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A rhapsody of colours from Madagascar: discovery of a remarkable new snake of the genus *Liophidium* and its phylogenetic relationships

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Abstract. We describe an extraordinarily bright-coloured new species of lamprophiid snake from Makira reserve in the North East of Madagascar, assigned to the subfamily Pseudoxyrhophiinae. *Liophidium pattoni* sp. n. is characterised by four pink-red longitudinal lines on a black dorsum, a yellow venter and a pink-red ventral side of tail. It had previously been photographed at Masoala National Park in northeastern Madagascar and possibly elsewhere, but its generic assignment was uncertain because no specimens were available for study. Molecular phylogenetic analyses on the basis of DNA sequences of the cytochrome *b*, 16S rRNA and nuclear c-mos genes are concordant in placing the new species sister to *Liophidium rhodogaster*, and these two species sister to a clade containing the remaining *Liophidium* species included. Besides its unique colour and a substantial genetic differentiation, *L. pattoni* differs from almost all *Liophidium* by meristic characters, the only exception being *L. torquatum* that exhibits overlaps in scale counts with the new species but differs by its colouration, with lack of pink-red colour on the back, a dark band in the neck, and transversal lines of spots on the venter. Next to the yellow-black *Stenophis citrinus*, this is the second pseudoxyrhophiine from Madagascar with such bright and potentially aposematic colour, although these two species both are not aggressive and, as far as is known, not dangerously toxic.

Key words. Lamprophiidae, *Liophidium pattoni* sp. n., Madagascar, molecular relationships, Serpentes, Squamata.

Introduction

Madagascar is inhabited by three or four families of snakes depending on the interpretation of recent phylogenetic studies of the "Colubridae sensu lato". The Boidae has three representatives, 14 species belong to Typhlopidae, and more than 76 belong to the Lamprophiidae (as defined by Vidal et al. 2008). Except for *Mimophis*, all Malagasy lamprophiids are classified in the subfamily Pseudoxyrhophiinae. This includes the genus *Liophidium*, a group of aglyphous, terrestrial snakes occurring both in Madagascar and the Comoro Island of Mayotte. The genus was erected by Boulenger (1896), and several species were described more than hundred years ago (Boulenger 1888, Mocquard 1901, Schlegel 1837), with further species named more recently (Domergue 1984, Franzen et al. 2009). A single species has been described from the Comoros, *L. mayottensis* (Peters, 1874), differing from all other *Liophidium* species by exhibiting 19 rows of dorsal scales instead of 17.

From Madagascar, eight nominal species of *Liophidium* are known so far, all of them exhibiting 17 rows of dorsal scales, a divided cloacal scale and divided subcaudals (Glaw & Vences 2007, Franzen et al. 2009). All these species have overall brownish to black dorsal colours, with or without dorsal stripes, and whitish, yellowish or pinkish ventral sides frequently scattered with regularly arranged dark spots or markings, except for *L. rhodogaster* which is characterised by a bright pink ventral colouration.

A molecular study of the Pseudoxyrhophiinae (Nagy et al. 2003) suggests a close relationship among *Liopholidophis* and *Liophidium*. The phylogenetic relationships within this genus are not fully resolved. Franzen et al. (2009) provided the most comprehensive molecular phylogenetic hypothesis so far, including six species of *Liophidium*.

In addition to the nine nominal species, three supposedly undescribed candidate species have been reported and need formal taxonomic study, but one of these was so far only known from photographs (Glaw & Vences 2007). Here we report this new species of snake from the highlands of the Makira Plateau in northeastern Madagascar, and based on the collected specimen we place it in the genus *Liophidium*. The species has a unique colour pattern that differs from that of all other snakes known from Madagascar. We compare this species to its closest relatives and provide new molecular phylogenetic data for several species that help to clarify the relationships within this poorly known genus.

Materials and methods

Sampling

Although referred to as *Liophidium* sp. "Masoala" by Glaw & Vences (2007), the generic assignment of the new species described herein was unclear due to the lack of meristic data and its unique colouration. Therefore, we included in our molecular genetic analysis a number of samples representing the majority of the Malagasy pseudoxyrhophiine snake genera, in addition to samples of all nominal species of *Liophidium* except for *L. apperti* and *L. trilineatum*. Specimens and samples were collected in field expeditions between 2000 and 2009. According to previous results (Nagy et al. 2003), the Socotran endemic *Ditypophis vivax* is a sister group of the Malagasy pseudoxyrhophiine radiation and was used as outgroup taxon in the phylogenetic analyses.

Voucher specimen numbers and GenBank accession numbers are summarized in Table 1. Museum abbreviations used: HLMD – Hessisches Landesmuseum Darmstadt, Germany; MRSN – Museo Regionale di Scienze Naturali, Torino, Italy; MVZ – Museum of Vertebrate Zoology, University of California Berkeley, USA; UADBA – Université d'Antananarivo, Département de Biologie Animale, Madagascar; ZFMK – Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZSM – Zoologische Staatssammlung München, Germany.

Laboratory techniques

DNA was extracted either using traditional phenol-chloroform protocols or by commercial kits (e.g. NucleoSpin Tissue Kit from Macherey-Nagel). DNA yields were checked by agarose gel electrophoresis or by spectrophotometry. The amplifications of the whole cytochrome *b* (cob) gene, fragments of the 16S ribosomal RNA gene (16S) and of the nuclear oocyte maturation factor mos (c-mos) were carried out by polymerase chain reactions (PCRs) using primers which were published elsewhere (see Nagy et al. 2003 for details). Purified PCR products were sequenced on automated capillary sequencers of ABI Genetic Analyzer 3100 and 3130xl (both Applied Biosystems) or MegaBACE 1000 (GE Healthcare/Amersham) according to the manufacturer's protocols.

Analysis of molecular data

All obtained DNA sequences were manually checked for errors, and for stop codons in protein-coding genes. 16S sequences were aligned using the web server of MAFFT 6 (Katoh et al. 2002, Katoh & Toh 2008). Phylogenetic analyses were carried out on the concatenated data set of cob, 16S and c-mos sequences. This data matrix included 24 samples with an aligned sequence length of 2206 base

Table 1. Voucher numbers, locality information and GenBank accession numbers of the specimens used for molecular genetic analysis.

Species	Sample ID	Voucher specimen	Locality	Accession no. cob	Accession no. 16S	Accession no. c-mos
Alluaudina bellyi	J87	MRSN-FAZC 10622	Berara	AY188005	AY188044	AY187966
Compsophis albiventris	J90	ZSM 497/2000	Mt. d'Ambre	AY188011	AY188050	AY187972
Ditypophis vivax	S76	HLMD-RA-2972	Yemen, Socotra	AY188013	AY188052	AY187974
Dromicodryas bernieri	J91	UADBA FGMV 2000-517	Ifaty	AY188014	AY188053	AY187975
Heteroliodon fohy	J89	ZSM 548/2000	Mt. des Français	AY188018	AY188057	AY187979
Ithycyphus miniatus	J95	MRSN-FAZC 10680	Berara	AY188019	AY188058	AY187980
Langaha madagascariensis	J88	ZSM 636/2000	near Ifaty	AY188020	AY188059	AY187981
Leioheterodon madagascariensis	J67	MRSN-FAZC 10621	Maromandia	AY188022	AY188061	AY187983
Liophidium chabaudi	Tp844	MVZ 238844	near Ifaty	FJ404307	FJ404210	FJ387210
Liophidium maintikibo	M07-3	ZSM 2052/2007	near Kirindy	EU394723	GQ913669	GQ913663
Liophidium mayottensis	F3220	ZSM 1693/2008	Mayotte	GQ913675	GQ913670	GQ913664
Liophidium pattoni	DRV5948	ZSM 186/2009	Makira	GQ913676	GQ913671	GQ913665
Liophidium rhodogaster	F467	UADBA FGZC 467	Mt. d'Ambre	DQ979992	GQ913672	GQ913666
Liophidium rhodogaster	J304	ZSM 784/2003	Ranomafana	DQ979978	DQ979964	DQ979971
Liophidium therezieni	M07-2	ZSM 2053/2007	Mt. des Français	EU394722	GQ913673	GQ913667
Liophidium torquatum	J84	No voucher	Mt. d'Ambre	AY188023	AY188062	AY187984
Liophidium vaillanti	M09-2	No voucher	Tsimanampetsotsa	GQ913677	GQ913674	GQ913668
Liopholidophis sexlineatus	J98	UADBA FGMV 2000-38	Mandraka	AY188024	AY188063	AY187985
Madagascarophis colubrinus	J69	ZSM 549/2000	Mt. des Français	AY586231	AY586194	AY586219
Micropisthodon ochraceus	J86	ZFMK 66658	Ambato	AY188030	AY188069	AY187991
Pseudoxyrhopus ambreensis	J102	No voucher	Mt. d'Ambre	AY188035	AY188074	AY187996
Stenophis betsileanus	J71	ZFMK 60500	Marojejy	AY188037	AY188076	AY187998
Stenophis citrinus	J298	No voucher	No data	AY612047	AY611865	AY611956
Thamnosophis lateralis	J93	UADBA FGMV 2000-36	near Mantasoa	DQ979977	DQ979963	DQ979970

pairs. Parsimony analysis was carried out with PAUP* v4b10 (Swofford 2002), with 2000 bootstrap replicates performed to infer branch supports. In addition, a Bayesian inference of phylogeny was carried out using MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003). The data matrix was split into seven partitions: for the protein-coding genes (cob and c-mos) each codon position was treated separately, while 16S was handled as a single partition. Nucleotide substitution models were compared and selected by jModeltest (Posada 2008) applying the AIC(c) and BIC criteria. In Bayesian analysis, two parallel runs with four chains each were run for 5 million generations. Every 100th generation was sampled, and the first half of the trees was discarded as "burn-in".

Morphological characters

We recorded meristic and measurable characters as well as colouration from the holotype, which were complemented with photographs from two other specimens from the Masoala Peninsula using standard definitions (e.g. Babocsay 2004). Diagnosis and description largely follows the scheme of Babocsay et al. (2004). Measurable characters were recorded with a vernier calliper to the nearest 0.1 mm and snout-vent length (SVL, from the rostral scale to the cloaca) and tail length was measured with a piece of string. For counting small details (like teeth) and scales we used a Zeiss Stereo Discovery V12 stereomicroscope. We measured SVL, tail length, head length (from the tip of the snout to behind the mandible), head width (at the widest point of the head) and eye diameter (as the longest diameter of the visible part of the eye). We analysed in detail the arrangement of head scales, the number of preocular and postocular scales (in contact with the eye), presence/absence of loreal scales (between preoculars and nasal), number of upper labials or supralabials (from the one in contact with the rostral to the one in the aperture of the mouth inclusively), number and position of upper labials in contact with the eye, number of lower labials or infralabials (from the one in contact with the mental scale to the one opposite to the last supralabial), arrangement of the first pair of lower labials, contact between lower labials with the genials, number of preventral scales (defined as gular scales anterior to ventrals which are broader than long; Nilson & Andrén 1986), number of ventrals, divided or undivided state of the cloacal plate, number of subcaudal pairs (excluding the apical spine and counting both sides), and number of dorsal scale rows counted across the forepart of the body, at mid-body and anterior to the cloacal plate. Terminology of hemipenis morphology follows Ziegler et al. (1996).

Systematics

Liophidium pattoni sp. n.
(Figs. 1–2)

Holotype: ZSM 186/2009 (field number DRV 5948), adult male, from a site locally named Angozongahy at the western side of the Makira plateau, within the newly created reserve „Makira Natural Park", 15°26'13.3" S, 49°07'07.0" E, 1009 m above sea level, district of Mandritsara, region of Sofia, province of Mahajanga, northeastern Madagascar, collected on 28 June 2009 by M. Vences, D. R. Vieites, F. M. Ratsoavina & R.-D. Randrianiaina.

Diagnosis: *Liophidium pattoni* sp. n. can be easily distinguished from all other *Liophidium* species and any other species of Malagasy snakes by its unique colour pattern. It presents an overall black dorsal side with four regularly discontinuous pink-red stripes, fading into blue-grey at mid-body, and a bright conspicuous yellow venter with a pink-red colouration on the ventral side of the tail. In addition, it differs from other nominal species of *Liophidium* as follows (based on data summarized in Glaw & Vences 1994, 2007, Franzen et al. 2009): From the Comoroan species, *L. mayottensis*, by presenting 17 rows of dorsal scales versus 19. From *L. vaillanti* by presence of a loreal scale (versus absence); presence of eight upper labials, with upper labials 4 + 5 touching the eye, versus 7 (3 + 4); and by having a lower number of ventral scales (160 vs. 220–255). From *L. therezieni* by presence of a loreal scale (versus absence); presence of eight upper labials, with upper labials 4 + 5 touching the eye, versus 7 (3 + 4); and by a lower number of ventral scales (160 vs. 218–235). From *L. maintikibo* by presence of a loreal scale (versus absence); presence of eight upper labials, with upper labials 4 + 5 touching the eye, versus 7 (3 + 4); and by a lower number of ventral scales (160 vs. 193). The remaining *Liophidium* species have 8 supralabials and a loreal scale, and differences from *L. pattoni* are mainly in SVL, number of ventrals and subcaudals. *Liophidium pattoni* is possibly larger than *L. apperti* (417 vs. 238 mm [total length of the two respective holotypes]), and has more ventral scales (160 vs. 145). *Liophidium pattoni* is also possibly larger than *L. trilineatum* (417 vs. 330 mm total length of the only known specimens for which data on size is available; see Guibé 1958), and has more ventral scales (160 vs. 145–152). *Liophidium pattoni* shows a higher number of ventral scales than *L. chabaudi* (160 vs. 150–154), and more subcaudals (54 vs. 34–46).

By external morphology, *L. pattoni* is most similar to *L. torquatum*. Both species overlap in body length and number of ventrals, but *L. torquatum* has a slightly higher number of subcaudals (58–75) than *L. pattoni* (54). The main differences are in the colouration, as *L. torquatum* shows a rather uniform light brown dorsal colouration, sometimes with small black spots arranged in longitudinal series (Boulenger 1888), lacking the bright colour stripes on a black dorsal background shown by *L. pattoni*. *Liophidium torquatum* exhibits a dark crossband behind the parietals, missing in *L. pattoni*; upper labials with black edges which are bright yellow in *L. pattoni*; a brown throat with white, dark-edged markings, whereas it is completely yellow in *L. pattoni*; whitish or pinkish ventrals with small dark spots which are bright yellow with a black crescent shape in *L. pattoni*; and a yellowish or light pink tail with black dots, which is bright pink-red in *L. pattoni*.

Liophidium pattoni differs from its sister taxon (according to molecular data; see below), *L. rhodogaster*, in exhibiting fewer ventral scales (160 vs. 181–192) and fewer subcaudals (54 vs. 61–81). Both species show a pinkish colour on the ventral side of the tail, although this colouration extends to the ventrals in *L. rhodogaster* while it is bright

Figure 1. Holotype of *Liophidium pattoni* (ZSM 186/2009) from Makira forest in life in (a,b) dorsolateral and (c) ventral views.

yellow in *L. pattoni*. They also differ significantly in dorsal colour pattern, with *L. rhodogaster* having a brown dorsum with a lateral dark brown thin line and a wide blackish dorsal band, and the new species showing four very conspicuous bright pink-red discontinuous stripes, which change to blue-grey at mid-body, on a black ground colour. The head colouration also differs among both species, with a dark brown head with few whitish scales behind the eye in *L. rhodogaster*, and a black and bright yellow pattern in *L. pattoni* consisting of bright yellow supralabials, a black stripe reaching from the nasal scale through the eye and towards the posterior border of the head, and bright yellow upper postocular and temporal scales. From the snout to the supraocular scales, *L. pattoni* shows a variable amount of bright yellow colour with small black patches.

Description of the holotype: Adult male in good state of preservation. SVL 329 mm, tail length 87.5 mm (total length 416.5 mm; tail length 21% of total length). Head length 12.4 mm, head width 7.4 mm; eye large, 1.8 mm in diameter, pupil round. Ventral scales 160, one preventral; cloacal plate divided; 54 subcaudals, all divided. Dorsal scales smooth, no apical pits, in 17–17–17 longitudinal rows. Rostral scale wide, reaching onto the dorsal side of the head. Internasals rounded in the anterior part and straight in the posterior. Prefrontals nearly rectangular. One loreal present. Two preoculars and two postoculars. Supraoculars elongate, posteriorly reaching to the posterior margins of the postoculars. Frontal scale elongate, pentagonal. Parietals triangular, very broad; anterior outer margins reaching down to the upper portions of the lower postoculars. Upper labials 8/8. Upper

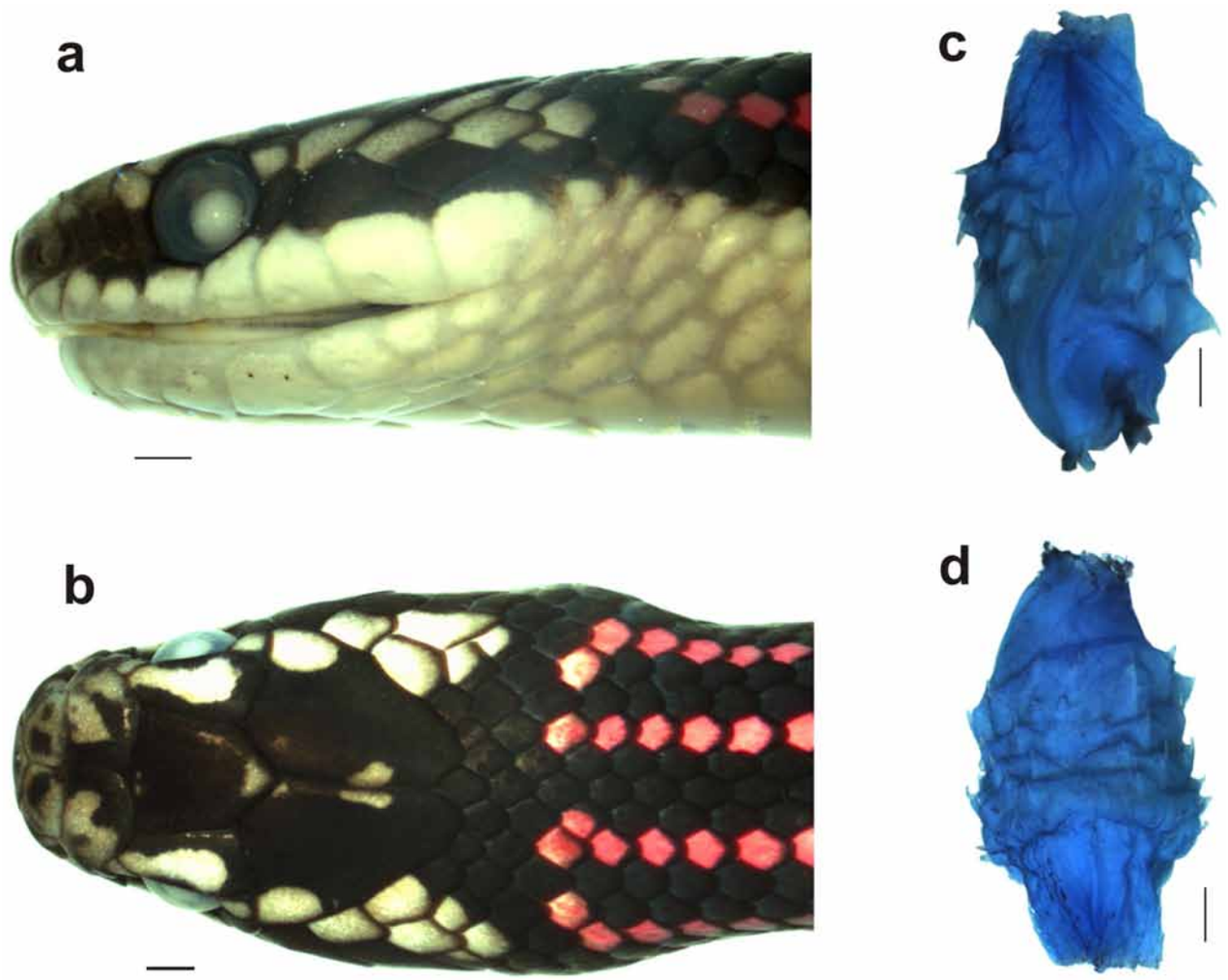

Figure 2. Head of preserved holotype of *Liophidium pattoni* (ZSM 186/2009) in (a) lateral and (b) dorsal views, showing details of scalation; and incompletely everted and apically damaged hemipenis of the holotype in sulcal (c) and asulcal (d) views, photographed after staining with methylen blue. Scale bars represent 1 mm.

labials 4 and 5 in contact with the eye. Lower labials 8/8, the first pair not in contact behind the mental; 1–4 touching the anterior genial, only the lower labial 5 touching a posterior genial in the right side and the 4–5 touching a posterior genial in the left side. Genials elongate, longer than broad. All head shields with tiny irregularly distributed black papillae. We counted 29 teeth on the left and right lower jaw, and 29 in the left upper jaw, apparently all ungrooved.

In life, overall colouration is black, with bright regularly discontinuous pink-red to blue stripes on the dorsal side, and bright conspicuous yellow to pink-red on the ventral side.

After two months in ethanol, the specimen has lost the brightness of the colours, especially on the ventral side, but not on the ventral side of the tail. The main dorsal head colouration is black, with some bright yellow areas. The supralabials are completely bright yellow, except the last two which also show a small black area on the upper part of the scales. A black stripe can be observed from the nasal scale through the eye and towards the posterior border of the head, covering the lower postocular scale but not the upper one that is bright yellow. Rostral, internasals and most of the surface of the prefrontals are bright yellow with few black patches. The yellow colouration extends above the eye, covering ca. 60% of the surface of the supraoculars, and the upper postoculars and seven temporal scales at each side bright yellow with a thin black border. Small yellow patches can be observed on the frontal and parietal scales. Four discontinuous stripes are present on the dorsum, consisting of pentagonal bright pink-red blotches arranged in lines of dorsal scales. These stripes are of a bright pink-red colour in the first half of the body and of a light blue colour in the second half of the body and tail. The change in colouration between the pink-red and blue happens around the central part of the body (corresponding to ventrals 83 to 87), where pink-red fades into blue. The discontinuity in the colour of the stripes is due to single scale colouration, with the posterior edge of each scale being dark black, while the rest of the scale is of vivid colour. The colour stripes correspond to dorsal scale rows number 4, 7, 11 and 14, all four lines originating in the same area behind the head, three scales separated from the parietals and one scale separated from another except the two central lines that have two scales of separation. Halfway to-

Figure 3. (a) Additional specimen of *Liophidium pattoni* (not collected), photographed by Goran Safarek at Masoala National Park on 15 October 2001 in Lohatrozona; (b-d) additional specimen of *L. pattoni* from a site named Tampolo in Masoala National Park, at about 150 m distance from the beach, found hidden in the leaf litter of secondary vegetation, photographed on 15 November 2006 around 14:00 h, by Sebastian Gehring; (d) shows the dorsal colour pattern of the second Masoala specimen in direct comparison to that of (e) the holotype from Makira (ZSM 186/2009).

wards the tail, both right and left lines merge. The first dorsal scale is bright yellow. The ventral colouration is bright yellow from the mental scale to ventral 158, where traces of pink-red can be observed towards the precloacal that is mostly pink-red. The ventral side of the tail is of a conspicuous pink-red. Each ventral scale shows a small black area of crescent shape that does not exceed half of the surface of each scale transversally, and does not reach the sides of the scales which are completely yellow.

Genital morphology: For examination of hemipenial structure, only incomplete preparations of the left hemipenis of the holotype of *L. pattoni* were available. Apparently the left hemipenis partly retracted during the fixation process after having initially been completely everted in the freshly dead specimen. We therefore cut the organ from the preserved holotype, and following the method of Pesantes (1994) and Ziegler & Böhme (1997), transferred it for 48 hours to 2% KOH before attempting to carefully evert the uneverted part of the organ, which was partly successful but caused considerable damage to the apical structures. Therefore, we divide our description in two parts: the unambiguously visible basis of the pedicel, and the tentatively reconstructed general shape of the terminal part of the hemipenis: (1) The pedicel of the hemipenis of *L. pattoni* is massive (maximum width 4.4 mm) and covered by large and strong spines at the basis. These spines are more strongly developed on the sulcal than the asulcal side (where they are missing centrally), but are missing at the sulcus spermaticus proper. The sulcus spermaticus runs singly for about 3 mm and then bifurcates. Distal from the massive basis, and ca. 1 mm after the division of the sulcus spermaticus, the spines become distinctly smaller (and are almost completely missing from the center of the asulcal side). There are no spines in between the two parts of the sulcus in the area distal to its bifurcation. There is no sign of a division of the hemipenis into two lobes until about 2.5 mm distally from the bifurcation of the sulcus spermaticus where the organ is damaged. (2) As far as is apparent from the partly damaged organ, the hemipenis does not seem to have long lateral lobes as known from *L. apperti, L. torquatum* and *L. trilineatum* (Domergue 1984, Ziegler et al. 1996). The area distal to the base of the pedicel seems to be less wide, but it is unclear whether this may be an artifact caused by the eversion after fixation. We also cannot exclude that the hemipenis may in fact contain (uneverted) long lobes (or short lobes as in *L. therezieni* and *L. vaillanti*; Domergue 1984).

Habitat and ecology: The holotype was collected during a sunny day while it was crossing a footpath in the Makira Plateau. The vegetation of the area was a primary rainforest, well preserved although with some recent areas of fragmentation because of human activities. The stomach of the snake contained a small lizard (an adult of *Madascincus melanopleura*) suggesting that *L. pattoni* probably hunts through the rainforest searching for small ground-living animals.

Intraspecific variation: Beside the holotype two other specimens were photographed in the lowlands of Masoala National Park (Fig. 3), but were not collected. From the comparisons of the photographs with the holotype from the Makira Plateau, several differences can be noted. The amount of yellow in the frontal part of the head (from the rostral to the frontal scale) is more extensive in the specimens from the lowlands. In one of the Masoala specimens this yellow extends above the eye to the posterior border of the head as in the holotype, although it reaches the beginning of the pink-red dorsal lines (Fig. 3a), while in the holotype and the other Masoala specimen (Fig. 3d) it does not. The temporal scales are almost completely yellow, with a much less conspicuous black border. In a lowland specimen (see Fig. 3d), the fusion of two of the temporal scales on the left side of its head can be observed, while those scales are not fused on the right side of the head. The main differences between specimens correspond to the dorsal lines. In the lowland individuals each pair of left and right dorsal stripes start in the same scale while in the holotype they are separated (see Fig. 3d, e). Also, in the holotype there are three black scales from the parietals to the first scale with colour in the external stripes, while there are four in the lowland individuals and the internal stripes start at least two scales further back in those lowland individuals (see Fig. 3d,e). The lateral stripes in the holotype are formed by single scale rows (rows 4 and 14), while in the lowland specimens a clear zig-zag pattern can be observed (Fig. 3a, b) as dorsal scales 4/5 and 14/15 show pink-red in every row becoming blue towards mid-body. A photograph of an additional specimen of unknown origin was published in Bradt et al. (1996) and originally identified as "probably a juvenile *Pseudoxyrhopus microps*". This specimen shows an uninterrupted connection of the elongated yellow spot behind the eye and the beginning of the pink stripes and agrees with the lowland specimens from Masoala by a zig-zag pattern in the lateral pink stripe, and (as far as recognizable) by a connection of the two pink stripes at their beginning (at least on the right side of the body) in the neck region. However, it differs from both, the specimens from Masoala and Makira, by the beige (vs. yellow) colour of the light spot on the anterior part of the head (covering the internasals and prefronatalia) and by lacking yellow colour on the supraoculars.

Phylogenetic position and genetic differentiation: All analyses of the combined data set (Fig. 4) are unambiguous to place *Liophidium pattoni* with strong support as the sister species of *L. rhodogaster*. The clade comprising these two taxa is sister to all other *Liophidium*, which are likewise placed in a monophyletic group with high support. Exploratory analyses of single-gene datasets for 16S, cytochrome *b* and c-mos were concordant in placing *L. pattoni* with *L. rhodogaster* (not shown). Uncorrected pairwise genetic distances in the cytochrome *b* gene were 10.7–11.3% between *L. pattoni* and *L. rhodogaster,* 11.8–15.7% between other nominal species of *Liophidium*, and 5.2% between the two included specimens of *L. rhodogaster* (from southern and northern Madagascar). Uncorrected pairwise distances in the 16S rRNA gene were 2.6–2.8% between *L. pattoni* and *L. rhodogaster,* 2.2–5.1% between other *Liophidium* species, and 1.0% between the two *L. rhodogaster* specimens. The genetic differentiation of *L. pattoni* from its sister species, *L. rhodogaster* is therefore in general at similar levels as observed among other *Liophidium* species, but surprisingly

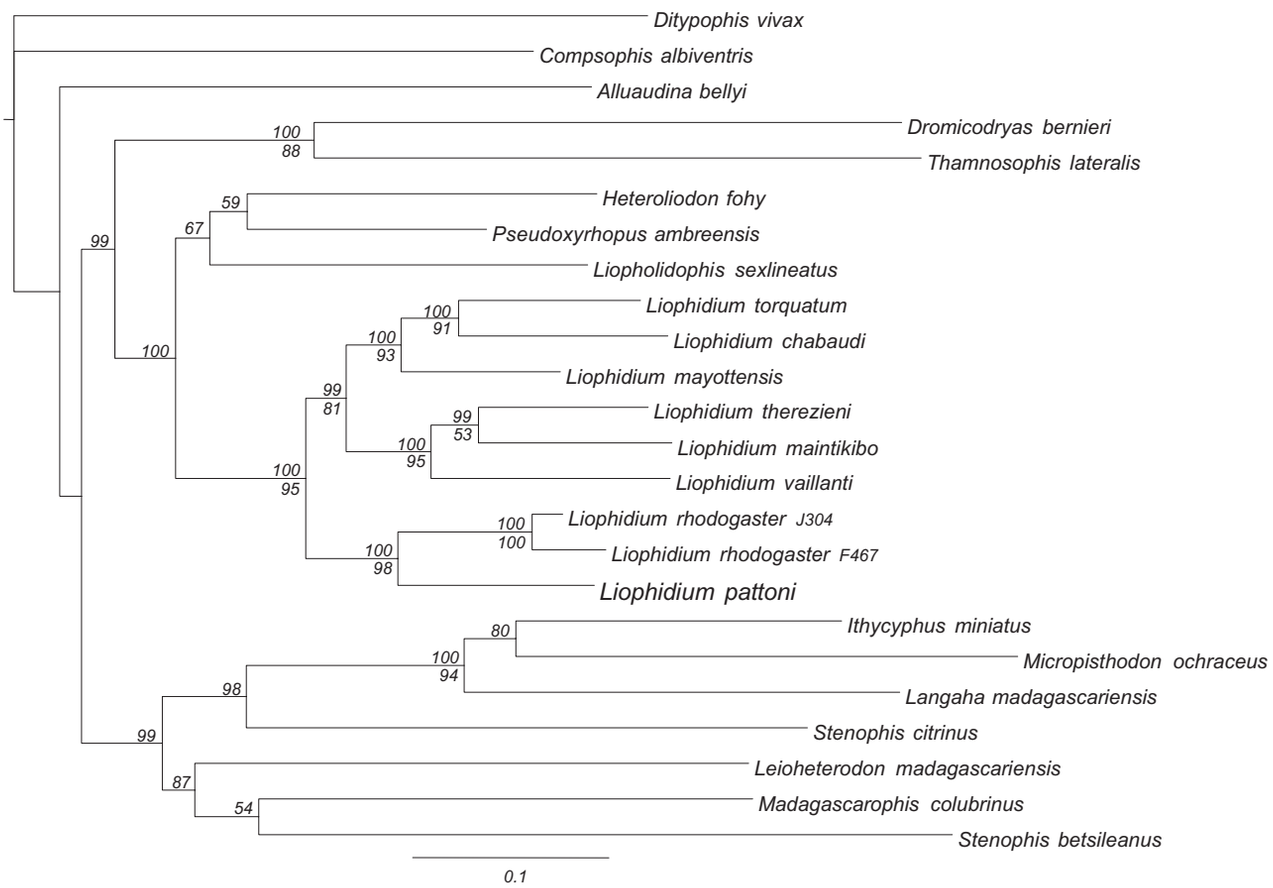

Figure 4. Bayesian phylogram based on combined sequences of the mitochondrial cytochrome *b* and 16S rRNA genes, and the nuclear c-mos gene (2206 bp aligned length). Posterior probabilities are shown above branches, parsimony bootstrap values below branches.

this species pair is at the lower bound of the range of differentiation values in the genus *Liophidium*. The Comoroan species, *L. mayottensis* is well supported as the sister species of *L. torquatum* and *L. chabaudi*, and nested within the genus.

Etymology: The species is named after Jim Patton, renowned mammalogist who recently developed a special interest in the Malagasy fauna. He and his wife Carol were amazing field companions from whom we learned a lot and enjoyed our time together during our recent joint field expeditions to Madagascar.

Distribution: So far, the species is known from two sites on the Masoala Peninsula, one site in the Makira Plateau, and possibly from one observation in the Ranomafana National Park (E. Rajeriarison pers. comm.). Although there is no picture from the Ranomafana individual, the observer is an experienced guide and the species is distinct enough that it cannot be confused with other snakes in Madagascar, but this record clearly is in need of confirmation. According to these few observations, the species may be widespread throughout the eastern coast of Madagascar, spanning a wide altitudinal range from sea-level to ca. 1100 m in the Makira Plateau, and occurring in very different environments from warm lowlands to relatively cool mountain rainforests.

Discussion

Snakes with bright colouration are usually strongly poisonous or they are mimics of some poisonous species, and such colourations are aposematic or warning signals to predators (e.g. Smith 1977, Savage & Slowinski 1992, Niskanen & Mappes 2005). In Madagascar, no snake has been reported to be strongly poisonous, although a few species have some poison that however is not lethal to humans (*Madagascarophis* spp., *Leioheterodon modestus* – Mori 2002, *Ithycyphus miniatus* – Mori & Mizuta 2006, *Langaha madagascariensis* – D'Cruze 2008). Out of more than 90 species of snakes described from Madagascar (belonging to the families Boidae, Lamprophiidae and Typhlopidae) only two species show a very bright dorsal colour pattern: *Stenophis citrinus* and *Liophidium pattoni*. *Stenophis citrinus* is an arboreal small-sized species with a unique colour pattern consisting of alternation of bright yellow and black cross bands on body and tail. Such a colouration pattern in potential prey is known to be avoided by birds for example (Schuler & Hesse 1985). Despite the colourations displayed by both species, neither of them seems to be poisonous, nor shows any aggressive behaviour. The origins of these aposematic colourations are unclear and can indicate either that these snakes are actually poisonous, which is not likely as they showed no biting behaviour when caught, or that they are distasteful to preda-

tors, or that they mimic poisonous species, e. g. black millipedes with red spots which resemble *L. pattoni* in size and colour pattern and are commonly encountered in Malagasy rainforests.

The unique and beautiful colour pattern of *L. pattoni* distinguishes it from any other species of snake from Madagascar. For the time being we consider the colour differences observed between the different specimens photographed from Masoala peninsula and the holotype of *L. pattoni* collected in the Makira plateau as intraspecific variation. However, it is interesting to observe such differences between highland and lowland specimens, indicating the possibility that the specimens from Masoala represent a very similar sibling species with slight differences in colouration, which needs to be investigated and clarified.

The phylogenetic data suggest three clades in *Liophidium*, the one constituted by *L. rhodogaster* and *L. pattoni* being sister to the rest of species, and one the well-supported clade formed by *L. therezieni, L. maintikibo* and *L. vaillanti* nested within *Liophidium*. This suggests that several morphological traits present in those three species, which distinguish them from other Malagasy *Liophidium* (like higher number of ventral scales, lack of a loreal scale and the presence of 7 supralabials with 3 and 4 in contact with the eye instead of 8 supralabials and 4 + 5 in contact with the eye), are derived. The species from Mayotte Island is deeply nested within the genus, and highly divergent from its sister taxa, suggesting that it dispersed to Comoros from Madagascar in the past. Here, we provide new molecular data for five species from this genus which helped to obtain a well supported phylogeny and clarify relationships at the species level. New molecular data are needed from *L. apperti* and *L. trilineatum* to complete and fully resolve the phylogenetic relationships in this genus.

Hemipenial morphology of *L. pattoni* unfortunately could not be satisfyingly determined. However, the presence of very large spines at the basis of the pedicel is not known from any other *Liophidium* except for *L. torquatum* (Ziegler et al. 1996). Because the genital morphology of *L. rhodogaster,* the apparent sister species of *L. pattoni,* is not known, we cannot draw a conclusion of possible evolutionary patterns in this character.

There is little information available for *Liophidium pattoni* and it is striking that this apparently widespread species has remained undescribed until now, despite its unique distinctive colouration. According to the available distribution records, the species may be present in much of eastern Madagascar, and it certainly spans a wide altitudinal range in the North East. It is unclear why so few records for this spectacular species are available, suggesting that it may occur only in low densities across its range.

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