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Morphological variation and taxonomic reassessment of the endemic Malagasy blind snake family Xenotyphlopidae

(Serpentes, Scolecophidia)

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We present morphological data of nine recently collected *Xenotyphlops* specimens from the coastal region east of Antsiranana in northern Madagascar, and compare them with data of the three hitherto known individuals of the family Xenotyphlopidae (the two type specimens of *X. grandidieri* and the holotype of *X. mocquardi*). We assign the newly collected material to *X. grandidieri* because of a lack of convincing and constant morphological differences from the types of this species. Our results indicate that the morphological variability of *X. grandidieri* is greater than formerly known. DNA sequences of the cytochrome b gene provide no indication of the occurrence of more than one species of *Xenotyphlops* in the Baie de Sakalava area despite the morphological variation found in specimens from this site. Due to the absence of clear diagnostic characters we propose to consider *X. mocquardi* a junior synonym of *X. grandidieri* resulting in a monotypic genus *Xenotyphlops* and a monotypic family Xenotyphlopidae. This conclusion is supported by the distribution ranges of both taxa, which are in close geographic proximity. To protect this unique relict species as well as other presumed endemics classified as Critically Endangered by the IUCN we suggest establishing a littoral (coastal) nature reserve along the coast east and southeast of Antsiranana.

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Fig. 1. The three reptile species originally described by Mocquard (1905, 1906) which were re-discovered in syntopy at Baie de Sakalava in northern Madagascar after more than 100 years without records. *Xenotyphlops grandidieri* (pink), together with the two skink species *Paracontias minimus* (brown with longitudinal lines of dark spots) and *P. rothschildi* (beige with black flanks). Note the extruded bifid tongue of the *Xenotyphlops* individual below on the left side.

Introduction

The enigmatic Malagasy blind snake family Xenotyphlopidae Vidal et al., 2010 currently comprises the single genus *Xenotyphlops* Wallach & Ineich, 1996 with the two species *X. grandidieri* (Mocquard, 1905) and *X. mocquardi* Wallach, Mercurio & Andreone, 2007, both presumably endemic to the same general area in northern Madagascar (Wallach & Ineich 1996, Wallach et al. 2007a, Köhler et al. 2010). Within the worm-like snakes (Scolecophidia), Xenotyphlopidae is most closely related to the species-rich and almost globally distributed family Typhlopidae Merrem, 1820 (Vidal et al. 2010). Together with the Asian family Gerrhopilidae Vidal et al., 2010, these families belong to the superfamily Typhlopoidea (Vidal et al. 2010). Scolecophidians are non-venomous, burrowing, worm-like snakes. They are usually small-sized and characterized by reduced vision, reduced

head scales, a tube-like body-shape and pinkish or brownish colour (Vidal et al. 2010). Their diet consists of social insects (ants and termites) and their larvae. A specialized feeding mechanism enables them to ingest a great number of prey items within a short amount of time (Kley & Brainerd 1999). The biogeographic pattern of this group is characterized by major vicariance events, such as the break-up of Gondwana and the split between India and Madagascar that might have promoted the diversification of major lineages (Vidal et al. 2010).

Considering the almost cosmopolitan distribution and species richness of the family Typhlopidae, the blind snake fauna of Madagascar appears relatively species-poor currently consisting of the three genera *Ramphotyphlops* Fitzinger, 1843 (one species), *Typhlops* Oppel, 1811 (11 species) and *Xenotyphlops* (two species). Since 1980, only three new species of Malagasy blind snakes have been described (*Xenotyphlops moc-*



Fig. 2. *Xenotyphlops grandidieri* in life: a. dorsolateral view; b. lateral view of head; c. ventral view of head.

quardi, *Typhlops rajeryi* Renoult & Raselimanana, 2009 and *Typhlops andasibensis* Wallach & Glaw, 2009), all discovered opportunistically rather than in the framework of a comprehensive revisionary work. With the exception of the probably introduced and parthenogenetic *Ramphotyphlops braminus* (Daudin, 1803), all Malagasy blind snake species are endemic to the island and occur in a wide variety of habitats, from xeric savanna at the coast to deciduous forest and rainforest at lower and mid-altitudes (Wallach

& Glaw 2009). Most of the species are known from few localities only. Although recent herpetological surveys have attempted to increase the records using pitfalls and targeted digging, blind snakes frequently remain undetected (Andreone et al. 2003). It is thus not surprising that ecological knowledge about these snakes is very incomplete and that the diversity of Malagasy blind snakes is presumably underestimated.

Until recently, both species of the genus *Xeno-*

typhlops were only known from their type specimens. In the beginning of the 20th century, the French zoologist François Mocquard described three species of reptiles with the imprecise type locality information “Madagascar”. The type specimens originated from the collection of Maurice de Rothschild and were donated to the Muséum National d’Histoire Naturelle, Paris (MNHN). The species described by Mocquard (1905, 1906) were the two limbless skinks *Paracontias minimus* (Mocquard, 1906) and *Paracontias rothschildi* Mocquard, 1905 and the typhlopoid snake *Xenotyphlops grandidieri* (Mocquard, 1905) (Fig. 1). Since none of the three species was rediscovered their status remained enigmatic and even their Malagasy origin was doubted (Brygoo 1981). The type specimens remained the only representatives known for the species for more than a century, until we collected all three of Mocquard’s taxa at the same locality within the same habitat, thus confirming their Malagasy origin (Köhler et al. 2010). Several years before, Wallach & Ineich (1996) had noticed the morphological uniqueness of the unusual blind snake *Typhlops grandidieri* and erected the genus *Xenotyphlops* for it. Wallach et al. (2007a) have rediscovered the genus based on a single specimen from northern Madagascar which they assigned to a new species, *X. mocquardi*, based on differences in morphological and anatomical characters to *X. grandidieri*.

Recently, a molecular phylogeny of the Scolecophidia suggested a Cretaceous split between the genus *Xenotyphlops* and its sister group, the family Typhlopidae (Vidal et al. 2010). This phylogenetic position of *Xenotyphlops* was not reflected in a DNA barcoding approach of Malagasy reptiles (Nagy et al. 2012), probably because the different Malagasy *Typhlops* lineages show deep mitochondrial divergences as well.

In general appearance, *Xenotyphlops* are purple to pinkish coloured, thin, medium-sized blind snakes (snout-vent length 163–276 mm), with a strongly pointed rostral scale and complete lack of eyes (Fig. 2). *Xenotyphlops* is unique in having a large, circular and nearly vertical rostral, and a single anal shield. Internally, it lacks a tracheal lung, has a type G foramen in the right bronchus, an anteriorly positioned heart and a large heart-liver gap (Wallach & Ineich 1996, Wallach et al. 2007a).

The new material collected by us in the far north of Madagascar allowed for the first time to examine morphological and molecular variation of *Xenotyphlops* based on an adequate number of specimens. The present study aims to reexamine the specific status of *X. mocquardi* using nine recently collected specimens, and the holotype of *X. mocquardi*.

Material and methods

Specimens were euthanized and preserved in 75 % ethanol after sampling tissue for potential DNA extraction. All studied specimens are stored in the Zoologische Staatssammlung München (ZSM), Germany. Additionally, we examined the holotype of *X. mocquardi* (MRSN R3208), stored in Museo Regionale di Scienze Naturali Torino (MRSN). The type material of *X. grandidieri* (MNHN 1905.271 and MNHN 1905.272), stored in the MNHN, and several additional specimens of *Xenotyphlops*, all collected by us around the Baie de Sakalava in 2007 and 2008 and stored in the Université d’Antananarivo, Département de Biologie Animale (UADBA) were not available for this study.

All measurements and scale counts were taken by J. E. Wegener and all drawings of head scales were made by S. Swoboda. Snout-vent length (SVL) was measured from the tip of the snout to the anterior end of the cloaca, measured with a ruler, to the nearest 0.5 mm. Measurements were taken twice and the mean value for SVL was calculated. Scale counts and drawings were made under a stereo-microscope. *Xenotyphlops* has smooth, unpigmented, small scales (<1 mm) that make counting of scales and drawing extremely challenging and we therefore used commercial highlighter to stain body and head scales temporarily. Middorsal scales were counted between the rostral and the posterior apical scale; longitudinal scale rows (around body) were counted anteriorly at level of the 20th midventral posterior to the mental, at midbody and posteriorly at the 10th scale anterior to the anal shield.

Head shields were examined using a stereo-microscope and illustrated with drawings of the ventral, dorsal and lateral (right side of the animal) aspects, following Wallach (1993), Wallach & Ineich (1996) and Wallach et al. (2007a) for nomenclature. We dissected one specimen (ZSM 2214/2007) to examine major visceral characters and to compare them with the holotype of *X. mocquardi*, which had been already dissected by Wallach et al. (2007a).

Eight of the nine newly collected and studied specimens (ZSM 2075/2007, ZSM 2193/2007, ZSM 2194/2007, ZSM 2213/2007, ZSM 2214/2007, ZSM 2215/2007, ZSM 2216/2007 and ZSM 2217/2007) were captured in and around the Baie de Sakalava (12°16'24" S, 49°23'33" E, 11 m a.s.l.) near Ramena, about 10 km eastwards of Antsiranana in northern Madagascar. ZSM 1594/2008 was collected 1.6 km southeast of Iovona (12°19'58.3" S, 49°24'19.5" E, 5 m a.s.l.), located 14 km southeast of Antsiranana, not far from the type locality of *X. mocquardi* (Fig. 3).

DNA was extracted from tissue samples of ten *Xenotyphlops* specimens using standard protocols. A fragment of the mitochondrial cytochrome b gene was amplified using primers CB-Typh1F (CTGAAAAAY-CACCGTTGTTATCAACTA) and CB-Typh1R (CTYTGGTTACAARAACARTGCTTT) and sequenced (both strands) on an Applied Biosystems 3730XL automated sequencer. Mega 5.0 (Tamura et al. 2011) was used to

check chromatograms, correct scoring errors, and create final alignments. Because of the relatively low variation among all sequences obtained we refrained from building a phylogenetic tree but rather describe the observed differences in the text below. All newly determined sequences were submitted to GenBank (accession numbers KF770842-KF770851).

Results

New records of *Xenotyphlops*: distribution, habitat and conservation status

During our field surveys in 2007 and 2008, we recorded specimens of *Xenotyphlops* at two coastal localities, Baie de Sakalava and 1.6 km southeast of Iovovona with a distance of ca. 6.5 km between them. The type locality of *X. mocquardi* (Ambodivahibe, corrected coordinates: 12°23'25" S, 49°26'20" E, ca. 40 m a.s.l.) is further 7 km south of the locality near Iovovona. These three localities are within 1 km distance from the coastline and obviously belong to the same littoral (coastal) habitat type without any obvious biogeographic barrier between them, and we therefore (Glaw & Vences 2007) first assigned the newly collected specimens to *X. mocquardi*. Our *Xenotyphlops* specimens were found at both localities in syntopy with the two historically described limbless skinks (*Paracontias rothschildi* and *P. minimus*) from the Rothschild collection, which all have the imprecise type locality "Madagascar". The rediscovery of all three species in this region suggests that the historical specimens were collected together in this area as well (see also Köhler et al. 2010). New evidence shows that the Rothschild collection actually included material from the Orangea region. In a revision of Malagasy stick insects Hennemann & Conle (2004: 11) listed a female specimen of *Achrioptera fallax* from the MNHN collection with the origin "Madagascar, Prov. d'Orangéa, Maurice de Rothschild, 1905", providing further evidence that also the types of *Xenotyphlops grandidieri* and the two *Paracontias* species were collected in this region.

An additional record of *X. grandidieri* from the Ampombofofo region north of the Antsiranana bay (*Xenotyphlops* locality probably 12°05'58" S, 49°20'20" E) was published by Megson et al. (2009) although a voucher specimen was apparently not collected at this locality. The known distribution range of the genus *Xenotyphlops* thus comprises a narrow coastal band of approximately 34 km length and an elevational range of 5 to approximately 40 m a.s.l. Although the actual range of these relict snakes might extend further north and south of the known localities, it is likely to be endemic to a nar-



Fig. 3. Map of northern Madagascar showing known localities of *Xenotyphlops grandidieri* (△) and the type locality of *X. mocquardi* (○).

row coastal band in the north of the island and it is not known from any protected areas.

The first specimen collected by us (ZSM 2075/2007) was discovered on a coastal dune when turning a piece of wood in the sand. Most other specimens were collected by local people who frequently encountered the species while digging for a special type of tuber for consumption. ZSM 1594/2008 was found when digging by hand in a depth of approximately 30 cm in fine, compact, and slightly humid sand below a thin layer of organic material (detritus, fallen leaves) close to a bush in scrub forest. Another individual (deposited in UADBA) was trapped in a pitfall line in the Orangea forest some 400–500 m inland from the Baie de Sakalava. All *Xenotyphlops* localities known to us are on fixed dunes of reddish fine sand, covered by very dense scrub forest (littoral forest sensu de Gouvenain & Silander 2003). Due to the presence of narrow foot paths all localities are semi-open with stretches of bare sand only along the paths. We visited the area only during the rainy season and found the soil and the organic layer always being slightly humid.

At Baie de Sakalava and near Iovovona, *Xenotyphlops* and the skinks *Paracontias minimus* and *P. rothschildi* were found in close syntopy within the

same square meters of soil. However, in contrast to the *Xenotyphlops* specimens, the skinks were always found close to the surface, within or near to the thin organic layer.

We observed strong destructive human impact especially in the coastal parts of the Orangea forest where *Xenotyphlops* occurs, including charcoal production, logging for timber and intensive zebu grazing. Less human impact was observed near Ifovona. We could not make any observations on the reproduction and diet of these snakes.

Morphological variation

Examination of the specimens available to us, most of which were newly collected from the same population at the Baie de Sakalava, revealed that the number of longitudinal scale rows around the body is more variable than previously suggested by Wallach et al. (2007a). As will be shown in the following, other major characters used to distinguish *X. mocquardi* and *X. grandidieri* were found to be highly similar in both taxa. We will here focus explicitly on the seven characters that were used by Wallach et al. (2007a) to distinguish between the two species. Data of five external characters are summarized in Table 1, and major head scale characters are shown in Figure 4. In addition we tried to verify the two major characters of internal anatomy as well.

(1) Direction of the anterior rostral point: Wallach et al. (2007a) used the anterior rostral point as character to differentiate *X. grandidieri*, which has an anteriorly directed anterior rostral point, from *X. mocquardi*, which has a ventrally directed one. Among the newly found specimens we observed variation in head shape, head size and shape of the rostral (Figs 5, 6), but the direction of the anterior rostral point was found to be ventral in all specimens. Remarkably, Wallach et al. (2007a) mentioned that the rostral of both type specimens of *X. grandidieri* has been ‘sloughed off’, a phenomenon not uncommon in hundred-year old specimens, and which might have influenced the direction of the rostral point in these specimens.

(2) Scale contacting inferior nasal suture: According to Wallach & Ineich (1996) supralabial II (SL2) contacts the inferior nasal suture in *X. grandidieri*, whereas in *X. mocquardi* the rostral contacts the inferior nasal suture (Wallach et al. 2007a). The specimens examined here, including the holotype of *X. mocquardi*, uniformly showed an inferior nasal suture contacting SL2 as described for *X. grandidieri*.

(3) Relative size of supralabials: The largest supralabial in the holotype of *X. mocquardi* is SL3 according to both Wallach et al. (2007a) and our own observations. In *X. grandidieri*, Wallach et al. (2007a) diagnosed SL4 to be the largest supralabial. Earlier, however, Wallach & Ineich (1996) described SL3 and SL4 to be equally sized in *X. grandidieri*. In

Table 1. Morphological characters of nine recently collected specimens of *Xenotyphlops grandidieri* and the holotype of *X. mocquardi* MRSN R3208 compared to morphological data from the literature of *X. mocquardi* MRSN R3208 (Wallach et al. 2007a) and the two type specimens of *X. grandidieri*, MNHN 1905.271 and MNHN 1905.272 (Wallach & Ineich 1996). Morphological characters are: number of scale rows at anterior, midbody and posterior position; absence or presence (“yes” vs. “no”) of posterior scale row reduction; largest supralabial (SL), “equal” refers to SL3 and SL4 being equally sized; scale that contacts the inferior nasal suture; direction of the anterior rostral point; number of middorsals; snout-vent length (SVL) in mm.

	<i>X. mocquardi</i>				
	MRSN R3208 (this study)	MRSN R3208 (Wallach et al. 2007a)	ZSM 2075/2007	ZSM 2193/2007	ZSM 2194/2007
DNA sequence	no	no	yes	yes	no
Anterior scale rows	21	22	20	20	20
Midbody scale rows	20	22	20	20	20
Posterior scale rows	20	20	20	20	22
Posterior scale row reduction	yes	yes	no	no	no
Largest supralabial	SL3	SL3	equal	equal	SL3
Scale contacting the inferior nasal suture	SL2	rostral	SL2	SL2	SL2
Anterior rostral point direction	ventral	ventral	ventral	ventral	ventral
Middorsals	517	478	521	485	531
SVL in mm	244.5	248.5	206.5	201.5	259

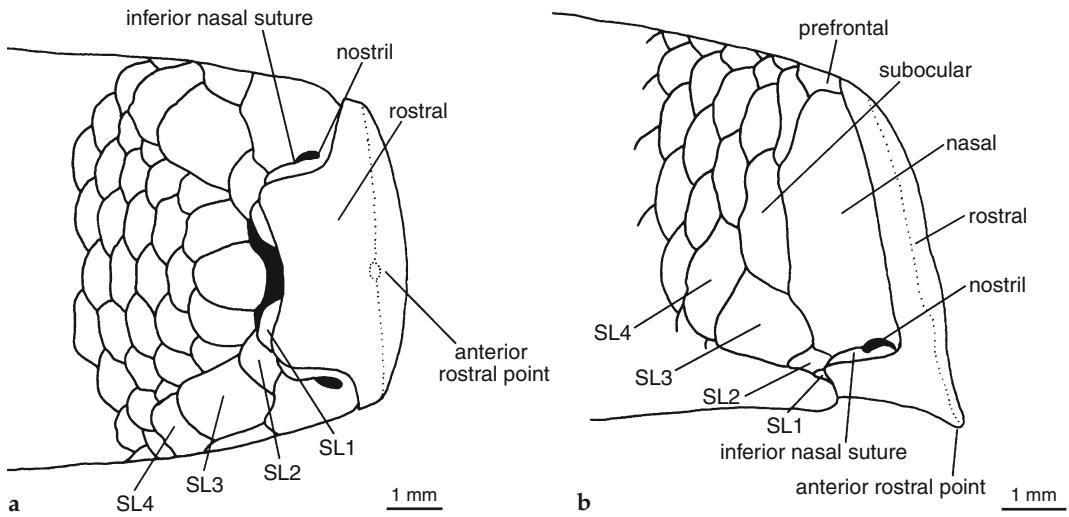


Fig. 4. Ventral (a) and lateral (b) view of major head scales of *Xenotyphlops grandidieri* following Wallach (1993) and Wallach & Ineich (1996) for nomenclature. Supralabials are referred to as SL.

the specimens examined here, we found SL3 to be the largest supralabial in most cases, but in three specimens SL3 and SL4 were equally sized. Comparing the size of the two supralabials is likely to be subjective, because SL3 is squared, while SL4 is rectangular, but see Figures 5 and 6.

(4) Scale rows around the body: *X. grandidieri* is characterized by 20 anterior longitudinal scale rows, 20 at midbody and 20 posteriorly whereas *X. mocquardi* shows a 22-22-20 pattern (Wallach et al. 2007a). We were unable to reproduce the scale count pattern for *X. mocquardi*, but counted 21 anterior scale rows, 20 at midbody and 20 posteriorly. We observed variation in the number of longitudinal scale rows reaching from 20 to 22 in all individuals

at different body regions. Five individuals showed a 20-20-20 scale row pattern, three individuals a 20-20-21 pattern, and for one specimen we counted 20-20-22 (Table 1). Ventral scales were found to split up once or twice and fused again within short sections several times throughout the body and/or in the posterior third (Fig. 7). In particular, we counted 21 longitudinal scale rows in four individuals (MRSN R3208, ZSM 2213/2007, ZSM 2216/2007, ZSM 2075/2007) a few times throughout the body, and 22 longitudinal scale rows in eight individuals anterior to the anal shield (see Fig. 7a). Specimen MRSN R3208 varies in the number of scale rows between the 20th and 22nd midventral from 21 to 22 scale rows and a similar observation was made

X. grandidieri

ZSM 2213/2007	ZSM 2214/2007	ZSM 2215/2007	ZSM 2216/2007	ZSM 2217/2007	ZSM 1594/2008	MNHN 1905.271 (Wallach & Ineich 1996)	MNHN 1905.272 (Wallach & Ineich 1996)
no	yes	no	no	no	no	no	no
20	20	20	20	20	20	20	20
20	20	20	20	20	20	20	20
21	20	21	21	20	20	20	20
no	no	no	no	no	no	no	no
equal	SL3	SL3	SL3	SL3	SL3	SL4	SL4
SL2	SL2	SL2	SL2	SL2	SL2	SL2	SL2
ventral	ventral	ventral	ventral	ventral	ventral	anterior	anterior
518	545	516	514	517	502	482	469
259.5	255	163	276	175	165.5	248	249

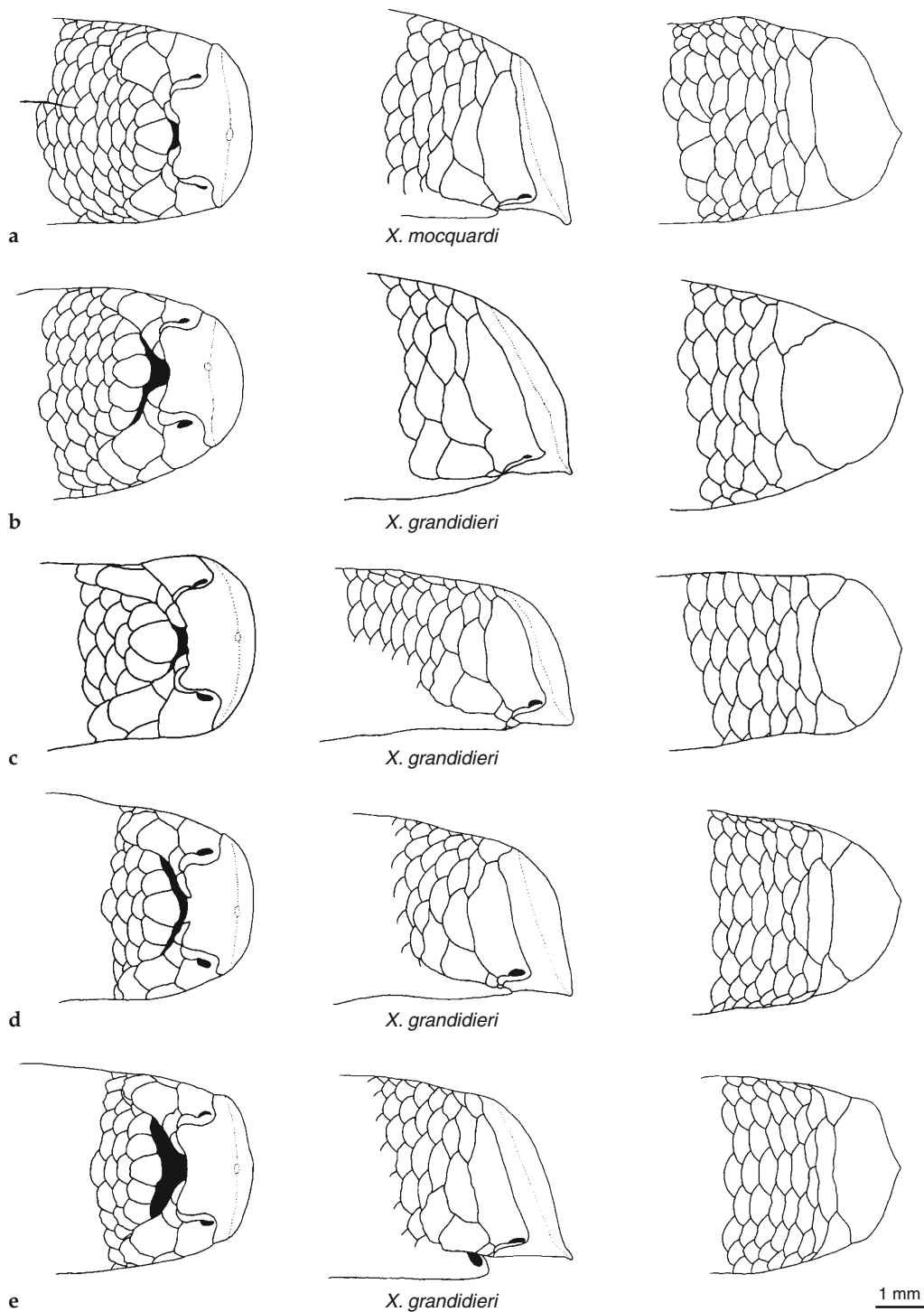


Fig. 5. Head drawings of *Xenotyphlops grandidieri* and *X. mocquardi*. From left to right: ventral, lateral and dorsal view. From top to bottom: **a.** holotype of *X. mocquardi* MRSN R3208; **b-e.** *X. grandidieri*; **b.** ZSM 1594/2008; **c.** ZSM 2075/2007; **d.** ZSM 2193/2007; **e.** ZSM 2194/2007.

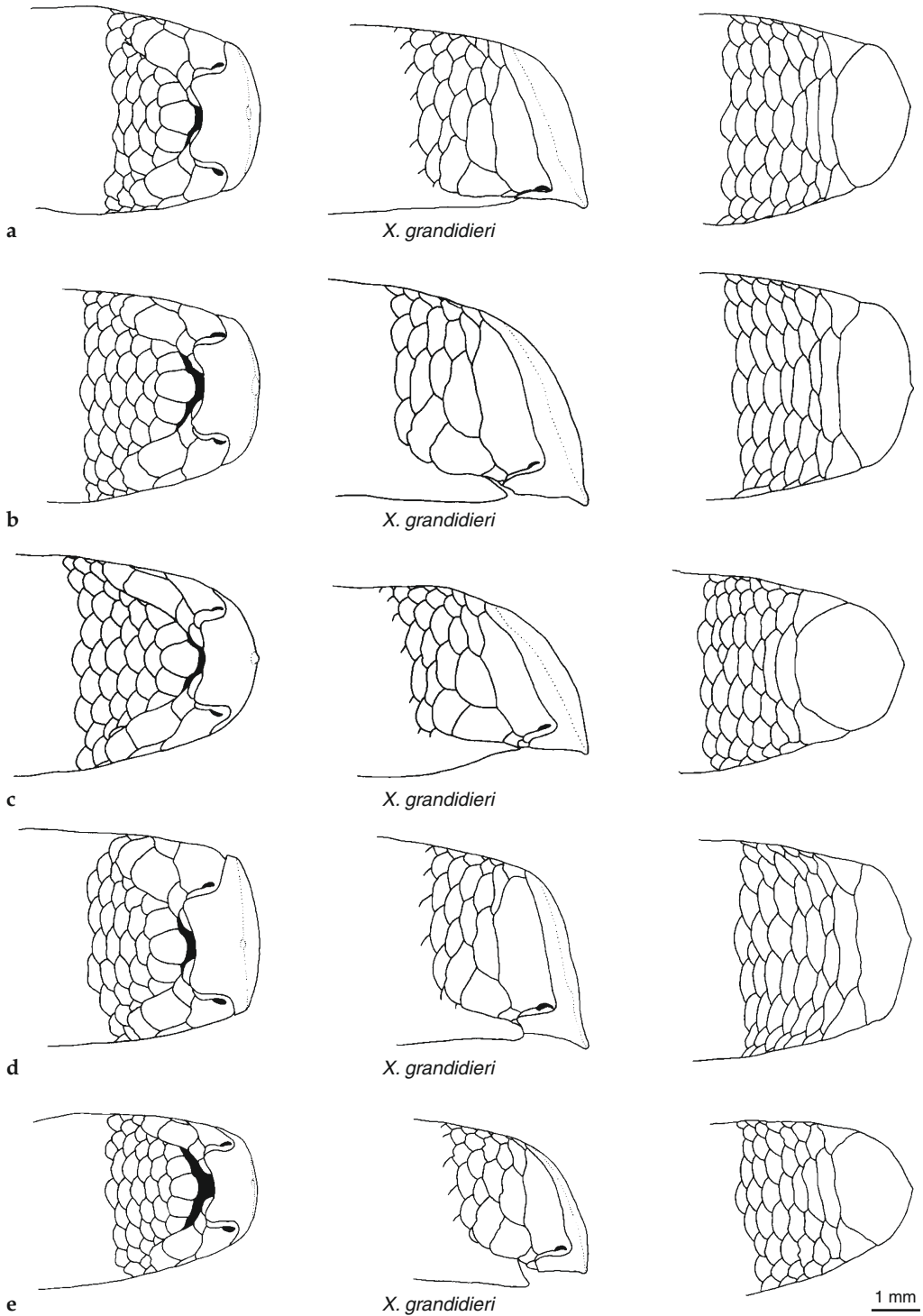


Fig. 6. Head drawings of *Xenotyphlops grandidieri*. From left to right: ventral, lateral and dorsal view. From top to bottom: a. ZSM 2213/2007; b. ZSM 2214/2007; c. ZSM 2215/2007; d. ZSM 2216/2007 and e. ZSM 2217/2007.

anterior to the midbody (Fig. 7b). However, we also observed dorsal or lateral insertions of single, small scales that were not part of a row and increase longitudinal scale rows, when included into the count. Consequently, the number of longitudinal scale rows depended on the individual and on the body position where the scales were counted. We could not observe any pattern or consistency in the occurrence of such variation in scale rows along the body. Scale patterns shown in Table 1 reflect the number of longitudinal scales at specific body regions as defined in the method section.

(5) Posterior scale row reduction: This refers to a decrease in number of scale rows from anterior to posterior, a phenomenon often occurring around the midbody in several blind snakes, reducing the number of scale rows by one or two (Schwartz & Henderson 1991). We observed a reduction from 21 to 20 scales only in MRSN R3208. All other individuals have a 20–20–20 pattern, or an increased number of posterior scale rows (to 21 or 22 scale rows) right before the anal shield.

(6) Anteriorly extended liver lobe: by internal anatomy, *X. mocquardi* was distinguished from *X. grandidieri* in having an anteriorly extended liver lobe on the left side vs. right side in *X. mocquardi*. The liver in *Xenotyphlops* is asymmetrically organized, with one segment extending anteriorly and the other segment extending towards the posterior end. The liver was found to be asymmetrically and identically organized in both examined dissected specimens (MRSN R3208 and ZSM 2214/2007) with an anterior left liver lobe and posterior right lobe. We therefore cannot confirm the observation of Wallach et al. (2007a) who described the right liver lobe extending anteriorly for MRSN R3208.

(7) Presence of a left lung for *X. mocquardi* (vs. absence in *X. grandidieri*): ‘Left lung’ refers to a teardrop-shaped, small (1.5 mm or 0.6 % of snout-vent length) vascularized tissue that is part of the right lung and located behind the heart apex. We could identify such structure in MRSN R3208, but not in the newly dissected specimen ZSM 2214/2007. However, we cannot rule out the presence of such a structure in ZSM 2214/2007 due to our limited knowledge of xenotyphlopoid internal anatomy and the difficulty in recognizing these minute organs.

Genetic variation

DNA sequences were obtained from ten *Xenotyphlops* specimens, among which three that were also examined morphologically (Table 1; ZSM 2075/2007, ZSM 2193/2007, ZSM 2214/2007), plus additional specimens deposited in the UADBA collection

(specimens with field numbers FGZC 1141, 1167, 1168, 1336, 1338, 1139) or severely damaged (ZSM 2125/2007). All these specimens came from the Baie de Sakalava. In the 1022 bp fragment of cytochrome b, each specimen had a unique haplotype, suggesting a rather important genetic diversity in these snakes, despite their very small distribution range. Nevertheless, the differences among most haplotypes amounted to only 2–6 substitutions (0.1–0.6 % uncorrected pairwise distance). The sole exception was the specimen ZSM 2075/2007 which differed from all other haplotypes by 15–17 substitutions (1.5–1.7 % uncorrected pairwise distance). This specimen was collected a few hundred meters apart from the others yet in the same general dune area, suggesting a rather strong degree of population structure across small distances in these snakes. Unfortunately, no sequence could be obtained from the Iovovona locality due to poor tissue quality (original tissue sample lost).

Discussion

Morphological and genetic differentiation and taxonomic conclusions

Several Malagasy fossorial squamates have been known only from the type specimens for decades before they were rediscovered and redescribed (Renoult & Raselimanana 2009, Köhler et al. 2010). Their species diversity is likely to be underestimated and information of their biology is scant (Wallach & Glaw 2009). Almost every newly found individual therefore adds to the knowledge about intraspecific variation, distribution range, life history and ecology of the Malagasy herpetofauna. Examination of the newly found individuals and the holotype of *X. mocquardi* revealed previously unknown variation in longitudinal scale rows and uncovered inconsistencies in the literature about *Xenotyphlops*.

After discovering *X. mocquardi* in 2005, Wallach et al. (2007a) noticed that the rostral shield of both *X. grandidieri* specimens was removed and made minor correction in their species description. Damage in hundred-year old specimens is not uncommon and often results from preservation issues and handling over several decades. Using such specimens for taxonomic tasks is challenging on its own, but especially in the case of *Xenotyphlops* where specimens are small and body and head scales are shiny and unpigmented.

A major discrepancy was found in the way characters are described in Wallach & Ineich (1996) and Wallach et al. (2007a). In their species description Wallach et al. (2007a) noted that the infranasal scale of *X. mocquardi* is separated from the supranasal by

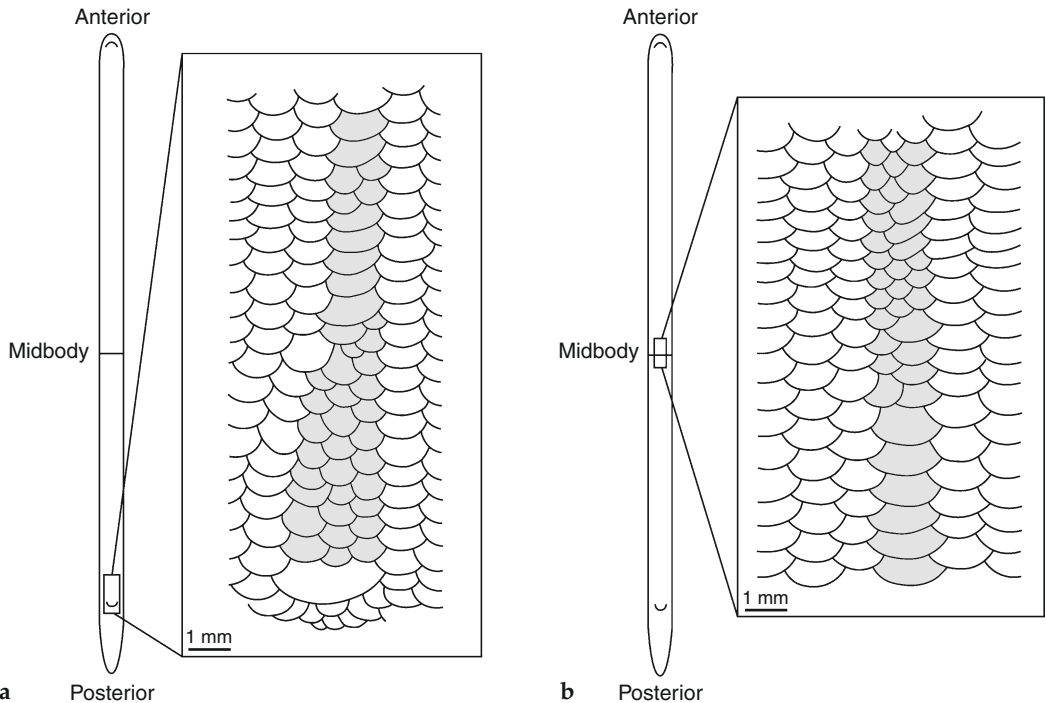


Fig. 7. Ventral scale rows were found to split up and fuse again within short sections of the body in several individuals. Drawings of two specimens are used here for illustration. Division of ventral scale rows of *Xenotyphlops grandidieri* (ZSM 2214/2007) anterior to the anal shield (a) and division of ventral scale rows of *X. mocquardi* (MRSN R3208) anterior to the midbody (b) are highlighted in grey. Ventral scale rows split up once or twice and fuse again within short body sections and increase the number of longitudinal scale rows (around the body) from normally 20 to 21 or 22 scale rows. Similar patterns anterior to the anal shield as shown in (a) were observed in eight out of nine examined specimens of *X. grandidieri*. Scale row division within sections throughout the body similar as shown in (b) was also observed in two other specimens of *X. grandidieri*.

the nostril and 'the inferior suture, which contacts supralabial II'. In the same article, the inferior suture is listed as contacting the rostral and was used as character to distinguish *X. mocquardi* from *X. grandidieri*. Since we found the contacting scale to be SL2 in all specimens including MRSN R3208, we conclude that the character state for *X. mocquardi* is similar to *X. grandidieri*.

Reduction in the number of scale rows from anterior to posterior has been observed in several blind snake species (*Typhlops dominicanus* Stejneger, 1904; *T. lumbricalis* Linnaeus, 1758; *Acutotyphlops banaorum* Wallach et al., 2007b; *T. rajeryi*) and is used as a taxonomic character. Scale rows commonly fuse between the anterior end and the midbody, reducing number of scale rows by up to two rows (Schwartz & Henderson 1991). In contrast, variation in scale row patterns within species is rare, but has been observed among others in *Typhlops epactius* Thomas, 1968, *T. hectus* Thomas, 1974, *T. jamaicensis* Shaw, 1802 and *T. pusillus* Barbour, 1914 (Schwartz & Henderson

1991). The frequently observed scale row pattern in *Xenotyphlops* is 20–20–20, but occasionally 21 or 22 scales can be counted at different body regions. For MRSN R3208, the holotype of *X. mocquardi*, we counted at the above-defined positions a 21–20–20 pattern, which stands in contrast to the 22–22–20 pattern found by Wallach et al. (2007a). However, counting at different body positions we also obtained scale rows of up to 22. In *Typhlops richardi* Duméril & Bibron, 1844 from St. Thomas (U.S. Virgin Islands) variation in scale row reduction is associated with population structure (Schwartz & Henderson 1991). To infer whether this is the case for *X. grandidieri*, more individuals have to be sampled from the type locality of *X. mocquardi* using molecular data to infer population structure. Unfortunately, we had no tissue sample of the *X. mocquardi* holotype to test its identity genetically, and tissue samples of a further individual collected near the *X. mocquardi* type locality (at Ivoivona) were lost by the air carrier.

Out of seven major characters that were used to

distinguish *X. grandidieri* and *X. mocquardi*, five were found to be similar throughout all examined specimens and the literature-based data of *X. grandidieri*. One character (longitudinal scale rows) was observed to be more variable than previously observed in the species and one internal character (presence of a left lung), could not be assessed with confidence here. Unfortunately, genetic data were present for only three of the specimens examined morphologically. These three specimens all had 20 scale rows but included some variation in the relative supralabial size (Table 1). The genetic variation observed among all ten haplotypes from Baie de Sakalava was at a level typically found within species of squamates, suggesting that at this locality only a single species of *Xenotyphlops* occurs – with considerable intrapopulational variation in mitochondrial DNA and with a possible substantial degree of population subdivision. DNA sequence divergence among individuals from the Baie de Sakalava is moderately low (0.1–2 %) both here and in Vidal et al. (2010). The 10-million-year split in the timetree of Vidal et al. (2010: fig. 1) between two individuals of *Xenotyphlops grandidieri*, was not caused by a large number of sequence changes but rather a slow rate of change inferred by the short branch length in the tree leading to the species. The unusually wide credibility interval of that estimate (1.3–26 Ma) indicates that it does not conflict with the conclusion here that only a single species is represented.

We are aware that the available evidence remains fragmentary and insufficient for a thorough taxonomic revision of these snakes, as is the case with many typhlopoids which often are known from few individuals. Taken together we derive the following conclusions from the data available:

(1) The newly collected specimens from Baie de Sakalava show no convincing differences to the types of *X. grandidieri*, and furthermore were found in syntopy with two fossorial skinks from the same historical collection (by Rothschild) with the same imprecise original locality information and apparently a similar microendemic occurrence in northern Madagascar. We therefore conclude that the collected material from Baie de Sakalava is to be assigned to the species *X. grandidieri*.

(2) No constant and convincing morphological characters are currently known to distinguish the so defined *X. grandidieri* from *X. mocquardi*. We therefore consider *Xenotyphlops mocquardi* a junior synonym of *X. grandidieri*.

Habitat and conservation

Xenotyphlops appear to be highly specialized to a fossorial life in sandy substrate. They have completely lost any visible traces of eyes, a character shared among Malagasy scoleophidians only with *Typhlops madagascariensis* Boettger, 1877 (Glaw & Vences 2007). Together with the sand-dwelling *T. arenarius* Grandidier, 1872 these are the only Malagasy typhlopoid snakes with a pinkish, pigmentless body coloration (Wallach & Glaw 2009), a character also shared with several fossorial, sand-dwelling skinks with reduced eyes (*Voeltzkowia* Boettger, 1893 and *Sirenoscinus* Sakata & Hikida, 2003; Miralles et al. 2012). Furthermore, *Xenotyphlops* is the only typhlopoid snake in Madagascar that is apparently restricted to coastal habitats although other species (e.g. *Typhlops arenarius*) can be found close to the coast as well. Remarkably, the sandy habitat where *Xenotyphlops* was found is populated by many other reptile species highly adapted to a fossorial life in the sand, especially of the genus *Paracontias* (*P. minimus*, *P. rothschildi*, *P. fasika* Köhler, Vences, Erbacher & Glaw, 2010, *P. cf. hildebrandti*) and *Madascincus arenicola* Miralles, Köhler, Glaw & Vences, 2011 (Miralles et al. 2011). Within Madagascar, such a concentration of fossorial or semi-fossorial, sand dwelling reptiles is otherwise only found in the Toliara region in south-western Madagascar where several species of the genus *Voeltzkowia* and *Pygomeles braconnierei* Grandidier, 1867 occur syntopically. Some of the limbless reptiles of northern Madagascar are classified as Critically Endangered by the IUCN (*Paracontias fasika*, *P. minimus*, *P. rothschildi*) and are probably endemic in this littoral (coastal) habitats (Köhler et al. 2010). The remarkably high number of fossorial sand-dwellers in the Orangea forest/Baie de Sakalava area suggests that the presence of sandy dune habitat in the north of Madagascar probably was continuous throughout evolutionary time for these squamates throughout evolutionary times (despite several distinct sea level changes during the glacial periods), allowing the relict *Xenotyphlops* lineage to survive and the other reptile species to adapt to the sandy habitat. We therefore expect that other, still unstudied groups of organisms might have evolved microendemic and fossorial species in this region as well. To protect this habitat and its unique microendemic sand biota we suggest to establish a new nature reserve along the sandy coast east and southeast of Antsiranana or, alternatively, the expansion of the Montagne des Français reserve to include the coastal habitats along the coast and the dry forest of Orangea. Together with the efforts to protect these areas concepts for the development of a sustainable mode of land use for local people should be developed.

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