rudimentary, poorly recognizable rostral appendage, and several details of their colouration (e.g. 2–3 red dorsolateral spots versus only one in *F. labordi*).

red spots in a line laterally on the body and a pattern of alternating white and brown crossbands is present across the vertebral column and continued onto the head. When displaying or showing gravidity *F. labordi* turn violet or blue with black vertical stripes and black spots except for the series of orange-brown spots along the dorsal line. Stressed *F. voeltzkowi* have a similar black pattern, but they only show violet in a broad lateral stripe, contrasting the red spots; the remaining body and the extremities are of a black ground colour with intense white spotting.

Distribution

The two unambiguous distribution records of *F. voeltzkowi* as summarized and mapped by Sentís et al. (2018) include (1) the type locality "Antema [sic] an der Bembatukabai" based on Boettger (1893), which probably refers to the coastal village Antrema (ca. -15.713307°, 046.167501°, 15 m a.s.l.) or to the adjacent forest, and (2) the coastal village Soalala (ca. -16.097426°, 045.348670°, 40 m a.s.l.) based on Boettger (1913). Our observations confirm the assumption of Sentís et al. (2018) that the locality Katsepy (a coastal village in the Bombetoka bay) listed by Brygoo (1978) as locality of *Furcifer labordi*, actually refers to

F. voeltzkowi. Photographic records of *F. voeltzkowi* from two additional localities, which were originally identified as *F. labordi*, were recently published on iNaturalist (https://www.inaturalist.org/taxa/797666-Furcifer-voeltzkowi) by Martin Mandak. One of these records, made on 23 November 2015, shows roosting juvenile and apparently subadult males near the type locality Antrema (-15.712145, 46.175033, precision of coordinates 150 m), less than 1 km from the coast. The second record, made on 13 November 2015, shows a roosting juvenile in the Tsiombikibo forest (-15.96822, 45.7163, precision of coordinates 1000 m, estimated altitude ca. 40 m a.s.l.), approximately half-way between Katsepy and Soalala and at 10 km distance from the coast. An additional record without exact locality data most likely referring to *F. voeltzkowi* was reported from the newly protected area Antrema as *Furcifer labordi* (Association Reniala 2013). Surprisingly, we could not find any individuals in the relatively intact private dry forest below the lighthouse near the type locality Antrema. In accordance with Rakotoarison et al. (2015) we also failed to record *F. voeltzkowi* at all surveyed localities east of the Betsiboka river. Brygoo (1971: 240) noticed an unconfirmed *voeltzkowi* record from Lakato (55 km from Moramanga) in eastern Madagascar by Arnoult & Bauchot (1963), which, however, must be erroneous for biogeographic reasons.
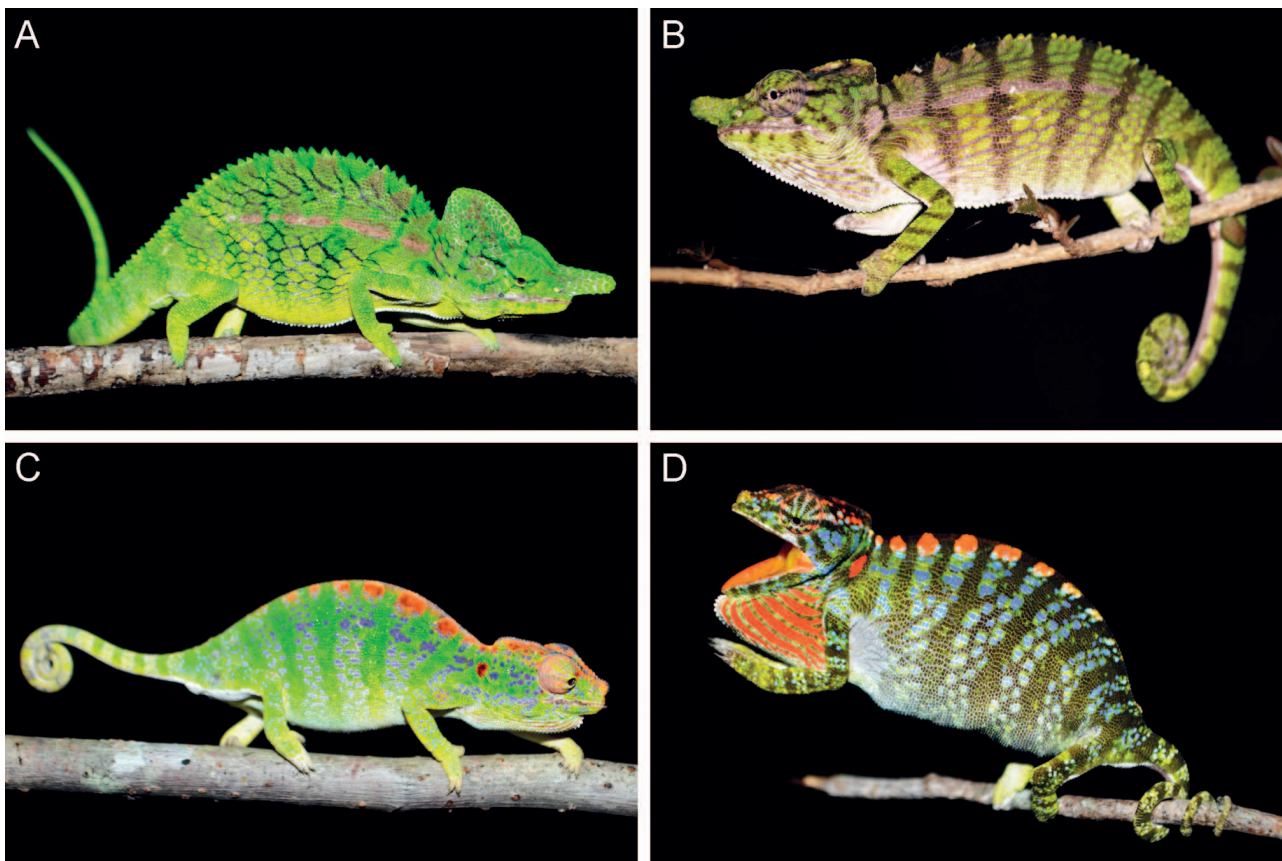

Figure 4. *Furcifer labordi* from Kirindy, western Madagascar. A) adult male, in relaxed state; B) subadult male, stressed colouration; C) adult female, relaxed; D) adult female in stressed/gravidity colouration.

Based on the reliable and precisely known records, the elevational range of *F. voeltzkowi* is between sea level and 40 m above sea level. This pattern matches with its sister species *F. labordi*, which also inhabits low elevation sites (< 100 m above sea level).

Conservation status

The available data support the assumption of Sentís et al. (2018) that the distribution range of *F. voeltzkowi* might extend at least 100 km along the coast between Katsepy at the Betsiboka river and Soalala at the Baly Bay, an area that is characterized by moderately high reptile species richness (Jenkins et al. 2014). However, it remains unclear if its distribution is largely continuous throughout its range or scattered in isolated populations (which is more likely) and if it is restricted to a narrow band along the coast or also occurs more inland. It is also unclear if records of *F. tuzetae* from coastal forests of Belambo and Sahamalaza (Raselimanana 2008), 180–240 km northeast of the Betsiboka, refer to *F. voeltzkowi* or another species. For these reasons, its extent of occurrence (EOO) cannot be reliably assessed at present, but might comprise ca. 1000 km² according to the currently available data. Thus it is clear that *F. voeltzkowi* is not a microendemic species and almost certainly occurs in the newly protected area Antrema, officially known as "Réserve de Ressources Naturelles du Site Bioculturel d'Antrema" (Goodman et al. 2018). Although Antrema suffers from anthropogenic pressures such as slash-and-burn agriculture and wildfires (Goodman et al. 2018) its protection as a reserve might mitigate these threats in the future. The observed high density of *F. voeltzkowi* in the secondary vegetation at the border of the village Katsepy demonstrates that the species is not dependent on intact dry forests and is probably adaptable to a certain degree of habitat degradation. We hypothesize that one reason why this brightly coloured species was overlooked for many decades is its assumed short life span of only few months in the rainy season, which makes it difficult and unlikely to record this species, since most roads in its distribution range are not accessible in the wet season.

We recommend that the extinction risk of this species is assessed for the IUCN Red List of Threatened Species. According to our current state of knowledge *F. voeltzkowi* might qualify as Endangered B1ab(iii) under the Red List Criteria of the IUCN (2012) as the extent of occurrence is estimated to be less than 5.000 km², the populations are expected to be severely fragmented, and there is continuing decline in the extent and quality of its habitat. However, with its relatively large extent of occurrence and an ability to survive in secondary habitats, *F. voeltzkowi* does not appear to be a species in urgent need of targeted conservation, but because its remaining habitat continues to decline and fragment, it is likely to require conservation in the long-term to prevent them from becoming more threatened.

Natural history

We observed three adult males and numerous (ca. 15) adult females of *F. voeltzkowi* at the end of the rainy season (between 30 March and 1 April 2018) on the property of the hotel "Madame Chabaud", which is a mosaic of garden, open secondary forest and plantations. All individuals were found roosting at night at estimated heights of 3–10 m above the ground on branches of trees. The males showed distinct signs (bite marks and smaller injuries) of interspecific fighting and subjective signs of ageing, suggesting that they were approaching the end of their life. On the other hand, the observation of small juveniles and subadult males in November 2015 (published by M. Mandak on iNaturalist, see above) suggests that juveniles might have hatched in October. These data are still rather rudimentary, but suggest that *F. voeltzkowi* might have a very short lifecycle similar to its sister species *F. labordi* (Karsten et al. 2008, Eckhardt et al. 2017) although probably less extreme since the prolonged rainy season in northwestern Madagascar might support a slightly longer post hatching life. Most observed females did not show obvious signs of ageing and had well-developed eggs in their body, which could be easily felt through the skin, suggesting that these chameleons were still in the peak of the egg-laying period. According to the owner of the hotel, a much higher density of *F. voeltzkowi* can be observed in February and March, when the rainy season is at peak (Ms. Chabaud pers. comm.).

Discussion
Specific distinctness of *Furcifer voeltzkowi*

According to the concept of integrative taxonomy decisions on species delimitation should be based on different and independent lines of evidence (e.g., Padial et al. 2010, Miralles et al. 2011, Hawlitschek et al. 2012). Our results confirm the morphological differences between males of *F. voeltzkowi* and *F. labordi* observed by Sentís et al. (2018) and revealed additional differences in the morphology and colouration of females. Furthermore, we found substantial and concordant genetic differentiation between *F. voeltzkowi* and *F. labordi* in two mitochondrial and one nuclear gene segments. Thus, the combination of four different lines of evidence (morphology, colouration, mitochondrial and nuclear DNA sequences) strongly supports the specific distinctness of *F. voeltzkowi*.

Morphological differentiation of *F. voeltzkowi* and *F. labordi*

Apart from the larger size female *F. voeltzkowi* are relatively similar to *F. labordi*, but differ, for example, by the number of red spots on each body side (mostly two, but rarely three in *F. voeltzkowi* versus only one in *F. labordi*). Similar to the differently coloured rostral appendages in the *Ca-*

lumma nasutum group (PARCHER 1974) these spots might function as a signal for species recognition. Although both species do not live syntopically, at the current knowledge, such signals could have function as drivers for speciation in the past, as was shown for anole lizards (INGRAM et al. 2016). Gravid females of *F. voeltzkowi* can show a spectacular stress colouration, including pattern of black-, blue- and white (Fig. 3). This colouration becomes very distinct when females catch sight of a male, and is similar to that of *F. labordi*, and – to a lesser extent – also to that of the *Furcifer lateralis* complex. All these species are short living and have rapid life histories with about 2–4 months from hatching to egg deposition (BLANC 1970a, 1970b, KARSTEN et al. 2008). This implements that there is only a short period for mating and the courtship of males must be as efficient as possible. In general, gravidity colouration functions as a signal to males that they should not even approach; the more conspicuous it is the better is the signal – even over a great distance. As a result, the males can recognize gravid females earlier and can focus on receptive females. This might work as a selective advantage for the species as both sexes save energy during the mating season.

Another interesting difference between *F. voeltzkowi* and *F. labordi* is the size of the rostral appendage. In female *F. voeltzkowi*, it is rather variable, ranging from almost completely absent to small but distinct, as it is typical for *F. labordi*. The reasons for this variability are unknown, but could be due to individual hormonal differences. A rostral appendage length difference is also evident between the males of both species, with *F. labordi* having longer rostral appendages than *F. voeltzkowi* (Table 1). It remains to be clarified in future studies, if there is a general intraspecific correlation between rostral appendage length of males and females in certain chameleon groups with bony rostral appendage, which could contribute to elucidate the evolution of ornamentation in chameleons (to be studied in a forthcoming paper by SCHERZ and colleagues). In certain species with a very pronounced male rostral appendage (*F. rhinoceratus*, *F. antimena*) females have a relatively distinct rostral appendage, whereas in species with a shorter male rostral appendage (*F. voeltzkowi*, *F. angeli*) those of females are very rudimentary. In any case, there seems to be a relatively strong and poorly understood intraspecific variability in rostral appendage length of males of *Furcifer* species with a single bony rostral appendage (*F. rhinoceratus*, *F. antimena*, *F. labordi*, *F. voeltzkowi*, *F. angeli*).

Biogeography

A large geographical gap of more than 450 km separates the currently known distribution ranges of the two apparent sister species, *F. labordi* and *F. voeltzkowi* (Fig. 1). Knowledge of the reptile and amphibian communities in this gap area is rather poor, especially in unprotected coastal forest rudiments, and new locality records could thus lead to significant range extensions of both species in the

future. A better geographical sampling is also necessary before a reliable biogeographic interpretation of the distribution of these chameleons can be drawn. For instance, their occurrence may be influenced by major river barriers (e.g., *F. labordi* apparently has not been found north of the Tsiribihina river so far) or by speciation in watershed refugia (see WILMÉ et al. 2006, VENCES et al. 2009).

Potential of life history studies on *Furcifer voeltzkowi*

Life history strategies in chameleons are very different, ranging from long-living species, which can live for more than nine years (TESSA et al. 2017), to short-living species like *F. labordi* (KARSTEN et al. 2008, ECKHARDT et al. 2017). *Furcifer labordi* has an extreme and unique life history with a posthatching lifespan of just 4–5 months, which is apparently the shortest among tetrapods (KARSTEN et al. 2008). This annual chameleon lives mostly as an egg, at least in the driest southernmost part of its range (KARSTEN et al. 2008). A recent study on *F. labordi* in the less arid Kirindy forest in west Madagascar revealed a similar but less extreme life cycle (ECKHARDT et al. 2017). The available data on the life history of *F. voeltzkowi* are still very rudimentary, but support the assumption, that its general lifecycle might be similar to its sister species *F. labordi*, although the less arid climate in northwestern Madagascar might allow for a prolonged lifespan. Due to the assumed correlation of life history traits with climate in the *F. labordi*/*F. voeltzkowi* species complex, future comparative studies on the life history of *F. voeltzkowi* might be an excellent model system to increase our knowledge on the evolution of extreme life histories and their constraints in tetrapods.

Necessary efforts to rediscover further Malagasy chameleons

Herpetological research in recent decades has led to an enormous progress of knowledge on Malagasy reptiles. For instance, many new species of chameleons have been described (e.g., GEHRING et al. 2010, 2011, CROTTINI et al. 2012, FLORIO et al. 2012, GLAW et al. 2009, 2012, PRÖTZEL et al. 2017, 2020, SCHERZ et al. 2019) and several endemic reptile species not seen for more than a century have been rediscovered, including the blindsnake *Xenotyphlops grandidieri*, which is the only representative of the family Xenotyphlopidae (WALLACH et al. 2007, VIDAL et al. 2010, WEGENER et al. 2013), and the scincid lizards *Paracontias rothschildi* and *P. minimus* (KÖHLER et al. 2010). With the rediscovery of *Furcifer voeltzkowi* we demonstrate that even a brightly coloured chameleon can become a "lost species" although it does not occur in a remote mountain massif, but just a few kilometres from the large town of Mahajanga. However, despite the substantial progress, numerous Malagasy species are still known from only a single or very few specimens, collected many decades ago and their con-

tinued existence is questionable: *Furcifer monoceras* is only known from the adult male holotype collected 115 years ago (Boettger, 1913) and characterized by a very long rostral appendage not known from any other Malagasy chameleon. It was only recently resurrected (Sentís et al. 2018), but our short survey around the type locality Betsako did not reveal any hints of its continued existence. *Furcifer tuzetae* is another large chameleon species (395 mm total length) so far only known from the holotype, which was collected in 1969 in southwest Madagascar (Brygoo et al. 1972). Not seen for many decades, a photograph of this species has recently appeared on the internet (e.g., at http://www.chameleondatabase.com/portfolio-item/furcifer-tuzetae/). The dwarf chameleon *Brookesia lambertoni*, known from only two type specimens probably collected in the year 1921 at the unidentified locality "Fito" (Brygoo 1978) awaits its rediscovery as well. Another example is the large snake *Pseudoxyrhopus ankafinaensis*, which is only known from the holotype collected in 1880 (Raxworthy & Nussbaum 1994) and is currently the only reptile species from Madagascar considered as Critically Endangered (Possibly Extinct) on the IUCN Red List. However, the only diagnostic characters of this species are based on the asymmetrical head scalation of the holotype, suggesting that this individual might well represent an aberrant specimen of *P. microps* rather than a distinct species.

In all these cases the lack of basic knowledge is evident and is a crucial impediment to clarify the conservation status of these species. This problem is not restricted to Malagasy reptiles, but true for many lizards (Meiri et al. 2018) and other species throughout the world. We therefore greatly acknowledge the "Search for lost species Initiative" of Global Wildlife Conservation and similar programs, which significantly contribute to fill the enormous gaps in our knowledge of the extant biodiversity on our planet.

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Supplementary data

The following data are available online:

Supplementary Video 1. *Furcifer voeltzkowi* in the natural habitat (FG and DP): https://youtu.be/Exen2NIb_bw