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Uncovering the herpetological diversity of small forest fragments in south-eastern Madagascar (Haute Matsiatra)

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Abstract

Madagascar has historically suffered from high fragmentation of forested habitats, often leading to biodiversity loss. Neverthless, forest fragments still retain high levels of biological diversity. The Haute Matsiatra Region (south-eastern Madagascar) hosts the renowned Andringitra National Park and several surrounding isolated forest fragments embedded in a matrix of human-dominated landscape. During a herpetological survey conducted in the Region, we visited a total of 25 sites. We applied a molecular taxonomic approach to identify the collected material and generate new reference sequences to improve the molecular identification of Malagasy herpetofauna. We identified a total of 28 amphibian and 38 squamate taxa and provided a systematic account for each one of them. Nine of the identified taxa are candidate species, amongst which one was newly identified. We extended the known distributional range of 21 taxa (nine amphibians and 12 squamates). Although the largest forest fragments hold a higher number of species, we also detected a relatively high herpetological diversity in small patches. Our results highlight the importance of investigating small forest fragments to contribute to a better understanding of the patterns of diversity and distribution of the amphibians and reptiles of Madagascar.

Key Words

Introduction

Ranked as one of the top megadiversity hotspots on Earth, Madagascar hosts exceptional and highly threatened fauna and flora (Myers et al. 2000; Wilmé et al. 2006). The proportion of native endemic vertebrate fauna is remarkable, with families, subfamilies and several genera being entirely limited to Madagascar. At the species level, 92% of native non-marine "reptiles" (intended as all Sauropsida, excluding birds) and 100% of native amphibians are endemic to the Island (Glaw and Vences 2007; AmphibiaWeb 2021; Uetz et al. 2021). Yet, some recent anthropogenic introductions are currently known (e.g. *Duttaphrynus melanostictus*, Licata et al. 2020;

Hoplobatrachus tigerinus, Mohanty et al. 2021; *Agama agama*, Wagner et al. 2009; *Indotyphlops braminus*, Uetz et al. 2021). The great environmental and bioclimatic heterogeneity of the Island has played a major role in the diversification of the rich Malagasy biota (Vences et al. 2009; Ganzhorn et al. 2014). Following Cornet (1974) and Schatz (2000), five major biomes are recognised in Madagascar: the eastern rainforest, the western dry deciduous forest, the sub-humid forest of the central highlands, the southern sub-arid spiny forest and the montane thickets. The main biodiversity distributional patterns largely follow this bioclimatic subdivision, with the highest abundance of both amphibian and reptile species found along the eastern rainforest belt (Goodman and Benstead 2003; Wollenberg et al. 2008; Crottini et al. 2012a; Brown et al. 2014, 2016).

Amphibians and reptiles are particularly diverse, with ca. 369 and 440 currently recognised species, respectively (Glaw and Vences 2007; AmphibiaWeb 2021; Uetz et al. 2021). Nevertheless, the level of undescribed diversity is high, as reported by Nagy et al. (2012) for reptiles and Perl et al. (2014) for amphibians. Field research efforts over the last three decades, the widespread use of large-scale species inventories and the application of an integrative taxonomic approach employing molecular, morphological and bioacoustic (for amphibians) identification, coupled with voucher collection (Yoder et al. 2005; Padial et al. 2010), enabled impressive progress in uncovering this hidden diversity (e.g. Rosa et al. 2012; Cocca et al. 2018). In times of major biodiversity loss, field research is fundamental to catalogue world biodiversity and represents a fundamental step for its conservation (Dijkstra 2016). As in several other places of the world (Böhm et al. 2013), a large portion of Malagasy herpetofauna is at high risk of extinction (e.g. Irwin et al. 2010; Jenkins et al. 2014), with 46.2% of the assessed amphibians and 37.7% of the assessed reptiles currently listed as threatened according to the IUCN Red List categories (Vulnerable, Endangered and Critically Endangered) (IUCN 2020).

With most species being forest dwellers, the major threat to Malagasy amphibians and reptiles is forest loss, degradation and fragmentation (e.g. Irwin et al. 2010; Böhm et al. 2013; Jenkins et al. 2014; Riemann et al. 2017). The extent of deforestation that Malagasy biota has historically undergone is dramatic (Hornac 1943; Jarosz 1993; Vieilledent et al. 2018). In the first 30 years of French colonisation (1895–1925), the amount of primary forest that was destroyed is estimated to be 70% of the vegetation present in the pre-colonial period (Hornac 1943; Jarosz 1993), while a further 44% of the remaining forest was estimated to be lost in the period of 1953–2014 (Vieilledent et al. 2018). Deforestation not only results in an overall decrease in the surface of forested areas, but is also responsible for the heavy fragmentation of remaining forests. In fact, Vieilledent et al. (2018) estimated that, in 2014, 46% of Malagasy remaining forests were less than 100 m distant from forest edges. Species richness tends to decrease with fragment size and species composition is also affected by fragmentation, with forest specialists disappearing rapidly with increasing degradation and fragmentation (e.g. Vallan 2002; Lehtinen and Ramanamanjato 2006; Riemann et al. 2015; Nopper et al. 2018). Nevertheless, the diversity and endemism in small forest fragments remain notable (e.g. Rosa et al. 2012). These small patches, embedded in a mosaic landscape, can act as refugia to local herpetofauna (Crottini et al. 2011a; Durkin et al. 2011; Riemann et al. 2015). The description of several new species, microendemic to these tiny forest fragments, has further increased the awareness on their conservation value (e.g. Gehring et al. 2010; Rosa et al. 2014; Jenkins et al. 2014; Crottini et al. 2015; Prötzel et al. 2018).

The Region of Andringitra is located in south-eastern Madagascar (Haute Matsiatra Region). This area is dominated by the Andringitra Massif, protected by Andringitra National Park (Fig. 1). Most of the herpetological research conducted in this Region has been focused on the protected area. The Andringitra Massif was first surveyed over 90 years ago and the first species inventories took place during the 1970s (see Paulian et al. 1971; Nicoll and Langrand 1989; Blommers-Schlösser and Blanc 1993; Goodman 1996; Raselimanana 1999; Goodman and Razafindratsita 2001). In 1993, Goodman (1996) carried out a thorough herpetological assessment within the framework of a multidisciplinary inventory of the eastern slopes of the massif. Several amphibian and reptile species were collected, providing a fundamental contribution to the knowledge of the local herpetofauna. The most updated species list of Andringitra National Park includes 50 amphibians and 40 reptiles (of which five are locally endemic to the Andringitra Massif), resulting from several biological inventories (both published and unpublished) and observations from the area (Goodman et al. 2018).

In the area surrounding the Andringitra Massif (especially the western side), several small patches of forest are the remains of a much more extensive forest cover (Fig. 1). This area is dominated by a human-modified landscape made of pastures, villages and rice fields (Crottini et al. 2012b; Gould and Andrianomena 2015). Knowledge of the herpetofauna that inhabits these small forest patches is scarce (see Glaw and Vences 2007) and most of the information comes from Anja Community Reserve (e.g. Crottini et al. 2011b, 2012b, 2015), a tiny forest fragment managed by the local community (Fig. 1A). Three reptile species were recently described from Anja and, to date, they are reliably known only from this Reserve (or from a few scattered isolated rock boulders close by): *Brookesia brunoi* Crottini, Miralles, Glaw, Harris, Lima & Vences, 2012; *Paragehyra felicitae* Crottini, Harris, Miralles, Glaw, Jenkins, Randrianantoandro, Bauer & Vences, 2014 and *Phelsuma gouldi* Crottini, Gehring, Glaw, Harris, Lima & Vences, 2011. These exceptional findings stress the conservation value of this small forest fragment and point to the importance and
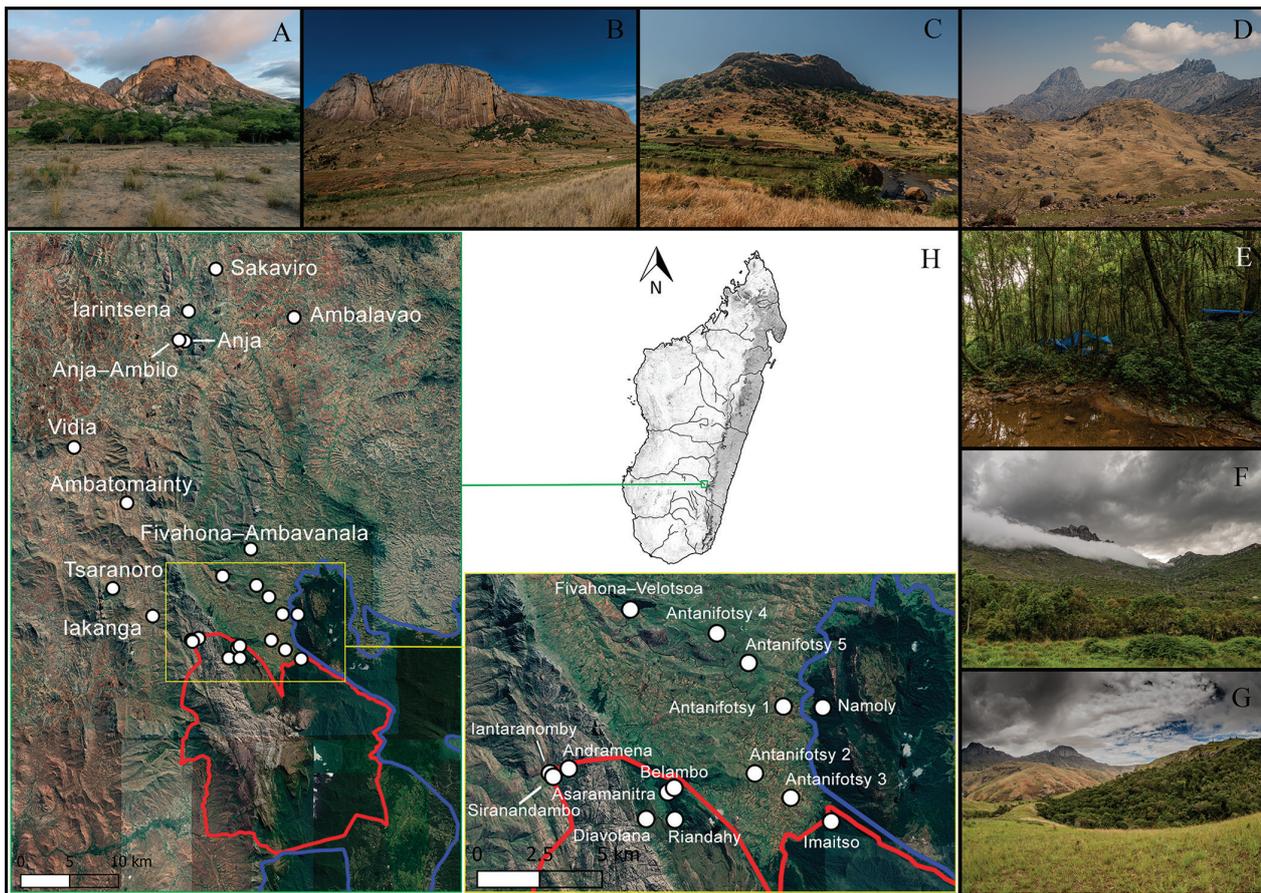
Figure 1. Map of the study area and sampling sites. The borders of Andringitra National Park (red) and Paysage Harmonieux Protégé du Corridor Forestier Ambositra–Vondrozo (Ambositra–Vondrozo Forest Corridor) (blue) are shown. See Suppl. material 1: Table S1 for more details on the sampled localities. Map data ©2015 Google (QGIS Development Team 2020). **ANP ES** – Andringitra National Park Eastern Slopes; **ANP WS** – Andringitra National Park Western Slopes. **A.** Anja; **B.** Sakaviro; **C.** Ambatomainty; **D.** Western slopes of the Andringitra Massif from Iantaranomby (ANP WS); **E.** Imaitso (ANP ES); **F.** Belambo (ANP ES); **G.** Fivahona–Velotsoa; **H.** Map with sampling sites. Photographs by Javier Lobón-Rovira.

potential herpetological interest of all other nearby fragments of the Region.

We surveyed the Region of Andringitra, collected tissue samples and specimens, and performed a species-level identification of the sampled amphibians and reptiles. Despite visiting some localities within the borders of Andringitra National Park, we focused our efforts on the several forest fragments surrounding the Massif, to fill the knowledge gap of the herpetological diversity of these poorly explored areas. Here, we provide a first barcoding reference database for the surveyed areas.

Methods

Study area

The study area is in the administrative region of Haute Matsiatra, encompassing a portion of the Andringitra Massif and the areas in the immediate surroundings (Fig. 1). This mountain chain dominates the area and is composed of several granitic peaks, amongst which Pic Boby soars as the highest of the region (2,658 m a.s.l.) and as the second highest in the whole country (Nicoll and Langrand 1989; Goodman 1996). The Massif is located at the south-eastern limit between the eastern escarpment and the central high plateau, which determines a sharp bioclimatic gradient with humid conditions in the eastern part and drier weather in the western (Goodman 1996). The regional climate can be defined as cold and humid with marked seasonality (Vidal Romani et al. 2002). Between May and October, the weather is cold and dry, with extreme temperatures that can drop below 0 °C at night, whereas the following season, from November to April, it is warm and wet with heavy rainfalls that represent 80% of the yearly precipitations (Vidal Romani et al. 2002). The strong elevational and climatic variability is responsible for the great diversity of habitats, amongst which there are lowland rainforest and dry forest in the eastern and western parts of the Region, respectively, and, at higher elevations, montane meadows, heathlands and rocky outcrops (Goodman 1996; Goodman et al. 2018).

Most of the Massif is included in Andringitra National Park, which protects an overall area of 31,160 ha (Nicoll

and Langrand 1989). Paysage Harmonieux Protégé du Corridor Forestier Ambositra–Vondrozo (thereafter "Ambositra–Vondrozo Forest Corridor") is eastwards of Andringitra National Park and protects the ca. 200 km of low-elevation forest corridor connecting Vondrozo, Andringitra and Pic d'Ivohibe Special Reserve (ca. 10 km further south than Andringitra National Park) with Ranomafana National Park and Ambositra further north (Fig. 1) (Goodman et al. 2018). Besides these protected areas, three private Reserves are present in the surroundings of the Andringitra Massif: Anja Community Reserve, Sakaviro Community Reserve and Tsaranoro Valley Forest (Fig. 1A and B). They are characterised by fragments of semi-arid deciduous forest located at ca. 950 m a.s.l. at the base of low-elevation granitic mountains rising a few hundred metres relative to the ground level. These forest fragments are particularly small: 36 ha (Anja), 14 ha (Sakaviro) and 46 ha (Tsaranoro) (Crottini et al. 2012b; Gould and Andrianomena 2015). Several other small forest fragments are scattered throughout the area, especially in the western part of the Region, but no legal protection is known for these sites. We sampled in 25 localities, eight of which are within Andringitra National Park, one locality within Ambositra–Vondrozo Forest Corridor and 16 sites are located in the surroundings of the Andringitra Massif (Fig. 1; Suppl. material 1: Table S1). In the present study, we refer to Andringitra as the overall study area comprising the eponymous Massif and the forest fragments in the surrounding areas that were investigated, irrespective of the limits of the protected areas present in the region (Fig. 1).

Sampling

The samples included in this study were collected between 2009 and 2018, although most of the sampling effort was deployed between the 13th of November and the 18th of December 2018. This period matches the onset of the rainy season and the peak of activity of reptiles and amphibians. We spent a minimum of two days at each sampling locality (defined as where campsites were established). Continuous opportunistic searches took place while moving amongst different sites (Suppl. material 1: Table S1). Animals were opportunistically sought in all microhabitats during both day and night searches, visually detected and caught by hand. Each individual was photographed and the geographic location was recorded with a GPS receiver. One tissue sample was taken from each collected individual. Samples were stored in 96% ethanol and the caught animals were released upon sampling. We identified each individual, based on the morphological descriptions provided in Glaw and Vences (2007) and subsequent descriptions and, in the case of putative candidate species, a limited number of specimens across different localities were collected as vouchers. These individuals were anesthetised and subsequently euthanised with an overdose of MS222 either by immersion in a

saturated solution (amphibians) or through intracoelomic injection (reptiles) of the same solution. All voucher specimens were fixed in 96% ethanol and placed in 70% ethanol for long-term storage.

Laboratory procedures

Total genomic DNA was extracted from tissue samples following the protocol described in Bruford et al. (1992), consisting of a high-salt extraction using proteinase K digestion (10 mg/ml concentration). We amplified a fragment of ca. 550 bp of the 3' terminus of the mitochondrial 16S rRNA gene (16S) for all amphibian samples (Palumbi et al. 1991) and a fragment of ca. 650 bp of the cytochrome oxidase I gene (COI) for reptiles (Nagy et al. 2012), both of which have been widely used for molecular taxonomic identification of Malagasy herpetofauna (Vences et al. 2005); Nagy et al. 2012. Whenever the amplification of the two markers was either unsuccessful or not informative to provide an accurate species identification, we amplified additional markers, namely the 5' terminus of the 16S fragment (16S 5') for amphibians and 16S, NADH dehydrogenase subunit 1 (ND1), NADH dehydrogenase subunit 2 (ND2) or Cytochrome b (Cytb) for reptiles (see Suppl. material 2: Table S2 for primers and PCR conditions). Successfully amplified samples were sequenced with an ABI 3730XL automated sequencer at Macrogen Inc. (Spain). Chromatograms were manually checked and edited, when necessary, with BIOEDIT 7.2.6 (Hall 1999).

Molecular species identification

Newly-generated sequences were aligned with the Clustal W algorithm implemented in BIOEDIT 7.2.6 (Thompson et al. 1994; Hall 1999). Neighbor joining trees, based on Kimura 2–parameter model distances, were computed for each investigated gene with MEGA X 10.0.5 (Kumar et al. 2018) to roughly divide the samples into genetically uniform groups (16S for amphibians and COI for reptiles). Each group was compared to the molecular database available in GenBank through the BLAST algorithm (https://blast.ncbi.nlm.nih.gov/Blast.cgi) (Altschul et al. 1997), using nblast default parameters, to retrieve the most similar homologous sequences available in the online database. Species identification was based on the inter-specific thresholds suggested by Vieites et al. (2009) for the 16S fragment in amphibians (3%) and the different thresholds for the different Malagasy reptile groups suggested by Nagy et al. (2012) for the COI fragment. Molecular identification was confirmed by the analysis of the photographic records. In a few instances where molecular data were not available, sample identification was based on the photographic records or the morphological examination of the collected specimens. We used MEGA X 10.0.5 (Kumar et al. 2018) to compute the average uncor-

rected pairwise genetic distances (uncorrected *p*–distances) for each identified taxon. Whenever it was not possible to assign a sample to a formally described species, we used the definitions of different categories of candidate species proposed in Vieites et al. (2009). The working names for the candidate species follow the nomenclature proposed in Vieites et al. (2009) and following publications (e.g. Zimkus et al. 2017) or, in case of first identification, we used the species epithet of the morphologically most similar species, which was prefixed with "sp. aff." and followed by the locality name in quotation marks.

To verify if each taxon was already reported from the Region, we retrieved information from Glaw and Vences (2007), Brown et al. (2014), the IUCN Red List of Threatened Species (IUCN 2020), Goodman et al. (2018) and taxon-specific publications. Species records that were found to be outside the known species distribution were considered range extensions. Information on species identification, distribution, microhabitat preferences and intra-specific genetic variability of each identified taxon are reported in the section Species accounts.

Results

We generated a total of 520 sequences (308 of amphibians and 212 of reptiles; see Suppl. material 3: Table S3 and Suppl. material 4: Table S4 for GenBank accession numbers (MZ285088–MZ285597) and sampling information and identification of each analysed sample; see Suppl. material 9: Table S7 for locality records of all identified species). Thirteen records (four for amphibians and nine for reptiles) were based on the inspection of photographic material or the morphological examination of the preserved specimens. Neighbor joining trees of the 16S (amphibians) and COI (reptiles) gene fragments are provided in Suppl. material 7: Fig. S1 and Suppl. material 8: Fig. S2.

We sampled a total of 28 amphibian taxa. Most of them belong to the Mantellidae family, of which were 11 Boophinae, 10 Mantellinae and two Laliostominae. We also recorded two hyperoliids and *Ptychadena mascareniensis* (Ptychadenidae). Only two microhylids, both belonging to the subfamily Scaphiophryninae, were sampled. We collected four candidate species (*Boophis* sp. Ca33, *Mantidactylus* sp. Ca14, *Mantidactylus* sp. Ca48 and *Ptychadena* sp. aff. *mascareniensis* "OTU1"). We contributed to extending the current species range for nine taxa (*Heterixalus luteostriatus*, *Scaphiophryne* (*Pseudohemisus*) *calcarata*, *Boophis* (*Sahona*) *doulioti*, *Boophis* (*Boophis*) *boppa*, *Boophis* (*Boophis*) *occidentalis*, *Boophis* (*Boophis*) *rhodoscelis*, *Gephyromantis* (*Phylacomantis*) *corvus*, *Mantella betsileo* and *Mantidactylus* (*Brygoomantis*) sp. Ca14). Amongst the collected material, two taxa are microendemic to the area: *Boophis laurenti* and *Mantidactylus bourgati*.

We identified a total of 38 squamate reptiles. Geckos and chameleons are the most represented groups in our sampling, with 10 taxa each. They are followed by pseu-

doxyrhophiid snakes (six), skinks (four), gerrhosaurids (three), oplurids (two), sanziniid snakes (two) and one psammophiid snake. We collected five candidate species (*Lygodactylus* sp. aff. *pictus* Ca01 "Isalo", *Paragehyra* sp. aff. *felicitae* "Tsaranoro", *Paroedura* sp. aff. *bastardi* Lineage D, *Trachylepis* sp. aff. *vato* and *Pseudoxyrhopus* sp. Ca2). Amongst these, *Paragehyra* sp. aff. *felicitae* "Tsaranoro" was unknown to science and identified in the present study for the first time. We contributed to extending the known distribution area for 12 taxa (*Furcifer nicosiai*, *Furcifer willsii*, *Lygodactylus* sp. aff. *pictus* Ca01 "Isalo", *Paragehyra felicitae*, *Paroedura rennerae*, *Paroedura* sp. aff. *bastardi* Lineage D, *Phelsuma gouldi*, *Phelsuma lineata elanthana*, *Zonosaurus laticaudatus*, *Trachylepis* sp. aff. *vato*, *Leioheterodon modestus* and *Pseudoxyrhopus* sp. Ca2). Amongst the collected material, five taxa are microendemic to the surveyed region (*Brookesia brunoi*, *Paragehyra felicitae*, *Paragehyra* sp. aff. *felicitae* "Tsaranoro", *Paroedura* sp. aff. *bastardi* Lineage D and *Phelsuma gouldi*).

Species accounts

Amphibians
Family Hyperoliidae
Subfamily Hyperoliinae

Heterixalus betsileo (Grandidier, 1872)
Fig. 2L

Heterixalus betsileo occurs in Madagascar's central highlands, where it can be found in swamps and rice fields (Glaw and Vences 2007). Reported within Andringitra National Park, which is close to the southern limit of its distributional range (Glaw and Vences 2007; Goodman et al. 2018), the species was sampled at night within the forests of Anja and Sakaviro, in the western part of the surveyed region, between ca. 930 and 1,020 m a.s.l. (Suppl. material 3: Table S3). The species resulted in being common in both fragments. The two sampled individuals are genetically almost identical to each other (Suppl. material 5: Table S5) and to published sequences of this taxon sampled in Andringitra (16S: EF646668, JQ346497; 16S 5': EF646633) and Andasibe (e.g. 16S: EF646661).

Heterixalus luteostriatus (Andersson, 1910)
Fig. 2M

Heterixalus luteostriatus has a wide and discontinuous distribution across north-western and western Madagascar, including the Isalo Massif. This species can commonly be found in swamps and rice fields (Glaw and Vences 2007; Mercurio et al. 2008) and the record reported here constitutes an extension of the known species distributional range by ca. 180 km to the east from the Isalo Massif (Glaw and Vences 2007). Our study found this taxon at Anja, Anja–Ambilo, Iarintsena,
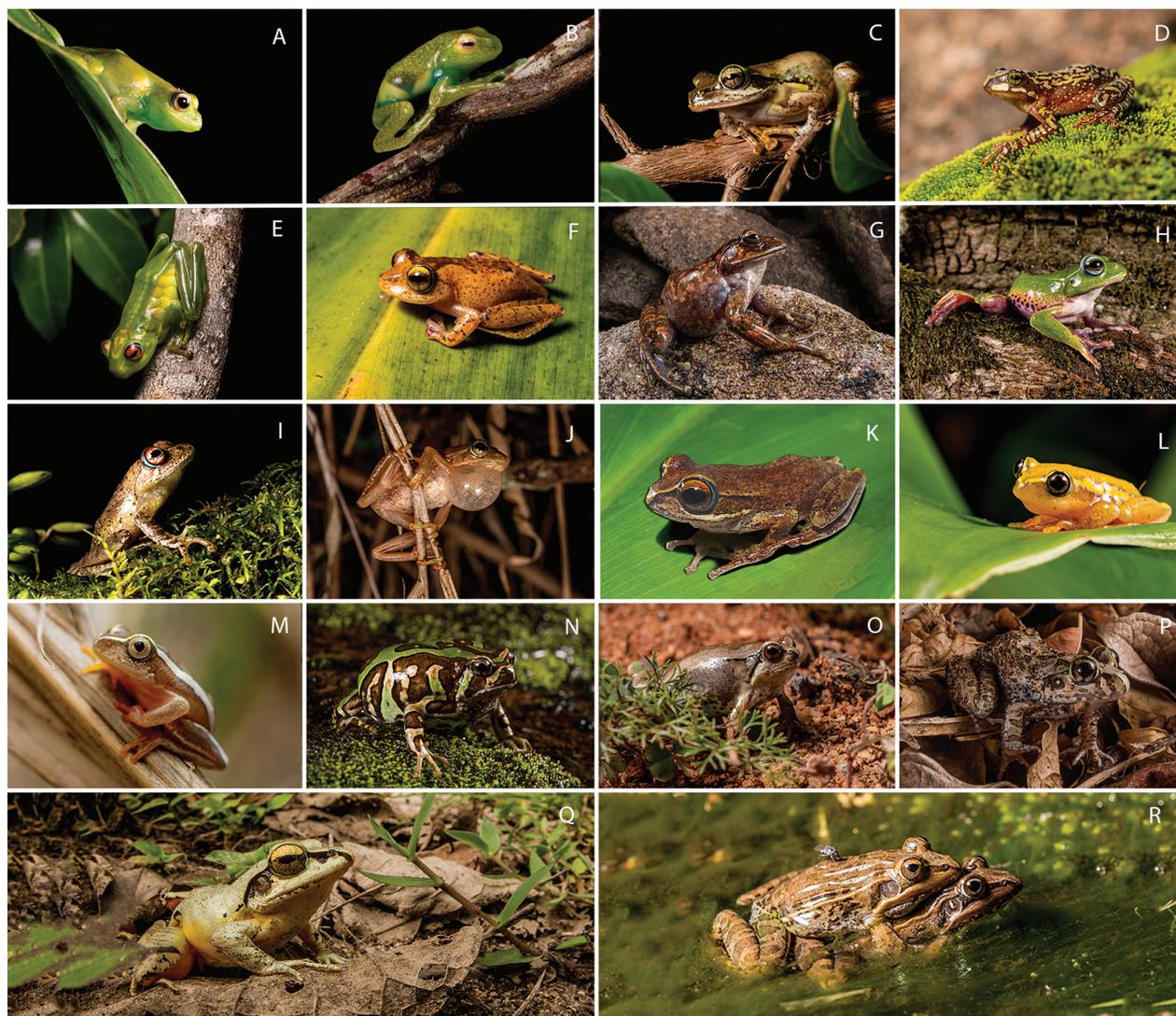
Figure 2. Hyperoliid, microhylid, ptychadenid and mantellid (subfamilies Boophinae and Laliostominae) species identified in this study. Sampling localities for each photographed individual are provided. **ANP ES** – Andringitra National Park Eastern Slopes; **ANP WS** – Andringitra National Park Western Slopes (Fig. 1; Suppl. material 1: Table S1). **A.** *Boophis* (*Boophis*) *ankaratra* from Imaitso (ANP ES); **B.** *Boophis* (*Boophis*) *boppa* from Iantaranomby (ANP WS); **C.** *Boophis* (*Sahona*) *doulioti* from Ambalavao; **D.** *Boophis* (*Boophis*) *laurenti* from Iantaranomby (ANP WS); **E.** *Boophis* (*Boophis*) *luteus* from Fivahona–Velotsoa; **F.** *Boophis* (*Boophis*) *majori* from Asaramanitra (ANP ES); **G.** *Boophis* (*Boophis*) *obscurus* from Imaitso (ANP ES); **H.** *Boophis* (*Boophis*) *occidentalis* from Andramena (ANP WS); **I.** *Boophis* (*Boophis*) *popi* from Imaitso (ANP ES); **J.** *Boophis* (*Boophis*) sp. Ca33 from Asaramanitra (ANP ES); **K.** *Boophis* (*Boophis*) *rhodoscelis* from Fivahona–Ambavanala; **L.** *Heterixalus betsileo* from Sakaviro; **M.** *Heterixalus luteostriatus* from Anja; **N.** *Scaphiophryne* (*Scaphiophryne*) *madagascariensis* from Andramena (ANP WS); **O.** *Scaphiophryne* (*Pseudohemisus*) *calcarata* from Ambalavao; **P.** *Laliostoma labrosum* from Anja; **Q.** *Aglyptodactylus madagascariensis* from Namoly; **R.** *Ptychadena* sp. aff. *mascareniensis* "OTU1" from Iantaranomby (ANP WS). Photographs by Javier Lobón-Rovira (A–J, L–R) and Francesco Belluardo (K).

Sakaviro and Tsaranoro (between ca. 940 and 1,020 m a.s.l.) (Suppl. material 3: Table S3), sometimes in syntopy with *H. betsileo*. This species seemed abundant and was found at both day (sleeping on leaves) and night on small shrubs in areas with degraded and open vegetation outside forests. The 16S sequences of the individual sampled during our survey are identical to each other (Suppl. material 5: Table S5) and individuals from Isalo (e.g. KX066672). The genetic distance between the individuals of *H. luteostriatus* and *H. betsileo* sampled in this study is 3.33%.

Family Microhylidae
Subfamily Scaphiophryninae

Scaphiophryne (*Pseudohemisus*) *calcarata* (Mocquard, 1895)
Fig. 2O

Scaphiophryne calcarata belongs to the subgenus *Pseudohemisus*. A recent study assigned the lectotype of five nomina (including *Calophrynus calcaratus* Mocquard, 1895) (Scherz et al. 2021). This taxonomic

proposal, together with the analysis of newly-collected material, enabled the restriction of the lineage of *Scaphiophryne calcarata* to the southern and south-western portion of the Island. The samples analysed in this study, collected at night in Ambalavao and Sakaviro (at ca. 1,000–1,010 m a.s.l.), are assigned to this lineage. They were included in Scherz et al. (2021) contributing to extend the known distributional range by ca. 180 km in a northern direction. This species was rare and only two individuals were found active at night: one in the garden of a hotel and the second on the ground in an open environment next to a small forest patch surrounded by pastures (Suppl. material 3: Table S3). The two analysed samples are identical to each other (Suppl. material 5: Table S5) and to individuals from Isalo (e.g. MH063283), and are almost identical to the other published sequences of this species (e.g. Berenty, AY834192; Tolagnaro AY834193). The genetic distance from individuals of *S. obscura* and the north-west lineage is ca. 3.3% (e.g. Kirindy, KU937802; Isalo, KX066692) and ca. 4% (Ampijoroa, KU937797), respectively.

Scaphiophryne (*Scaphiophryne*) *madagascariensis* (Boulenger, 1882)
Fig. 2N

This species is distributed in the central highlands, between the Ankaratra Massif in the north and the Andringitra Massif, in the south. This frog generally inhabits high elevation sites, both above and below the tree line (Glaw and Vences 2007; Goodman et al. 2018). *Scaphiophryne madagascariensis* was sampled at Andramena, Asaramanitra and Belambo, on both the eastern and western slopes of the Massif and between ca. 1,580 and 1,740 m a.s.l. The species was frequently encountered during our surveys. The individuals were often spotted in clearings next to a forest (Suppl. material 3: Table S3), both during day and night. We observed no genetic difference amongst the analysed samples (Suppl. material 5: Table S5). When comparing the samples analysed here with the sequences available in Genbank, we found no difference between our samples and individuals collected in the same area (Andohariana Plateau, DQ787110) and they are less than 1% divergent from individuals from Ankaratra (KC180053).

Family Ptychadenidae

Ptychadena sp. aff. *mascareniensis* "OTU1" UCS
Fig. 2R

Ptychadena mascareniensis (Duméril & Bibron, 1841) is the most widespread amphibian in Madagascar. It is usually found next to any pond, swamp and rice field, often outside the forest. Until a few years ago, Malagasy populations were considered conspecific to the populations from mainland Africa and it was thought that the species had been recently introduced to the Island (Glaw and Vences 2007). A recent study showed that *P. mascare-*

niensis is a species complex. Malagasy populations are not conspecific with the populations of the African continent and the populations assigned to *P. mascareniensis* from Madagascar belong to three operational taxonomic units (OTUs) in need of taxonomic revision (Zimkus et al. 2017). All the samples analysed in this study belong to *P.* sp. aff. *mascareniensis* "OTU1" (sensu Zimkus et al. 2017). This species was amongst the most frequent and abundant frogs we recorded, found both during day and night, despite being more commonly active during the day. It was normally found in rice fields or close to temporary water bodies, between ca. 870 and 1,650 m a.s.l. (Suppl. material 3: Table S3). We sampled this taxon at Andramena, Asaramanitra, Iantaranomby, Imaitso, Ambalavao, Ambatomainty, Antanifotsy 1, 3, 5, Anja, Fivahona–Ambavanala, Fivahona–Velotsoa, Namoly and Tsaranoro. The individuals, analysed for this study, are genetically uniform amongst each other (Suppl. material 5: Table S5) and are almost identical to other individuals collected in the area (Andohariana: AY517587 and AY517588) and across Madagascar (e.g. Toliara, KX836419; Ranomafana, KX836413; Bemaraha, KX836392; Andohahela, KX836390; Isalo, KX066671).

Family Mantellidae
Subfamily Boophinae

Boophis (*Sahona*) *doulioti* (Angel, 1934)
Fig. 2C

Distributed in western and southern Madagascar, this taxon is mostly found in open areas and secondary vegetation (Glaw and Vences 2007). *Boophis doulioti* had not been reported to this area before and our finding represents an extension of the species distributional range by ca. 150 km towards the east. Individuals were spotted active at night in Anja and Iarintsena (on the western side of the Andrinditra Massif), perching on trees and shrubs within semi-arid deciduous forest, in open environments next to villages, close to rice fields and within the town of Ambalavao at an elevation of ca. 950–1,030 m a.s.l (Suppl. material 3: Table S3). The analysed samples are all identical to each other (Suppl. material 5: Table S5) and samples collected at Isalo (KX066561), Tranomaro (MK132751) and Ranomafana (AY848515; this record being reported as *Boophis tephraeomystax* (Duméril, 1853)).

Boophis (*Boophis*) *ankaratra* Andreone, 1993
Fig. 2A

Boophis ankaratra is commonly found in the central highlands at high-elevation locations, both in rainforest and degraded gallery vegetation (Glaw and Vences 2007; IUCN SSC Amphibian Specialist Group 2016a). We collected a single individual during a night search at Imaitso, within an area of dense rainforest (ca. 1,670 m a.s.l.), perching on riverine vegetation surrounding a small stream (Suppl. material 3: Table S3). This sample

is identical to other available sequences from the Andringitra Region (Andringitra: AF411611; Imaitso Forest: DQ068396, DQ068397, DQ068398). The individual analysed in this study is molecularly almost identical to the population from Ranomafana (difference: 0.30%; GU974475).

Boophis (*Boophis*) *boppa* Hutter, Lambert, Cobb, Andriampenomanana & Vences, 2015
Fig. 2B

Boophis boppa has been recently described from Ranomafana National Park and Antoetra (Andreone et al. 2007; Hutter et al. 2015). This record represents a range extension for the species by ca. 80 km towards the south. Individuals were locally abundant and were collected at Asaramanitra (along the eastern slope of the Massif) and Iantaranomby (on the western slope), at an elevation of ca. 1,580–1,600 m a.s.l. Sampled individuals were perching at night on riverine vegetation along large streams in both forested areas and open environments with scattered trees (Suppl. material 3: Table S3). The analysed samples collected in this study are identical (Suppl. material 5: Table S5). They are also identical to individuals from the type locality (Ranomafana: KT588038) and very similar (99.80% similarity) to individuals from Antoetra (e.g. AY848438).

Boophis (*Boophis*) *laurenti* (Guibé, 1947)
Fig. 2D

This species is currently known only from Andringitra National Park, where it can be found in montane heathlands above 1,500 m a.s.l. (IUCN SSC Amphibian Specialist Group 2016b; Goodman et al. 2018). We sampled *Boophis laurenti* either on mossy rocks in streams or perching on dense vegetation and scattered trees close to running water. The species was detected during day and night (although more frequently active at night) and seemed common along both the western (Andramena, Iantaranomby) and the eastern (Diavolana) slopes of the Massif (between ca. 1,580 and 1,740 m a.s.l.) (Suppl. material 3: Table S3). Our samples are genetically uniform to each other (Suppl. material 5: Tables S5) and in comparison with previously available sequences (Andohariana: AY848599, AY659964; Andringitra: AY659963; Cuvette Boby: AY848575).

Boophis (*Boophis*) *luteus* (Boulenger, 1882)
Fig. 2E

This species can be found along streams in rainforest and secondary vegetation in several localities of eastern Madagascar (including Andringitra National Park), but also in Isalo in the south-west and Ambohitantely in the central highlands (Glaw and Vences 2007; Cocca et al. 2018; Goodman et al. 2018). The species was rare and only two individuals were spotted at Fivahona–Velot-soa, in the eastern part of the surveyed region, at ca. 1,270 m a.s.l. (Suppl. material 3: Table S3). Both individuals were found in roosting positions on trees near a stream at night. They show limited genetic differentiation and are almost identical to individuals collected at Ranomafana (e.g. FJ559330) and Isalo (FJ559354) (Suppl. material 5: Table S5).

Boophis (*Boophis*) *majori* (Boulenger, 1896)
Fig. 2F

Boophis majori is distributed in eastern Madagascar within a restricted region comprised of Antoetra, Ranomafana, Andringitra National Park (Imaitso Forest) (Brown et al. 2014) and Ivohibe, where it can be found on trees along rainforest streams (Glaw and Vences 2007; IUCN SSC Amphibian Specialist Group 2016c; Goodman et al. 2018). *Boophis majori* was a common species. During a night search, we collected three samples perching on trees along a large stream within rainforest habitat in Asaramanitra, on the eastern slope of the Massif, at ca. 1,590 m a.s.l. (Suppl. material 3: Table S3). These samples are identical to each other (Suppl. material 5: Table S5) and have 0.50% genetic distance with samples from Ranomafana (e.g. AY848586).

Boophis (*Boophis*) *obscurus* (Boettger, 1913)
Fig. 2G

Boophis obscurus was recently resurrected from the synonymy with *Boophis goudotii* Tschudi, 1838 (Glaw et al. 2010). The species is distributed in south-eastern Madagascar between Ranomafana, Isalo and Andringitra National Park (Andohariana Plateau) (Glaw et al. 2010; IUCN SSC Amphibian Specialist Group 2016d; Goodman et al. 2018). *Boophis obsurus* was common and abundant across the Region and was sampled in Andramena, Asaramanitra, Belambo, Iantaranomby, Imaitso, Riandahy, Siranandambo, Fivahona–Ambavanala, Fivahona–Velotsoa, Namoly and Tsaranoro (Suppl. material 3: Table S3). *Boophis obscurus* was collected between ca. 950 and 1,740 m a.s.l., normally found on rocks and boulders along water streams. It was sampled during both diurnal and nocturnal searches, despite being more frequent at night. The samples analysed in this study are molecularly similar to each other (Suppl. material 5: Table S5) and another sample collected from the same area (AY848568). They show only limited genetic difference to samples from other localities (e.g. Ranomafana: GU975058; Isalo: KX066565).

Boophis (*Boophis*) *occidentalis* Glaw & Vences, 1994
Fig. 2H

Boophis occidentalis has a discontinuous distribution in western (Tsingy de Bemaraha) and central Madagascar (between Isalo, Zazafotsy and Antoetra), where it is found in dry deciduous forest (Vences et al. 2003; Glaw

and Vences 2007). This species was previously not reported from our study area and this record extends the species distributional range by ca. 50 km towards the east. This species was collected in the eastern and western part of the Region (Andramena, Iantaranomby, Ambatomainty, Fivahona–Velotsoa and Tsaranoro; Suppl. material 3: Table S3) between ca. 920 and 1,740 m a.s.l., where it was often found on high trees close to streams. *Boophis occidentalis* was particularly common in Tsaranoro, whereas, in the other sampling sites, it was rarer. The individuals were all spotted at night. The collected samples are identical (Suppl. material 5: Table S5) and show high genetic affinity with individuals from Isalo (e.g. KX066570) and Antoetra (AY341720), with less than 1% genetic distance.

Boophis (*Boophis*) *popi* **Köhler, Glaw, Rosa, Gehring, Pabijan, Andreone & Vences, 2011**
Fig. 2I

Boophis popi is distributed in central-eastern Madagascar between Tsinjoarivo and Andringitra. This species can be found along streams in montane rainforest in a narrow elevational range of 1,000–1,500 m a.s.l. (Andreone et al. 2007; Köhler et al. 2011; Goodman et al. 2018). The samples included in the present study were collected on the eastern slopes of the Massif at Imaitso (where other individuals were previously sampled) at higher elevation (ca. 1,520–1,690 m a.s.l.), slightly above the currently known range for the species (Köhler et al. 2011) (Suppl. material 3: Table S3). The species was particularly abundant in this site. The collected individuals were found along small slow-flowing streams within rainforest, perching on the riverine vegetation. They were mostly spotted at night, despite a single individual being found during the day. The analysed samples are almost identical to each other (Suppl. material 5: Table S5) and to previously available sequences (Andringitra: e.g. JN679879; Antoetra: e.g. AY848551).

Boophis (*Boophis*) *rhodoscelis* **(Boulenger, 1882)**
Fig. 2K

This species is distributed between Ranomafana and Antoetra, where it can be found in swampy areas. Previous records from Ambohitantely have recently been assigned to *Boophis andrangoloaka* (Ahl, 1928) (Glaw et al. 2010). *Boophis rhodoscelis* was not yet reported from the study area and this record represents a range extension by ca. 70 km to the south. The species was rare. Two calling males were sampled at Fivahona–Ambavanala, in the eastern part of the surveyed region. The individuals were found during the night at ca. 1,480 m a.s.l. perching on trees next to a fast-flowing stream within rainforest (Suppl. material 3: Table S3). These two samples are identical to each other (Suppl. material 5: Table S5) and to samples collected at Antoetra (AY848616) and Ranomafana (e.g. AY848619).

Boophis (*Boophis*) sp. Ca33 UCS
Fig. 2J

This unconfirmed candidate species is part of the species group comprising *Boophis microtympanum* (Boettger, 1881) and *B. laurenti*. *Boophis* sp. Ca33 (following the terminology as in Vieites et al. (2009) and reported in Glaw and Vences (2007) as *B.* sp. aff. *microtympanum*) is morphologically similar to *B. microtympanum* from which it is distinguished by a more uniform dorsal colouration rather than the vermiculated pattern described in the nominal species. Vocalisations of the two taxa are very similar and present only some quantitative difference in note duration (Glaw and Vences 2007; Vieites et al. 2009). Glaw and Vences (2007) report the presence of *Boophis* sp. Ca33 in the surveyed area at Cirque Namoly and Vieites et al. (2009) states that this taxon was found to live in sympatry with *B. microtympanum*, an observation that might support the distinction of these taxa (sensu Miralles et al. 2021), although the genetic differentiation at the 16S marker is below the standard threshold of 3% (Vieites et al. 2009). The species was not abundant. We sampled three individuals of *Boophis* sp. Ca33 at Asaramanitra, on the eastern slopes of the Massif. These individuals were found at night perching on branches next to a large fast-flowing stream at ca. 1,590 m a.s.l. of elevation (Suppl. material 3: Table S3). The samples analysed here are identical to each other (Suppl. material 5: Table S5), to other available sequences from the area (AY848597) and Mahahira (AY848604; in the Ranomafana area). They are also almost identical to samples from Itremo (JF903885). Individuals from Ankaratra (HM769929), Col des Tapias (AJ315918), Ambohitantely (HM769928) and Andasibe (AY848598) attributed to *B. microtympanum* are ca. 1.60% different.

Subfamily Laliostominae

Aglyptodactylus madagascariensis **(Duméril, 1853)**
Fig. 2Q

This species inhabits rainforest in northern and eastern Madagascar. The Andringitra Massif represents the southernmost limit of its distributional range and the highest elevational record (Imaitso forest, 1,509 m a.s.l.) for the species (Köhler et al. 2015; Goodman et al. 2018). It is an explosive breeder reproducing in temporary ponds, but it can often be found on the forest floor outside the breeding season (Glaw and Vences 2007). The four analysed individuals were found on the floor of the rainforest at Imaitso and Namoly, in the eastern part of the Region at an elevation range between ca. 1,550 and 1,650 m a.s.l. (Suppl. material 3: Table S3). They were recorded during both night and day, although more frequently spotted at night. The collected samples are genetically identical to each other (Suppl. material 5: Table S5) and to other samples from the Region (e.g. KT159884). They are slightly different (ca. 0.40% ge-

netic distance) from individuals collected in Ranomafana (e.g. AY847991).

Laliostoma labrosum (Cope, 1868)
Fig. 2P

This species is widely distributed in dry habitats of western, northern and southern Madagascar (Glaw and Vences 2007). Within the Region of Andringitra, this species was already reported from the town of Ambalavao (e.g. AY848009). *Laliostoma labrosum* was not frequently encountered during our surveys. Individuals were spotted at night in the western portion of the Region in Iantaranomby and Anja. The encounters took place on the floor of semi-arid deciduous forest, close to large streams in open environments and within the town of Ambalavao, in a hotel garden, at an elevation between ca. 980 and 1,560 m a.s.l. (Suppl. Material 3: Table S3). The analysed samples are genetically identical to each other (Suppl. material 5: Table S5) and to other populations from different parts of Madagascar (e.g. Toliara: KR337974; Ankarafantsika: KR337954; Kirindy: KR337951; Isalo: KX066667; Tsaratanana: KR337858).

Subfamily Mantellinae

Gephyromantis (*Phylacomantis*) *corvus* (Glaw & Vences, 1994)
Fig. 3H

The samples of this taxon, collected at Anja, Sakaviro and Tsaranoro (in the western portion of the surveyed area; Suppl. material 3: Table S3), have been included in a recent taxonomic study (Cocca et al. 2020) where the authors synonymised *Gephyromantis azzurrae* Mercurio & Andreone, 2007 with *G. corvus* and described the second *Phylacomantis* lineage inhabiting Isalo as *Gephyromantis kintana* Cocca, Andreone, Belluardo, Rosa, Randrianirina, Glaw & Crottini, 2020. Previously known only from the Isalo Massif, where it inhabits large and deep canyons with fast-flowing water and gallery forests (Glaw and Vences 2007; Mercurio and Andreone 2007), these records represent an important range extension for the species by ca. 180 km towards east (Cocca et al. 2020). This species was rare. The individuals were found during night searches at an elevational range of ca. 950–1,020 m a.s.l. along small canyon-like streams in banks, ravines and crevices both within semi-arid deciduous forest and in open habitats. The analysed samples are identical (Suppl. material 5: Table S5) and have a limited genetic differentiation (ca. 0.60%) from the individuals of Isalo (KX066651).

Gephyromantis (*Gephyromantis*) *blanci* Guibé, 1974
Fig. 3G

Males of *Gephyromantis blanci* are easily found in rainforest and secondary vegetation while calling on the forest floor or low branches. Ambalamarovandana,

located in the eastern slopes of the Andringitra Massif, is the type locality of the species (Glaw and Vences 2007; IUCN SSC Amphibian Specialist Group 2016e; Goodman et al. 2018). *Gephyromantis blanci* was locally abundant and was sampled at Imaitso and Namoly, in the eastern part of the Region, at an elevation range of ca. 1,540–1,690 m a.s.l. (Suppl. material 3: Table S3). All collected individuals were males calling from the forest floor within dense rainforest, spotted both during day and night-time. The analysed samples are genetically identical to each other and to sequences previously available from the area (e.g. AY848324) (Suppl. material 5: Table S5).

Mantella betsileo (Grandidier, 1872)
Fig. 3I

This species is discontinuously reported from multiple localities in western Madagascar between the Isalo Massif, at the south, and Bemaraha, at the north. Within Isalo National Park, this species can be observed around both temporary and permanent water bodies, generally outside of the canyons (Glaw and Vences 2007; Mercurio et al. 2008). Although not yet confirmed from the surveyed area, the species was described from individuals likely collected in the Betsileo Region, which includes the Region of Andringitra. Sightings of *Mantella betsileo* were rare in our survey. We found this taxon during the night in the western portion of the Region at Ambatomainty, where two individuals were spotted active within a humid pit in the ground at ca. 930 m a.s.l. of elevation. Another individual was found in Anja, in an open area close to a granitic boulder. These records extend the known distributional range of the species by ca. 180 km towards east (Suppl. material 3: Table S3). The analysed samples are identical (Suppl. material 5: Table S5) and very similar to individuals from Isalo (e.g. EF674841) and Morondava (AF215288).

Mantidactylus (*Brygoomantis*) *betsileanus* (Boulenger, 1882)
Fig. 3B

This species is distributed in central-eastern Madagascar where it is often found along slow-flowing streams within rainforest, but it can also be found in degraded vegetation and human-dominated areas (e.g. rice fields) (Glaw and Vences 2007). We sampled *M. betsileanus* at Fivahona–Ambavanala, Fivahona–Velotsoa, Namoly and Tsaranoro, both in the eastern and western sides of the surveyed area (between ca. 930 and 1,650 m a.s.l.) (Suppl. material 3: Table S3). The species seemed abundant, especially in Fivahona–Velotsoa and Tsaranoro. The individuals were spotted both during day and night-time along the banks of slow-flowing streams within forest. Molecularly, the individuals analysed here are uniform (Suppl. material 5: Table S5) and are almost identical to individuals collected at Itremo (JF903887), Ranomafana (AY848275), Andasibe

Figure 3. Amphibians of the mantellid subfamily Mantellinae identified in this study. Sampling localities for each photographed individual are provided. **ANP ES** – Andringitra National Park Eastern Slopes; **ANP WS** – Andringitra National Park Western Slopes (Fig. 1; Suppl. material 1: Table S1). **A.** *Mantidactylus* (*Bryogoomantis*) *bourgati* from Namoly; **B.** *Mantidactylus* (*Bryogoomantis*) *betsileanus* from Namoly; **C.** *Mantidactylus* (*Chonomantis*) *delormei* from Imaitso (ANP ES); **D.** *Mantidactylus* (*Ochthomantis*) *femoralis* from Asaramanitra (ANP ES); **E.** *Mantidactylus* (*Bryogoomantis*) sp. Ca14 from Tsaranoro; **F.** *Mantidactylus* (*Hylobatrachus*) sp. Ca48 from Fivahona–Velotsoa; **G.** *Gephyromantis* (*Gephyromantis*) *blanci* from Imaitso (ANP ES); **H.** *Gephyromantis* (*Phylacomantis*) *corvus* from Sakaviro; **I.** *Mantella betsileo* from Ambatomainty; **J.** Subadult and tadpoles of *Spinomantis elegans* from Imaitso (ANP ES). Photographs by Javier Lobón-Rovira.

(e.g. FJ559234), Fierenana (e.g. EF606877) and Mandraka (AY848238).

Mantidactylus (*Brygoomantis*) *bourgati* Guibé, 1974
Fig. 3A

Endemic to the Andringitra Massif (already reported from Imaitso Forest and Andohariana Plateau), the species is known to live along streams within forest above the tree line (Glaw and Vences 2007). Ambalamarovandana, located in the eastern slopes of the Massif, is the type lo-

cality of the species. We sampled *Mantidactylus bourgati* across a large portion of the surveyed sites (Andramena, Asaramanitra, Belambo, Iantaranomby, Imaitso, Riandahy, Siranandambo, Fivahona–Ambavanala, Fivahona–Velotsoa, Namoly and Tsaranoro; Suppl. material 3: Table S3), both on the western and eastern portion of the Region at a wide elevational range (between ca. 930 and 1,740 m a.s.l.). In all sites, *M. bourgati* was abundant and the individuals were spotted during both day and night along the banks of streams within forest. Analysed individuals are genetically almost identical (Suppl. material 5: Table S5).

Mantidactylus (*Brygoomantis*) **sp. Ca14 UCS**
Fig. 3E

Mantidactylus sp. Ca14 is closely related to *Mantidactylus alutus* (Peracca, 1893) and morphologically similar to *Mantidactylus ulcerosus* (Boettger, 1880), relative to which it exhibits significant bioacoustic differences, slight morphological dissimilarities and substantial mitochondrial divergence (Vieites et al. 2009). This taxon is already known from Isalo and Tsingy de Bemaraha where it is typically encountered along slow-flowing streams in forested areas (Glaw and Vences 2007; Cocca et al. 2018). This record extends the known distributional range of this taxon by ca. 180 km towards the east from the Isalo Massif. The species was rare, with only two individuals sampled at night in Tsaranoro (at ca. 910 m a.s.l.), in the western part of the Region (Suppl. material 3: Table S3). They were spotted in a small pond below a large boulder. These two samples show no genetic differentiation to each other (Suppl. material 5: Table S5) and with samples from Isalo (e.g. KX066586).

Mantidactylus (*Chonomantis*) *delormei* **Angel, 1938**
Fig. 3C

This species is typically found along streams in montane forests between Ranomafana and the Andringitra Massif, which is also its type locality (Glaw and Vences 2007; Goodman et al. 2018). We sampled *Mantidactylus delormei* at Asaramanitra, Belambo and Imaitso, along the eastern slopes of the Massif between ca. 1,570 and 1,710 m a.s.l. Although a leaf litter-dwelling species, invididuals were always in proximity to streams within rainforest (Suppl. material 3: Table S3). The animals were sampled during both day and night searches, although they were more frequent at night. The analysed individuals are almost identical to each other (Suppl. material 5: Table S5) and to a previously available sequence from Andringitra (AY848148) and 1.1% distant from individuals from Ranomafana (e.g. GU975171).

Mantidactylus (*Ochthomantis*) *femoralis* (**Boulenger, 1882**)
Fig. 3D

The type locality of this taxon is "East Betsileo", which roughly corresponds to the surveyed area and the lineage currently assigned to this name is known from Andringitra and the Isalo Massifs (Glaw and Vences 2007; Cocca et al. 2018; Goodman et al. 2018). This locally abundant species was recorded at Asaramanitra, Iantaranomby, Imaitso, Riandahy, Siranandambo, Anja, Fivahona–Velotsoa and Tsaranoro, at an elevation range between ca. 930 and 1,730 m a.s.l., both in the eastern and western portions of the study area, showing a similar distribution to *M. bourgati* (Suppl. material 3: Table S3). The sampled individuals were observed along streams banks within forest and were collected during both day and night-time, despite being more frequent at night. They are genetically identical to each other (Suppl. material 5: Table S5) and almost identical with pre-

viously available sequences (e.g. Andringitra: HQ610918; Isalo: AY324813).

Mantidactylus (*Hylobatrachus*) **sp. Ca48 UCS**
Fig. 3F

Mantidactylus sp. Ca48 is morphologically similar to both *Mantidactylus lugubris* (Duméril, 1853) and *Mantidactylus cowanii* (Boulenger, 1882). This undescribed lineage is widely distributed amongst Isalo, Itremo, Antoetra (in sympatry with *M. cowanii*), Ranomafana, Ambohitsara, Vondrozo and Manombo (Cocca et al. 2018; Scherz et al. 2019). Goodman et al. (2018) report the possible presence of *M. lugubris* in the species list of Andringitra National Park although the record is considered as doubtful. We found this taxon at Asaramanitra, Iantaranomby and Fivahona–Velotsoa, in both the eastern and western parts of the Region (between ca. 930 and 1,650 m a.s.l.) (Suppl. material 3: Table S3). The species seemed common in Fivahona–Velotsoa, whereas, in the other sites, it was rarer. Individuals were found at night on rocks along streams. The analysed samples are genetically identical (Suppl. material 5: Table S5) and ca. 100% identical to individuals from Ranomafana (e.g. MK447667), Ambohitsara (e.g. MK447637), Ambatolahy (MK447645), Valohoaka (MK447661), Miranony (MK447658) and Manombo (AY848186).

Spinomantis elegans (**Guibé, 1974**)
Fig. 3J

Spinomantis elegans is distributed in south-eastern Madagascar between Ranomafana to the north and Andohahela to the south, including the area of the Andringitra Massif, which is close to the type locality (Ivohibe). This species lives at high elevations and is often found within small caves, between outcrops or hiding below rocks, both within forest and above the tree line (Glaw and Vences 2007). *Spinomantis elegans* was rarely encountered in our surveyes. We sampled a tadpole in a small pond at Imaitso and a subadult next to a large permanent stream at Asaramanitra, on the eastern slopes of the Massif at ca. 1,540–1,600 m a.s.l. of elevation (Suppl. material 3: Table S3). Both individuals were found at night. The two analysed samples are identical to each other (Suppl. material 5: Table S5) and previously available sequences (e.g. Cuvette Boby: AY659960; Ranomafana: AY848405).

Reptiles
Family Chamaeleonidae
Subfamily Brookesiinae

Brookesia brunoi **Crottini, Miralles, Glaw, Harris, Lima & Vences, 2012**
Fig. 4A

This species is currently known only from Anja Community Reserve where it is typically encountered on
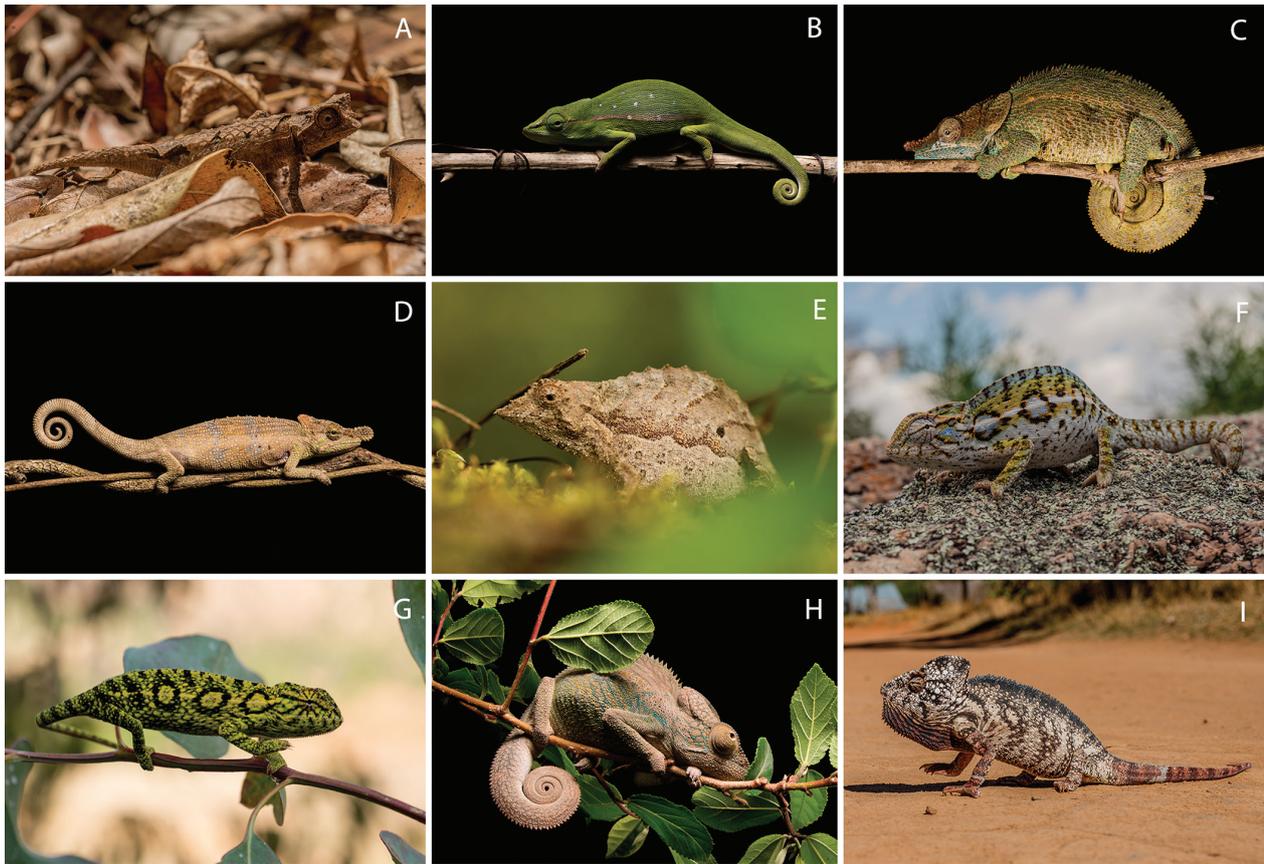
Figure 4. Chameleonid species identified in this study. The picture of the individual identified as *Furcifer willsii* from Fivahona–Velotsoa, found within the stomach content of a *Mimophis mahfalensis*, is not shown. Sampling localities for each photographed individual are provided. **ANP ES** – Andringitra National Park Eastern Slopes; **ANP WS** – Andringitra National Park Western Slopes (Fig. 1; Suppl. material 1: Table S1). **A.** *Brookesia brunoi* from Anja; **B.** *Calumma andringitraense* from Imaitso (ANP ES); **C.** *Calumma crypticum* from Imaitso (ANP ES); **D.** *Calumma fallax* from Asaramanitra (ANP ES); **E.** *Palleon nasus* from Namoly; **F.** *Furcifer lateralis* from Iantaranomby (ANP WS); **G.** *Furcifer major* from Anja; **H.** *Furcifer nicosiai* from Tsaranoro; **I.** *Furcifer oustaleti* from Anja. Photographs by Javier Lobón-Rovira.

the leaf litter during the day or roosting at a few centimetres height after the sunset, within the semi-arid deciduous forest patches of the Reserve (Crottini et al. 2012b). *Brookesia brunoi* was found only at Anja, at an elevation of ca. 970–980 m a.s.l. (Suppl. material 4: Table S4). The species seemed common in this forest fragment. All sampled individuals were found during the day moving on the leaf litter. Their sequences are molecularly uniform (Suppl. material 6: Table S6, COI) and show a maximum genetic distance of ca. 1.50% from previously available sequences (e.g. ND2: JX101752).

Palleon nasus (Boulenger, 1887)
Fig. 4E

Palleon nasus has originally been described from "Ekongo", which probably refers to Ikongo, ca. 55 km north-east of the Andringitra Massif. This species is distributed in south-eastern Madagascar between Ranomafana and Andringitra to the north and Tolagnaro to the south-east. *Palleon nasus* has been subdivided into two subspecies, based on morphological differ-

ences: *P. n. nasus* (Boulenger, 1887) and *P. n. pauliani* (Brygoo, Blanc & Domergue, 1972), the latter being described from Manjarivolo (in the Andringitra Massif), where it was collected at an elevation of 1,620–1,650 m a.s.l. Based on morphological examination, Goodman (1996) identified *P. n. nasus* (specimens collected at an elevation of 720–1,630 m a.s.l.) during a herpetological assessment on the eastern slopes of the Massif. We collected six individuals of *P. nasus* in the eastern parts of the Region (Imaitso and Namoly), at an elevation range between ca. 1,580 and 1,640 m a.s.l. (Suppl. material 4: Table S4). The species was common. The animals were all found at night within rainforest while roosting on branches (one individual close to the floor and the other at ca. 2 m from the ground) and they were not active. The analysed samples are genetically uniform to each other (Suppl. material 6: Table S6) and they show 10.5% genetic distance to sequences obtained from individuals of Andohahela (COI: JQ909283) and are ca. 4% distant to an individual from Ranomafana (16S: HQ130509). Morphological examination of the collected individuals suggests a closer affinity with *P. n. nasus*.

Subfamily Chamaeleoninae

Calumma andringitraense (Brygoo, Blanc & Domergue, 1972)
Fig. 4B

This species is known from Andringitra, which represents the type locality, and the Andohahela Massif (Glaw and Vences 2007), where it inhabits montane rainforest at an elevation range of 1,550–1,680 m a.s.l. (Goodman 1996; Goodman et al. 2018). We collected samples of this species at Imaitso and Fivahona–Ambavanala, in the eastern part of the Region, while roosting on branches in dense rainforest at an elevation between ca. 1,480 and 1,560 m a.s.l. (Suppl. material 4: Table S4). They were all spotted at night in a sleeping position. The species was abundant in Imaitso, while rarer in Fivahona–Ambavanala. The analysed individuals are genetically uniform to each other (Suppl. material 6: Table S6) and they have ca. 5.5% genetic distance to individuals from Andohahela (COI: JQ909303).

Calumma crypticum Raxworthy & Nussbaum, 2006
Fig. 4C

Calumma crypticum has a scattered distribution including the Tsaratanana Massif in the north and several localities in the central highlands, Ranomafana and Andohahela. It inhabits montane forests at an elevation between ca. 1,050 and 1,850 m a.s.l. (Boumans et al. 2007; Glaw and Vences 2007; Randrianantoandro et al. 2010). Boumans et al. (2007) showed that the species is composed of several intra-specific lineages characterised by a certain degree of mitochondrial differentiation at the 16S gene. This species was the most common chameleon we encountered during our sampling. We collected the species at Asaramanitra, Belambo, Imaitso, Fivahona–Velotsoa and Namoly, in the eastern portion of the Region (Suppl. material 4: Table S4). The sampled individuals were found both during the day and at night (sleeping) while roosting on branches in dense rainforest. They are genetically quite similar to each other (Suppl. material 6: Table S6) and show limited genetic differentiation compared to other samples collected in Ranomafana (COI: ca. 3%, JQ909308; 16S: ca. 0.50%, EF210643).

Calumma fallax (Mocquard, 1900)
Fig. 4D

Following its new definition, *Calumma fallax* is distributed in eastern Madagascar from Andohahela, to the south, to Mandraka to the north, where it can be found in rainforest at low and middle elevations (Glaw and Vences 2007; Gehring et al. 2011, 2012; Prötzel et al. 2020). The type locality of this taxon is Ikongo, which is located ca. 55 km north-east of the Andringitra Massif. We sampled this species at Asaramanitra, Fivahona–Ambavanala,

Fivahona–Velotsoa and Namoly in the rainforest of the eastern part of the surveyed area at an elevation range between ca. 1,490 and 1,670 m a.s.l. (Suppl. material 4: Table S4). The species was common in Namoly, while in the other sites, it was rarer. The animals were spotted at night on tree branches while sleeping. The analysed individuals are molecularly uniform across the different sampling localities (Suppl. material 6: Table S6) and show a 4% genetic distance from individuals of the same species from Ranomafana (ND2: JQ734064).

Furcifer lateralis (Gray, 1831)
Fig. 4F

Florio et al. (2012) revised the taxonomy of the *F. lateralis* complex, assigning the populations of southern and north-western Madagascar to *Furcifer major* (Brygoo, 1971) and *Furcifer viridis* Florio, Ingram, Rakotondravony, Louis Jr. & Raxworthy, 2012, respectively. The distribution of *F. lateralis* was restricted to eastern Madagascar, where it can be found within rainforest, at forest edges, in shrubby grasslands and more degraded vegetational formations (Raselimanana and Rakotomalala 2003; Glaw and Vences 2007). The species is reported from Andringitra (Goodman et al. 2018) and was sampled on the western slopes of the Massif (Iakanga and Iantaranomby) where it was encountered with low frequency. Only two individuals were collected during the day, actively perching in open grassland with scattered trees at an elevation between ca. 900 and 1,560 m a.s.l. (Suppl. material 4: Table S4). The analysed samples are molecularly identical to each other (Suppl. material 6: Table S6) and show limited genetic differentiation (16S) from samples collected at Cirque Namoly (EF210582; within the study area), Vondrozo (EF210589) and Tampina forest (EF210593).

Furcifer major (Brygoo, 1971)
Fig. 4G

Distributed in southern Madagascar, *F. major* inhabits almost any arid habitat including human-disturbed environments (Raselimanana and Rakotomalala 2003; Florio et al. 2012). We sampled this species at Ambatomainty, Anja, Anja–Ambilo and Sakaviro (Suppl. material 4: Table S4), on the western part of the Region at only ca. 10 km from the localities where we collected *F. lateralis*. Individuals were spotted during both day and night (sleeping), perching on tree branches. Despite present in multiple sites, the species was locally rare to encounter. Relative to *F. lateralis*, *F. major* was found at a lower elevation (between ca. 930 and 1,030 m a.s.l.) and in semi-arid deciduous forest. The analysed samples are genetically identical to each other (Suppl. material 6: Table S6) and show 2.6% genetic distance (COI) from conspecific populations from Isalo (e.g. MH063344).

Furcifer nicosiai Jesu, Mattioli & Schimmenti, 1999
Fig. 4H

This chameleon was first described from Tsingy de Bemaraha, in western Madagascar, where it is mostly found within dense sub-humid and dry forests. This species has been later reported from Paysage Harmonieux Protégé de Beanka, Paysage Harmonieux Protégé du Complexe Tsimembo Manambolomaty, Paysage Harmonieux Protégé du Complexe Lac–Forêt Ambondrombe, Paysage Harmonieux Protégé de Menabe Antimena and Réserve Spéciale d'Andranomena (Goodman et al. 2018). We sampled *Furcifer nicosiai* at Tsaranoro, in the western part of the region, at ca. 960–970 m a.s.l. (Suppl. material 4: Table S4). This record was included in Belluardo et al. (2021), along with other new records from central and western Madagascar, significantly expanding the known distribution of this species by ca. 300 km towards the south-east. *F. nicosiai* did not seem abundant. We sampled three individuals both during night (sleeping) and day while roosting on branches within semi-arid deciduous forest. The analysed individuals are genetically identical to each other (Suppl. material 6: Table S6) and they show 4% (COI: JQ909373) and 3% (16S: HF57045) genetic distance with individuals from the type locality (Tsingy de Bemaraha).

Furcifer oustaleti (Mocquard, 1894) Clade D
Fig. 4I

This species is widely distributed in Madagascar. It can inhabit a wide variety of habitats, including degraded vegetation and human-dominated environments (Glaw and Vences 2007; Florio and Raxworthy 2016). We identified this species at Ambalavao, Anja, Anja–Ambilo and Sakaviro (in the western part of the Region) at an elevation range of ca. 980–1,010 m a.s.l. (Suppl. material 4: Table S4). The species seemed quite common. The individuals were found during the day, both within semi-arid deciduous forest and in human-associated environments, actively perching on tree braches. The analysed animals are molecularly identical to each other (Suppl. material 6: Table S6) and to individuals from Isalo (COI: MH063345; 16S: MH063288) attributed to Clade D (sensu Florio and Raxworthy 2016), which is distributed in southern, central and north-western Madagascar.

Furcifer willsii (Günther, 1890)

This chameleon is distributed in central-eastern Madagascar and in the north, in the area of Tsaratanana, while records from western Madagascar require verification (Glaw and Vences 2007). *Furcifer willsii* can be found in rainforest where it is usually spotted roosting high above the ground. The only recorded individual was sampled in Fivahona–Velotsoa, in the eastern part of the study area (ca. 1,270 m a.s.l.) and it was recovered in the stomach of a specimen of *Mimophis mahfalensis* (Grandidier, 1867) (ACZC11133) (Suppl. material 4: Table S4) (Lobón-Ro-

vira et al. 2020). The previous southernmost record of this chameleon (Ikongo) is at ca. 55 km north-east from Fivahona–Velotsoa. The sample was included in Lobón-Rovira et al. (2020), contributing to extend the species distributional range further south. The sample shows 7.2% genetic distance from a conspecific individual collected at Ranomafana (COI: JQ909382).

Family Gekkonidae
Subfamily Gekkoninae

Hemidactylus mercatorius Gray, 1842
Fig. 5A

This species is widely distributed in Madagascar, commonly found in human-dominated areas (Glaw and Vences 2007). *Hemidactylus mercatorius* was found at Iantaranomby, Ambalavao, Ambatomainty, Anja–Ambilo, Iarintsena, Sakaviro and Tsaranoro (Suppl. material 4: Table S4), in the western part of the Region (between ca. 930 and 1,580 m a.s.l.), mostly in human settlements and sometimes also within semi-arid deciduous forest. The individuals were normally found in nocturnal activity on rocks, despite one individual being sampled during the day in Ambalavao. The species was common in Tsaranoro. The analysed samples show limited genetic differentiation (Suppl. material 6: Table S6). To the best of our knowledge, the population from Isalo is genetically the closest to the samples analysed here (ca. 2.70%, MH063351).

Lygodactylus pictus (Peters, 1883)
Fig. 5B

This diurnal gecko is known from south-eastern Madagascar and a few other localities in the central highlands. It is commonly found in degraded and secondary forest patches and in human-dominated environments. The Andringitra Massif and the surrounding areas are at the southern limit of the distributional range of the species (Puente et al. 2005; Glaw and Vences 2007). We sampled *Lygodactylus pictus* in degraded and secondary forest at Asaramanitra, Belambo, Fivahona–Ambavanala and Tsaranoro, both in the eastern and western parts of the surveyed region and in the town of Ambalavao at an elevational range between ca. 970 and 1,610 m a.s.l. (Suppl. material 4: Table S4). This gecko was mostly found in human-associated environments (e.g. roofs, houses) and only rarely on tree trunks. The individuals were mostly found active during the day, despite two being spotted at night, probably sleeping. The species was common in Belambo, while it seemed rarer in the other sites. The analysed samples are genetically homogeneous (COI, Suppl. material 6: Table S6) and almost identical to an individual from Ambositra (JQ909452, COI). There is some genetic difference (in 16S) between the individuals collected in Tsaranoro and Fivahona–Ambavanala. The sample from Tsaranoro (ACZC10950) is ca. 1% distant (16S) from an
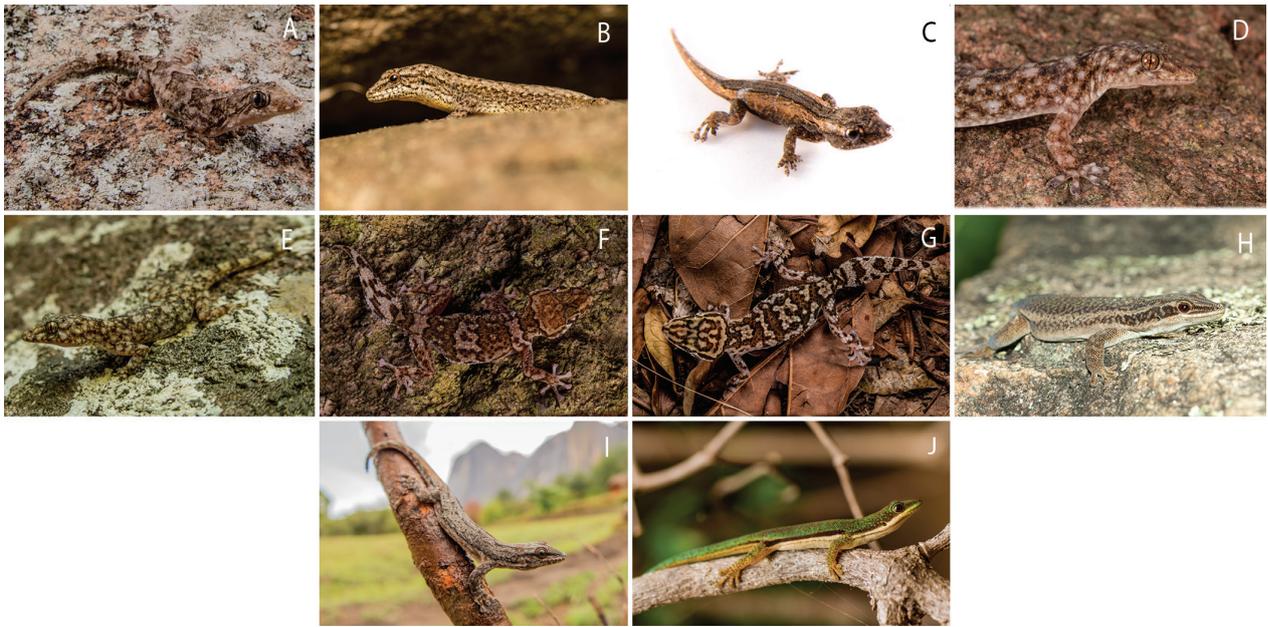
Figure 5. Geckos species identified in this study. Sampling localities for each photographed individual are indicated. **ANP ES** – Andringitra National Park Eastern Slopes; **ANP WS** – Andringitra National Park Western Slopes (Fig. 1; Suppl. material 1: Table S1). **A.** *Hemidactylus mercatorius* from Tsaranoro; **B.** *Lygodactylus pictus* from Belambo (ANP ES); **C.** *Lygodactylus* sp. aff. *pictus* Ca01 "Isalo" from Ambatomainty; **D.** *Paragehyra felicitae* from Anja; **E.** *Paragehyra* sp. aff. *felicitae* "Tsaranoro" from Tsaranoro; **F.** *Paroedura rennerae* from Anja; **G.** *Paroedura* sp. aff. *bastardi* Lineage D from Anja; **H.** *Phelsuma barbouri* from Belambo (ANP ES); **I.** *Phelsuma gouldi* from Tsaranoro; **J.** *Phelsuma lineata elanthana* from Fivahona–Velotsoa. Photographs by Javier Lobón-Rovira (A–G, I–J) and Gonçalo M. Rosa (H).

individual from Ambositra (AY653269), while the sample from Fivahona–Ambavanala (ACZC11175) is identical (16S) with two individuals of *L. pictus* from Ambositra (GU593455) and Sendrisoa (AY653270), a locality only ca. 6 km away from Fivahona–Ambavanala.

Lygodactylus sp. aff. *pictus* Ca01 "Isalo" UCS
Fig. 5C

We sampled a juvenile within the semi-arid deciduous forest of Ambatomainty (ca. 970 m a.s.l.) (Suppl. material 4: Table S4). The collected individual was found at night on a rock along a trail. This sample shows limited genetic distance from an individual collected at Analalava forest in Isalo (16S: 2.7%, AY653238; COI: 4.50%, JQ909445). The new record significantly extends the known distributional range of this taxon by ca. 180 km towards the east from the Isalo Massif.

Paragehyra felicitae Crottini, Harris, Miralles, Glaw, Jenkins, Randrianantoandro, Bauer & Vences, 2015
Fig. 5D

This gecko was known only from Anja Community Reserve and from a site a few km away from Anja. This species can be observed on granitic boulders associated with both semi-arid deciduous forest and grasslands. Even though the other geckos of the genus *Paragehyra*

are nocturnal, these animals can also be spotted during the day (Crottini et al. 2015). We sampled this species in Anja and Sakaviro, the latter record representing a distributional range extension (ca. 8 km). The collected samples were active at night on granitic boulders and rocks within semi-arid deciduous forest, sometimes in clearings within the forest, at ca. 950–990 m a.s.l. (Suppl. material 4: Table S4). The species was present in high densities in both sites. Collected samples show some genetic differentiation at the COI fragment (Suppl. material 6: Table S6) and they are almost identical (16S) to individuals from Anja (e.g. KP025816).

Paragehyra sp. aff. *felicitae* "Tsaranoro" CCS
Fig. 5E

This taxon was collected at Iantaranomby, Ambatomainty and Tsaranoro, all localities in the western part of the surveyed region (between ca. 910 and 1,610 m a.s.l.) (Suppl. material 4: Table S4). Animals were found active at night on granitic boulders both in open habitats and semi-arid deciduous forest. The species was particularly abundant in Tsaranoro and, to a less extent, in Ambatomainty, whereas only one individual was sampled in Iantaranomby. The analysed samples show limited genetic differentiation amongst sampled localities (Suppl. material 6: Table S6). The genetic distance between this taxon and *P. felicitae* sampled in Anja is ca. 15% (COI:

ACZC10432) and 7.6% (16S: KP025811), while it has 17% genetic difference with *Paragehyra petiti* Angel, 1929 (COI: JQ909497). This taxon is morphologically similar to *P. felicitae*. However, the analysis of the collected specimens highlighted the presence of a distinct number of longitudinal rows of enlarged turbercles on the dorsolateral surfaces of the body relative to the sister species *P. felicitae* (which is a morphological diagnostic character of this species), confirming its distinction also at the morphological level and determining the status of confirmed candidate species. The description of this candidate species is currently in progress.

Paroedura rennerae Miralles, Bruy, Crottini, Rakotoarison, Ratsoavina, Scherz, Schmidt, Köhler, Glaw & Vences, 2021
Fig. 5F

The *Paroedura bastardi* (Mocquard, 1900) species complex has been recently revised (Miralles et al. 2021). This work identified at least three evolutionary lineages within this species group. Following this finding, the authors propose a new definition for *P. bastardi* sensu stricto. They resurrected the binomen *Paroedura guibeae* Dixon & Kroll, 1974 and formally described a third lineage as *P. rennerae*. The latter species is currently known from Miandrivazo, Kirindy, Marofandilia, Anja and Isalo. We sampled this gecko at Ambatomainty, Anja, Sakaviro and Tsaranoro, all sites in the western part of the surveyed region (at ca. 930–990 m a.s.l.) (Suppl. material 4: Table S4), extending the known distribution of this species by ca. 25 km towards the south from Anja. This species was abundant in all visited sites. The animals were always found active at night on boulders, mostly within semi-arid deciduous forest, but sometimes also at the edge of the forest and in human settlements. The collected samples are molecularly uniform (Suppl. material 6: Table S6) and almost identical to an individual collected from Anja (COI: MG734947). They are slightly differentiated from conspecific populations from other localities (COI: 2.60%, MG734948, Kirindy; 16S: 1.4%, GU128989, Miandrivazo; 1.8%, GU129005, Marofandilia).

Paroedura sp. aff. *bastardi* Lineage D UCS
Fig. 5G

Individuals belonging to this lineage of the *P. bastardi* species complex were previously known only from Anja (Miralles et al. 2021). We collected this taxon at Anja and Tsaranoro, in the western part of the Region (at ca. 930–970 m a.s.l.), extending the distributional range by ca. 25 km towards the south (Suppl. material 4: Table S4). In both sites, this lineage was found in syntopy with *Paroedura rennerae*, which is very similar in morphology, and in high densities The individuals were found active at night on boulders within semi-arid deciduous forest and show a limited degree of genetic differentiation (Suppl. mate-

rial 6: Table S6). The collected samples are almost 100% identical to ZCMV 12790 (COI: MW311368), which is the only individual molecularly characterised for this taxon before our study (Miralles et al. 2021).

Phelsuma barbouri Loveridge, 1942
Fig. 5H

This diurnal gecko is known from a few montane areas on the central highlands and in south-eastern Madagascar. The area of Andringitra represents the southern limit of its distributional range. Unlike most *Phelsuma* geckos, which are arboreal, this species is normally found in montane rocky habitats on the ground and boulders (Glaw and Vences 2007; Goodman et al. 2018). We sampled a single individual of *Phelsuma barbouri* active during the day on a small wooden bridge at Belambo in the eastern slopes of the Massif, at ca. 1,570 m a.s.l. (Suppl. material 4: Table S4). This sample is 96% similar to a conspecific individual from Tsiafajavona (Ankaratra) (COI: JQ909518).

Phelsuma gouldi Crottini, Gehring, Glaw, Harris, Lima & Vences, 2011
Fig. 5I

This species was reliably known only from Anja, where a single individual (the holotype) was spotted on a trunk within the forest patch of the Reserve (Crottini et al. 2011b). The species is confirmed to be quite rare. Two individuals were sampled at night on lianas in the semi-arid deciduous forest of Tsaranoro, in the western part of the Region, at an elevation range of ca. 910–950 m a.s.l. (Suppl. material 4: Table S4). This finding extends the known distributional range of the species by ca. 25 km to the south. The two analysed samples are identical to each other (Suppl. material 6: Table S6) and identical to the holotype (16S: JF810252).

Phelsuma lineata elanthana Krüger, 1996
Fig. 5J

Phelsuma lineata elanthana is distributed in the central highlands and the northern part of central-eastern Madagascar (Boumans et al. 2007; Gehring et al. 2013). It inhabits a great variety of habitats, from the rainforest to bushes in more arid areas and it is also commonly found in human settlements (Glaw and Vences 2007). This gecko was rare. We sampled *P. lineata* only in Fivahona–Velotsoa, in the eastern part of the Region (at ca. 1,290 m a.s.l.), where the animals were found active during the day on *Pandanus* trees within the rainforest (Suppl. material 4: Table S4). This record represents a range extension for this taxon by ca. 350 km towards the south. The analysed samples show a 3% genetic distance (16S) from samples from Andasibe (EF210615) and Ambohitantely (EF210617).

Family Gerrhosauridae
Subfamily Zonosaurinae

***Zonosaurus aeneus* (Grandidier, 1872)**
Fig. 6E

This species is distributed at a wide latitudinal range between the central highlands and the eastern and south-eastern escarpment. It is typically found on the edges of rainforest or in open areas within forest (Glaw and Vences 2007). *Zonosaurus aeneus* was previously reported from Andringitra (Goodman et al. 2018) and was found at Fivahona–Ambavanala and Namoly, in the eastern part of the studied region (between ca. 1,480 and 1,650 m a.s.l.). *Zonosaurus aeneus* was sampled during the day. The animals were active on the ground in grassy clearings inside rainforest and in open areas immediately next to rainforest patches. One individual was found next to a ricefield (Suppl. material 4: Table S4). The analysed individuals are identical (Suppl. material 6: Table S6) and they show a 3.3% genetic distance from a sequenced individual from Ranomafana (COI: JQ909624) and a 1.5% genetic distance from individuals from Torotorofotsy (16S: KC515131).

***Zonosaurus laticaudatus* (Grandidier, 1869)**
Fig. 6C

This large plated lizard lives over a wide latitudinal range throughout western Madagascar (Glaw and Vences 2007). This species is reported from dry forest, rocky open areas, degraded and human-disturbed habitats (Glaw and Vences 2007; Recknagel et al. 2013). This taxon was not previously reported from the area of Andringitra and was collected at Ambatomainty, Anja and Tsaranoro, all localities in the western part of the Region (between ca. 870 and 960 m a.s.l.) (Suppl. material 4: Table S4). This record extends the known distributional range of the species by ca. 180 km to the East. The individuals were found both in open areas on rocky substrate and on large boulders next to semi-arid deciduous forest patches. They were active during the day. Analysed samples show 2.2% genetic distance from the population of Isalo (e.g. COI: MH063372) and 1% genetic distance from the population of Hazofotsy, close to Tolagnaro (16S: AY167372).

***Zonosaurus ornatus* (Gray, 1831)**
Fig. 6D

This species is found in central-eastern Madagascar where it inhabits open habitats and forest edges at a wide elevational range. In Ankaratra and Andringitra, this species is found in montane savannah and heathlands above the tree line (Glaw and Vences 2007; Goodman et al. 2018). We sampled *Zonosaurus ornatus* at Antanifotsy 2, Fivahona–Ambavanala and Namoly, in the eastern part of the Region (between ca. 1,450 and 1,650 m a.s.l.) in open environments next to rainforest, often in human-disturbed areas (Suppl. material 4: Table S4). One of the individuals was spotted next to a ricefield. The animals were all active during the day. The analysed samples are identical (Suppl. material 6: Table S6) and show a 2.3% genetic distance from individuals from Ambatolahy (e.g. COI: JQ909633). However, the population from Ambatolahy is almost identical at the 16S marker (e.g. KC515145).

Family Opluridae

***Oplurus grandidieri* Mocquard, 1900**
Fig. 6A

This species is distributed in the south-central part of the central highlands where it is often found in rocky environments (Glaw and Vences 2007). We found this species at Andramena, Iantaranomby, Siranandambo, Ambatomainty, Anja, Sakaviro and Tsaranoro in the western portion of the studied area (Suppl. material 4: Table S4). The animals were normally found in high densities on boulders and outcrops at an elevation range between ca. 930 and 1,740 m a.s.l. They were all active during the day. The analysed samples show a limited degree of genetic differentiation (Suppl. material 6: Table S6) and low genetic distance to the population from Isalo (COI: 3.5%, MH063380; 16S: 3.2%, MH063315). In Iantaranomby, two adult males were observed displaying an aggressive interaction on a sunny boulder (Lobón-Rovira et al. 2019).

***Oplurus quadrimaculatus* Duméril & Bibron, 1851**
Fig. 6B

Oplurus quadrimaculatus is distributed in the south and the south-eastern part of the central highlands, including the area of Andringitra (Glaw and Vences 2007; Münchenberg et al. 2008). It was also recently identified at Isalo (Cocca et al. 2018). *Oplurus quadrimaculatus* is a saxicolous species, normally observed on large boulders within arid environments and, in some cases, also next to forest patches. We found this species at Andramena, Asaramanitra, Imaitso, Ambatomainty, Anja, Fivahona–Velotsoa, Sakaviro and Tsaranoro in both the eastern and western parts of the surveyed area (Suppl. material 4: Table S4). The animals were present in high densities and active during the day on large boulders and outcrops both in open and forested areas at an elevation between ca. 870 and 1,740 m a.s.l. Within forest, they were normally spotted in rocky clearings or next to large streams delimited by outcrops. *Oplurus quadrimaculatus* was sometimes found in syntopy with *O. grandidieri* and, in some cases, the two species shared the same rocks. Analysed samples show limited genetic differentiation among them (Suppl. material 6: Table S6) and in relation to other individuals collected in the Andringitra Region (e.g. 16S: EU099752). They show a 4.4% genetic distance from the population from Andohahela (COI: JQ909486) and no differentiation from the population from Antoetra (e.g. 16S: EU099737) and Ambositra (16S: EU099742).
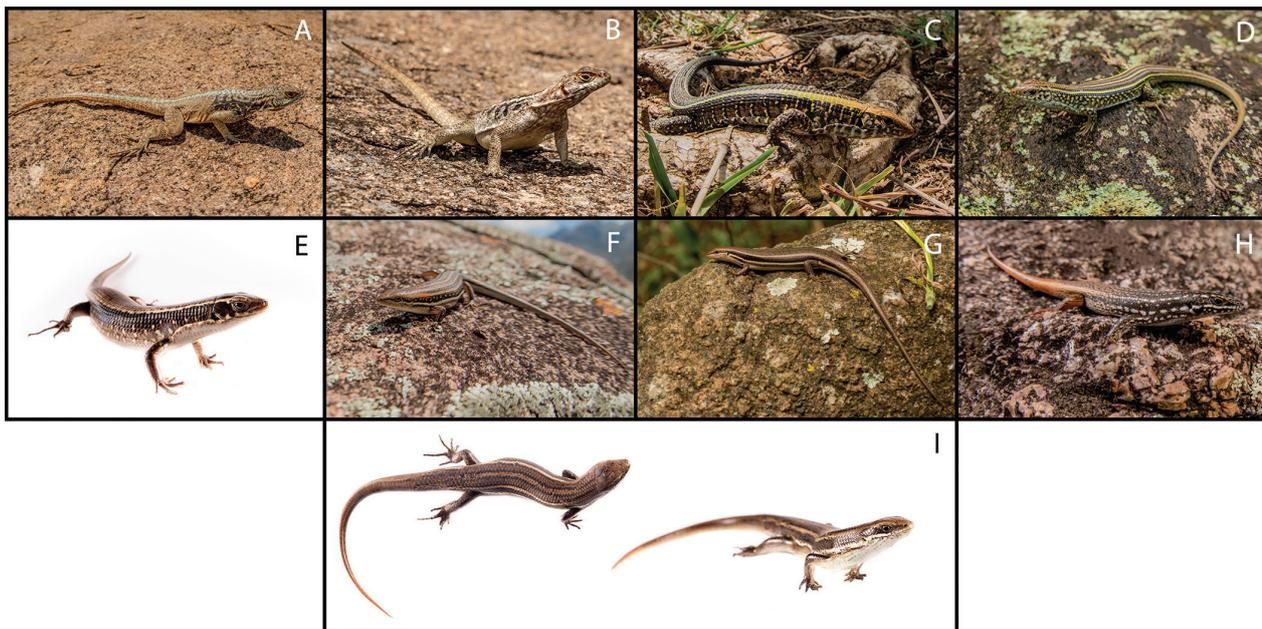
Figure 6. Scincid, gerrhosaurid and oplurid species identified in this study. Sampling localities for each photographed individual are provided. **ANP ES** – Andringitra National Park Eastern Slopes; **ANP WS** – Andringitra National Park Western Slopes (Fig. 1; Suppl. material 1: Table S1). **A.** *Oplurus grandidieri* from Anja; **B.** *Oplurus quadrimaculatus* from Anja; **C.** *Zonosaurus laticaudatus* from Anja; **D.** *Zonosaurus ornatus* from Antanifotsy 2; **E.** *Zonosaurus aeneus* from Namoly; **F.** *Trachylepis elegans* from Iantaranomby (ANP WS); **G.** *Trachylepis gravenhorstii* from Anja; **H.** *Trachylepis* sp. aff. *vato* from Asaramanitra (ANP ES); **I.** *Trachylepis boettgeri* from Antanifotsy 3. Photographs by Javier Lobón-Rovira.

Family Scincidae
Subfamily Mabuyinae

Trachylepis boettgeri **(Boulenger, 1887)**
Fig. 6I

Trachylepis boettgeri is found in central-eastern Madagascar where it inhabits the open habitats of the central highlands, including the Region of Andringitra (Goodman et al. 2018). We sampled one individual at Antanifotsy 3, in an area dominated by grasslands and rice fields in the eastern part of the Region at ca. 1,440 m a.s.l. (Suppl. material 4: Table S4). The animal was active on the ground during the day. The analysed sample is genetically almost identical to a population from Ankaratra (COI: JQ909591; 16S: DQ238879) and Ambatolampy (16S: AY070355).

Trachylepis elegans **(Peters, 1854) Lineage A**
Fig. 6F

This skink is distributed throughout Madagascar, except for the eastern escarpment (Glaw and Vences 2007). It mostly inhabits open habitats in both dry and humid environments and can be found in cities and other human-dominated environments (Glaw and Vences 2007; Vences et al. 2014). We found this taxon in high densities at Iantaranomby, Ambalavao, Ambatomainty, Anja–Ambilo and Fivahona–Velotsoa (in the western part of the surveyed region) and in Antanifotsy 4 (in the eastern) be-

tween ca. 830 and 1,670 m a.s.l. (Suppl. material 4: Table S4). All individuals were found in grassy open areas, sometimes next to small boulders, either close to forest patches or in human-dominated areas. They were found active during the day. The analysed samples show a limited degree of genetic differentiation (Suppl. material 6: Table S6) and they show a 2% genetic distance from the population of Isalo (e.g. COI: KF250670) attributed to lineage A (sensu Vences et al. 2014), which is the most widespread lineage in Madagascar.

Trachylepis gravenhorstii **(Duméril & Bibron, 1839)**
Lineage 4A
Fig. 6G

Trachylepis gravenhorstii is found almost everywhere in Madagascar up to 1,400 m a.s.l. (Glaw and Vences 2007; Vences et al. 2014; Goodman et al. 2018). We sampled this taxon at Belambo, Iantaranomby, Riandahy and Anja, in both the eastern and western part of the Region at an elevation between ca. 960 and 1,640 m a.s.l. (Suppl. material 4: Table S4). *Trachylepis gravenhorstii* was often found in syntopy with *T. elegans*, although less common than the latter species. Where *T. elegans* was not present, *T. gravenhorstii* was found in less human-disturbed habitats. The individuals were sampled during the day, both in grassy open areas with presence of small boulders and within forest active on the ground. The analysed samples show some degree of intra-populational variability

(Suppl. material 6: Table S6) and are identical to a sample collected at Ranomafana (COI: KF250703) attributed to lineage 4A (sensu Vences et al. 2014) distributed in central-eastern Madagascar. Previously available data of this species from the area (Ambalavao) belong to the lineage 4B (COI: KF250708). As previously reported for Isalo (Cocca et al. 2018), it seems that these two lineages occur sympatrically in the surveyed area.

Trachylepis sp. aff. *vato* UCS
Fig. 6H

Trachylepis vato (Nussbaum & Raxworthy, 1994) is distributed in central and southern Madagascar where it inhabits arid environments with boulders and rocks (Glaw and Vences 2007). It was described from a locality close to Andohahela (Type locality: Mananara River between Bevia and Hazofotsy, 24°51.00'S, 46°31.00'E), in south-eastern Madagascar (Nussbaum and Raxworthy 1994). We collected this lineage at Asaramanitra, Iantaranomby, Anja, Fivahona–Velotsoa, Iarintsena and Sakaviro, both in the eastern and western parts of the surveyed region (between ca. 990 and 1,660 m a.s.l.), mostly on boulders, both in open environments and within forest (Suppl. material 4: Table S4). The animals were all active during the day. This skink was not common in the sampling sites we visited. These records represent a slight range extension within the area of Andringitra. Lima et al. (2013) assigned individuals from Ambalavao (16S: KC345435; ND1: KC345095), Andringitra (16S: KC345394; ND1: KC345053) and Col des Tapias (16S: KC345432; ND1: KC345092) to a candidate species *T.* cf. *vato*. Our samples show some sign of genetic differentiation (Suppl. material 6: Table S6) and the genetic distance between our samples and the samples of *T.* cf. *vato* included in Lima et al. (2013) is between 1% and 2.3% (ND1: KC345092, KC345053, KC345095). Our samples are also almost identical to individuals from Ibity (16S: AY159097), close to Col des Tapias.

Family Psammophiidae

Mimophis mahfalensis (Grandidier, 1867)
Fig. 7G

This snake is widely distributed across almost all of the southern half of Madagascar, where it can be found in rainforest, dry forest, arid spiny thornbush savannah and human-dominated areas (Glaw and Vences 2007; Ruane et al. 2017). We sampled this species at Iakanga, Anja, Fivahona–Velotsoa and Sakaviro, both in the western and eastern parts of the surveyed area, at an elevation between ca. 900 and 1,270 m a.s.l. (Suppl. material 4: Table S4). The animals were found during the day active on the ground in a wide variety of habitats: rainforest, semi-arid deciduous forest and grassland. The analysed samples are molecularly similar to each other (Suppl. material 6: Table S6) and 0.8% distant (COI) to the population from

Ibity (JQ909481) and Isalo (MH063403). The individual collected at Fivahona–Velotsoa was found with a *Furcifer willsii* chameleon (ACZC11200) in its stomach (Lobón-Rovira et al. 2020).

Family Pseudoxyrhophiidae

Compsophis infralineatus (Günther, 1882)
Fig. 7A

This semi-arboreal snake is distributed in eastern and south-eastern Madagascar where it is normally found along ponds and small streams (Glaw and Vences 2007). *Compsophis infralineatus* was already reported from Andringitra (Goodman et al. 2018). Two individuals were found at night in Fivahona–Velotsoa and Namoly, in the eastern part of the Region, within the rainforest at an elevational range of ca. 1,270–1,640 m a.s.l. (Suppl. material 4: Table S4). In Fivahona–Velotsoa, this snake was found active on the ground along the banks of a small stream. The analysed individuals are genetically identical amongst each other (Suppl. material 6: Table S6) and they are ca. 1% distant (COI) from the population from Manjakatompo (e.g. JQ909355).

Leioheterodon modestus (Günther, 1863)
Fig. 7B

This snake has a patchy distribution in central, western and southern Madagascar, where it is generally found in dry areas, both inside and outside the forest and in anthropogenic environments (Glaw and Vences 2007). This species has not yet been reported from the study area and we found it at Antanifotsy 1, Fivahona–Ambavanala and Fivahona–Velotsoa in the eastern part of the Region, contributing to the extension of its known distributional range by ca. 200 km towards the east. Two individuals were spotted during the day active on the ground close to rice fields and villages near forest patches at an elevational range between ca. 1,280 and 1,460 m a.s.l. (Suppl. material 4: Table S4). The analysed samples are genetically identical to each other (Suppl. material 6: Table S6) and 0.60 % distant to an individual collected at Zazafotsy (COI: MH063415).

Liophidium torquatum (Boulenger, 1888)
Fig. 7F

This terrestrial snake is distributed in eastern and northern Madagascar where it mostly inhabits rainforest, despite being also found in dry deciduous forest (Glaw and Vences 2007). This species is reported from Andringitra (Goodman et al. 2018) and we sampled a single individual inside the semi-arid deciduous forest fragment of Anja, in the western part of the surveyed region (at ca. 990 m a.s.l.) (Suppl. material 4: Table S4). The animal was active during the day. This sample is almost 100% identical to the population of *L. torquatum* from Ranomafana (Cytb: DQ979984).

Figure 7. Psammophiid, pseudoxyrhophiid and sanziniid snakes identified in this study. Sampling localities for each photographed individual are provided. **ANP ES** – Andringitra National Park Eastern Slopes; **ANP WS** – Andringitra National Park Western Slopes (Fig. 1; Suppl. material 1: Table S1). **A.** *Compsophis infralineatus* from Namoly; **B.** *Leioheterodon modestus* from Antanifotsy 1; **C.** *Madagascarophis meridionalis* from Anja; **D.** *Thamnosophis lateralis* from Anja; **E.** *Pseudoxyrhopus* sp. Ca2 from Ambatomainty; **F.** *Liophidium torquatum* from Anja **G.** *Mimophis mahfalensis* from Sakaviro; **H.** *Sanzinia* cf. *volontany* from Anja; **I.** *Acrantophis dumerili* from Sakaviro. Photographs by Javier Lobón-Rovira (A–E, G, I), Gonçalo M. Rosa (F) and Franco Andreone (H).

Madagascarophis meridionalis Domergue, 1987
Fig. 7C

This species inhabits arid environments in southern and south-western Madagascar (Glaw and Vences 2007). *Madagascarophis meridionalis* is known to inhabit the Andringitra Region (Nagy et al. 2007) and was sampled at Ambatomainty, Anja, Iantaranomby and Tsaranoro, in the western part of the Region at an elevation range between ca. 930 and 1,580 m a.s.l. (Suppl. material 4: Table S4). The animals were mostly found active on the ground in open areas next to semi-arid deciduous forest, sometimes along streams and in human-disturbed environments. They were mostly spotted at night, although one individual was found during the day. The analysed samples are genetically uniform (Suppl. material 6: Table S6). They are identical to a published sequence from the area (16S: AY586213) and almost identical to the population from Antoetra (16S: AY586212). They are 1% distant (COI) from the population from Andranovorivato (KU925345).

Pseudoxyrhopus sp. Ca2 UCS
Fig. 7E

This taxon was sampled in Ambatomainty, in the western part of the Region (at ca. 960 m a.s.l.) (Suppl. material 4: Table S4). The only collected individual was moving on the ground at night in an open area with a few scattered trees next to a small fragment of semi-arid deciduous forest. This specimen is genetically very similar (2.7% distance at COI) to a candidate species collected at Zombitse–Vohibasia National Park (RAN 43545–UMMZ 203648, Burbrink et al. 2019). Our finding extends the known distribution of this taxon by ca. 230 km to the north-east.

Thamnosophis lateralis (Duméril, Bibron & Duméril, 1854)
Fig. 7D

This is one of Madagascar's most common snakes (Glaw and Vences 2007), being mostly found outside dense forest and often in degraded areas (Vences 2011). We

sampled this species at Antanifotsy 3, Anja, Tsaranoro, Fivahona–Ambavanala and Fivahona–Velotsoa in both the western and eastern parts of the surveyed region at an elevation between ca. 930 and 1,480 m a.s.l. (Suppl. material 4: Table S4). We found this species active on the ground during the day, both within forest and in anthropogenic environments (next to ricefields). Analysed samples are genetically uniform (Suppl. material 6: Table S6) and show 1% distance from the population from Isalo (COI: MH063410).

Family Sanziniidae

Acrantophis dumerili Jan, 1860
Fig. 7I

Acrantophis dumerili is distributed in central and southern Madagascar where it inhabits dry forest, savannah, as well as open and cultivated areas (Glaw and Vences 2007). *Acrantophis dumerili* is reported from Ambalavao (Glaw and Vences 2007) and was sampled at Sakaviro and Vidia, in the western part of the surveyed region (at ca. 850–990 m a.s.l.) (Suppl. material 4: Table S4). While the specimen sampled in Sakaviro was found after dusk active on the ground at the edge of semi-arid deciduous forest, the other was found dead on the Route Nationale 7. The samples are identical to each other (Suppl. material 6: Table S6) and to an individual from an imprecise sampling locality (COI: JQ909244, "300 km from Tana") and the population from Ambositra (16S: AY336072). They are also almost identical to the population from Isalo (16S: EU419793).

Sanzinia cf. *volontany* Vences & Glaw, 2004
Fig. 7H

Following a recent taxonomic revision, the genus *Sanzinia* comprises two species, *Sanzinia volontany* and *S. madagascariensis* (Duméril & Bibron, 1844) (Reynolds et al. 2014). The two species are genetically divergent and show some degree of morphological differentiation in colouration and pholidosis (Vences and Glaw 2003; Orozco-terWengel et al. 2008; Reynolds et al. 2014). They are divergently distributed, with *S. madagascariensis* occurring in eastern Madagascar and *S. volontany* throughout the west. An individual of *Sanzinia* sp. was photographed at night in Anja while moving on the florest floor, in the western part of the Region, but no tissues were collected from that specimen (Suppl. material 4: Table S4). The analysis of the photographic material would lead to assign the individual to *S. volontany*, although the record requires further confirmation. *Sanzinia madagascariensis* is known from Ivohibe (Glaw and Vences 2007), whereas *S. volontany* from Isalo (Orozco-terWengel et al. 2008). Given the geographic proximity of these records and the presence of both rain and dry

forests in the Region, there is the possibility that both species inhabit this area.

Discussion

We provided the first list and barcoding reference database for 28 amphibians and 38 reptiles of the area surrounding the Andringitra Massif and extended the known distributional range of nine amphibians and twelve reptiles. Species composition is probably influenced by the environmental diversity of the Region (Goodman 1996; Goodman et al. 2018). Besides the several microendemics (*Boophis laurenti*, *Mantidactylus bourgati*, *Brookesia brunoi*, *Paragehyra felicitae*, *Paragehyra* sp. aff. *felicitae* "Tsaranoro", *Paroedura* sp. aff. *bastardi* Lineage D and *Phelsuma gouldi*), many taxa are distributed only in the eastern part dominated by rainforest (e.g. *Boophis ankaratra*, *B. boppa*, *B. majori*, *B. popi*, *B. rhodoscelis*, *Aglyptodactylus madagascariensis*, *Gephyromantis blanci*, *Mantidactylus delormei*, *Spinomantis elegans*, *Calumma crypticum*, *Phelsuma lineata*, *Zonosaurus ornatus* and *Compsophis infralineatus*), while others are only present in the western dry habitats (e.g. *Laliostoma labrosum*, *Mantella betsileo*, *Scaphiophryne calcarata*, *Heterixalus luteostriatus*, *Furcifer major* and *Madagascarophis meridionalis*) (Glaw and Vences 2007).

Surveyed sites are highly fragmented and embedded within a matrix of anthropogenically-modified landscape. Despite the likely loss in species richness and the alteration of species composition, forest fragments retain high levels of diversity in Madagascar (Crottini et al. 2011a; Durkin et al. 2011; Jenkins et al. 2014; Riemann et al. 2015). Such diversity can be irreplaceable when it includes microendemics. These species are reliably known only from a few geographically close localities, therefore fragments alteration and destruction may lead to their extinction. As already reported by Jenkins et al. (2014), Anja Community Reserve stands out at the national level for its multiple microendemic taxa and, in our sampling, Anja resulted as the most species-rich (24 species) amongst the surveyed fragments (Fig. 1A; Suppl. material 9: Table S7). Meaningful comparisons of the number of recorded species amongst sampling sites are hampered by the non-standardised sampling effort and the limited time spent in each locality, which was probably not enough to sample the actual total diversity. However, we can still notice an expected positive relationship between fragment area and species richness. We sampled 21 and 19 species in Tsaranoro and Fivahona–Velotsoa (Fig. 1G), respectively, the two largest fragments along with Anja. In the smallest patches, we found a lower number of species. In both Sakaviro and Ambatomainty (Fig. 1B and C), we found 14 species and, in Fivahona–Ambavanala, we recorded 12 species. Beyond species numbers, it is interesting to note that even the smallest fragments could host taxa that were

not detected in any other locality, some of which represent relevant range extensions. Ambatomainty is probably the most interesting example in this sense. In this highly degraded forest of only two hectares (Fig. 1C), we recorded two candidate new species: *Lygodactylus* sp. aff. *pictus* Ca01 "Isalo" and *Pseudoxyrhopus* sp. Ca2, to date reliably known only from a few other sites some hundreds of kilometres away (i.e. Isalo and Zombitse–Vohibasia National Parks, respectively).

Deforestation and habitat fragmentation are more pronounced in the western part of the surveyed region where, even within the National Park borders, the forest cover is reduced (Goodman 1996). The taxa that inhabit these fragments may not find large forests at a similar elevation within the Park and may consequently lack available legally protected habitat. These small forest fragments can thus play a fundamental role as refugia to the local herpetofauna. Their conservation should, therefore, be prioritised for the long-term survival of their unique herpetological diversity and, more in general, for the conservation of the biodiversity of the entire Region. Finally, the improved knowledge on the species distribution of the candidate taxa, identified in this study, will now likely enable their formal description (e.g. in the case of *Paragehyra* sp. aff. *felicitae* "Tsaranoro" and *Paroedura* sp. aff. *bastardi* Lineage D).

Conclusions

In a country plagued by centuries of forest loss and fragmentation (Hornac 1943; Jarosz 1993; Vieilledent et al. 2018), species inventories of remnant forest fragments are of paramount importance to achieve a better understanding of Malagasy biodiversity. We highlighted the herpetological significance of the small forest patches surrounding the Andringitra Massif, where we identified several taxa that were previously unknown from this area and, in several instances, we contributed to the extension of their known distributional ranges by hundreds of kilometres (e.g. Belluardo et al. 2021). Many of these taxa are candidate new species and the newly-collected specimens will enable future taxonomic evaluations and descriptions. We also identified one candidate species previously unknown to science and provided a better characterisation of the distribution of several microendemic species that inhabit the study area. We generated a first barcoding reference database for this area that will facilitate future systematic research, both at the regional and country level. These results emphasise the relevance of the Region of Andringitra in terms of microendemic diversity hosted in highly altered habitats. Apart from three private reserves managed by local communities, and despite their herpetological value, the other investigated fragments are not officially protected. Granting some legal protection to these sites is highly desirable to warrant the conservation of this unique biodiversity.

Acknowledgements

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Supplementary material 1

Table S1. Sampling localities visited in this study, with associated coordinates and elevation

Supplementary material 2

Table S2. Amplified genes, primers and PCR conditions used in this study

Supplementary material 3

Table S3. Amphibian samples identified in this study

Supplementary material 4

Table S4. Reptile samples identified in this study

Supplementary material 5

Table S5. Within taxa uncorrected p–distances (16S) of amphibian taxa identified in this study

Supplementary material 6

Table S6. Within taxa uncorrected p–distances (COI) of reptile taxa identified in this study

Supplementary material 7

Figure S1. Amphibians Neighbor joining tree of the 16S rRNA gene 3' terminus

Authors: Francesco Belluardo, Darwin Díaz Quirós, Javier Lobón-Rovira, Gonçalo M. Rosa, Malalatiana Rasoazanany, Franco Andreone, Angelica Crottini

Data type: phylogenetic tree

Explanation note: The tree was computed with MEGA X 10.0.5 (Kumar et al. 2018) setting 1000 bootstrap replicates. The evolutionary distances were computed with the Kimura 2–parameter method, and ambiguous positions were removed with the pairwise deletion option.

Link: https://doi.org/10.3897/zse.97.63936.suppl7

Supplementary material 8

Reptiles Neighbor joining tree of the cytochrome oxidase I gene

Authors: Francesco Belluardo, Darwin Díaz Quirós, Javier Lobón-Rovira, Gonçalo M. Rosa, Malalatiana Rasoazanany, Franco Andreone, Angelica Crottini

Data type: phylogenetic tree

Explanation note: The tree was computed with MEGA X 10.0.5 (Kumar et al. 2018) setting 1000 bootstrap replicates. The evolutionary distances were computed with the Kimura 2–parameter method, and ambiguous positions were removed with the pairwise deletion option.

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Table S7. Locality records of amphibian and reptile species identified in this study

Authors: Francesco Belluardo, Darwin Díaz Quirós, Javier Lobón-Rovira, Gonçalo M. Rosa, Malalatiana Rasoazanany, Franco Andreone, Angelica Crottini

Data type: occurrences

Explanation note: Species records from this study are marked with '+'. Records from previous publications are labelled with '*', and the source is reported in the column 'Reference'. Localities coordinates are available in Suppl. material 1: Table S1.

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