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# New insights into the systematics and molecular phylogeny of the Malagasy snake genus *Liopholidophis* suggest at least one rapid reversal of extreme sexual dimorphism in tail length

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**Abstract** The pseudoxyrhophiine snake genus *Liopholidophis* Mocquard, 1904 (family Lamprophiidae) is endemic to Madagascar and according to its present definition comprises six medium-sized, terrestrial and diurnal snake species, most of which are characterised by an unusual and extreme sexual dimorphism in tail length. We performed molecular phylogenetic analyses using nucleotide sequences of three mitochondrial genes (16S rRNA, cytochrome *b* and cytochrome oxidase I) and one nuclear gene (c-mos) for all described and two additional species newly described herein. The two new species are very small sized (total length: 234–312.5 mm), have comparatively short tails and a reduced number of dorsal scale rows (15 at midbody), the lowest value among all non-scolecophidian snakes of Madagascar. Both species are secretive or rare, and they have a reddish belly in life that fades in preservative. In terms of colouration and morphology, they are most similar to each other and furthermore to *Liopholidophis rhadinaea.* Together with this species and *L. dimorphus*, they form a well-supported clade. *Liopholidophis baderi* sp. nov. from central eastern Madagascar is characterised by 149–158 ventrals and 71–77 subcaudals, whereas the similar *L. oligolepis* sp. nov. from the northeast has even fewer ventrals (137) and subcaudals (54). The phylogenetic tree suggests that the tail length dimorphism in the genus *Liopholidophis* has evolved in a complex pattern including at least one reversal. The phylogenetic position of the two new dwarf species indicates that both the absence of extreme sexual dimorphism in tail length and their body size reduction are derived and probably correlated features. Also the close phylogenetic relationships between the long-tailed *L. sexlineatus* and the similar but relatively short-tailed *L. varius* demonstrate that dimorphism in tail length can be strongly mitigated in short evolutionary time periods.

**Keywords** Serpentes · Lamprophiidae · Miniaturisation · Sexual dimorphism · Tail length

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## Introduction

Sexual dimorphism has always fascinated biologists, even more so since Darwin (1859) proposed sexual selection as a mechanism generating in many cases the striking differences between males and females of the same species. According to him, the two main forms of selection are natural and sexual selection (although mainly proposed for human evolution, see Darwin 1871), representing the major forces in evolution. Other researchers have subsumed sexual selection as a subcategory of natural selection, but this alternative view does not downgrade the evolutionary relevance of the former. Many sexually dimorphic organisms have since been identified throughout the animal kingdom (for an overview about sexual selection, see Kirkpatrick 1987), and the role of sexual selection in speciation has also been thoroughly discussed (reviewed by Ritchie 2007). One possible hypothesis to explain sexual dimorphism is Fisher's runaway model (1915): traits that do not directly increase fitness may also be objects

of sexual preference and hence sexual selection. The resulting secondary sexual characters can be ornaments that serve as visual attraction or weapons (reviewed by Emlen 2008) used in male-male competition. However, sexual selection by females and intrasexual competition (for example for breeding opportunities) may be also crucial factors and therefore should not be neglected (Clutton-Brock 2007). In some cases, signalling of putatively superior quality — in order to attract recognition of the opposite sex — becomes very costly. Zahavi's handicap principle (1975, 1977) states that these extreme costs cannot be afforded by low-quality signallers; hence, the signals resulting from such an extreme investment become reliable. The most well-known example is probably the beautiful and 'costly' plumage of the peacock, which is preferred by peahens and therefore favoured and selected over many generations (Petrie et al. 1991).

However, sexual dimorphism can also occur in the absence of obvious sexual selection. For example, female-biased size dimorphism in many vertebrates apparently results from natural selection for maternal quality or for offspring number, indicating that both natural and sexual selection are potentially important. Furthermore, sexual dimorphism might also result from morphological constraints imposed on members of one sex but not on members of the other sex (King 1989). Sexual dimorphism in snakes is typically reflected in both snout-vent length and tail length: The snout-vent length may be male-biased or female-biased, whereas sexual dimorphism in tail length is nearly always male-biased (Shine 1978, 1989; King 1989). Male snakes typically have longer tails relative to their body length than females, but the extent of this dimorphism varies among species (King 1989). Based on the study of one species (*Thamnophis sirtalis parietalis*), Shine et al. (1999) suggested that males with longer tails relative to body length have longer hemipenes and that sex divergence in tail length relative to body length in snakes reflects the action of sexual selection for male mating success. Nevertheless, in some cases it seems that the actual tail length of male snakes may be the result of complex, and even counteracting or counterbalancing actions. In the case of the sea-snake *Laticauda colubrina*, Shine and Shetty (2001) found that both sexual and natural selection affect tail length in an unexpected complexity: male snakes with longer tails grew slower and they were more likely to survive, but males with normal tails swam faster and had better mating chances. Concerning body size, males grow larger, relative to conspecific females, in species with male-male combat than in species not recorded to show such behaviour (Shine 1994).

Among the endemic radiation of pseudoxyrhophiine snakes from Madagascar and the Comoro islands strong sexual dimorphism is rare, although the dimorphic projections of the snout tip in the genus *Langaha* are one of the most spectacular cases overall in snakes. Few species, including the Madagascan *Langaha madagascariensis*, *Ithycyphus miniatus* and the two *Lycodryas* species occurring on the Comoros, show distinct sexual dichromatism (Cadle 2003; Hawlitschek et al. 2012).

The genus *Liopholidophis* Mocquard 1904, is endemic to Madagascar and part of a large and diverse radiation of lamprophiid snakes, the Pseudoxyrhophiinae (Nagy et al. 2003). According to the most recent revisions (Cadle 1996a, 1998; Glaw et al. 2007), six species are currently recognised: *L. dimorphus, L. dolicocercus*, *L. grandidieri*, *L. rhadinaea*, *L. sexlineatus* and *L. varius*. All described species generally share 17 dorsal scale rows at midbody, and all but *L. varius* are characterised by an extreme sexual dimorphism in tail length. Males have much longer tails, a higher number of subcaudal scales and usually a longer snout-vent length than females; consequently, their total length is also longer. Cadle (1996a) noted that *L. rhadinaea* shows remarkable similarities to species of the genus *Liophidium* in morphology and colouration, making a clear definition and delimitation of these two genera difficult. These uncertainties prompted him even to classify one snake specimen, collected in 1966 at Perinet (= Andasibe) and originally identified as *Liophidium* sp. (Domergue 1988), as "genus and species inquirenda" (Cadle 1996a: 454–458). In 1996 we collected a second specimen of this mysterious snake from the same locality with very similar characteristics, indicating that an undescribed species is involved rather than an aberrant specimen. Furthermore, in 2005 we found a superficially similar specimen in northeastern Madagascar that however differed by various morphological characters from the Andasibe specimens. In the following we study these dwarf snakes and conclude that they belong to two new species for which we provide formal taxonomic descriptions. In addition we provide a molecular phylogenetic analysis of *Liopholidophis* based on a complete sampling at species level that allows new and unexpected insights into the evolution of the extreme sexual dimorphism of tail length in this genus.

## Materials and methods

The snakes were anaesthetised by injection with chlorobutanol, fixed in formalin or 98% ethanol, and stored in 70% ethanol. Muscle tissue samples were taken from freshly killed specimens in the field and preserved in 98% ethanol. Snout-vent length (SVL) and tail length were measured to the nearest millimetre with a calliper. We follow Cadle (1996a) regarding the terminology of meristic and mensural data. Ventral scales were counted without preventrals. Museum acronyms are: Muséum national d'Histoire naturelle, Paris (MNHN); Museo Regionale di Scienze Naturali, Torino (MRSN); Université d'Antananarivo, Département de Biologie Animale (UADBA); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); Zoologische Staatssammlung München (ZSM).

FGMV, DRV and ZCMV are field numbers of specimens that will be catalogued in one of the mentioned museum collections.

Measurements and counts were taken as follows: snout-vent length (from the rostral to the posterior margin of the anal scute); tail length (from the posterior margin of the anal scute to tip of tail); total length (sum of snout-vent length and tail length); head length (from the rostral to the posterior margin of the angle of the jaws); head width (measured at the widest point at the level of the temporal region). Scale dimensions were ascertained at their widest point by using a digital calliper under a dissecting microscope. Measurements were rounded as follows: snout-vent length and tail length to the nearest 0.5 mm; all remaining measurements to the nearest 0.1 mm. Ventral counts follow Dowling (1951). Preventrals are defined as scales anterior to the ventrals, which are broader than long. Dorsal scale rows were counted at the tenth ventral, at midbody (half of snout-vent length), and at the tenth ventral anterior to the anal scute. The exact position of the reduction from 17 to 15 scale rows at the neck is given in the specimen descriptions. Dorsocaudal scale rows include all scale rows around the tail without counting subcaudals. Subcaudal counts are given in the left/right order. Symmetrical characters are given in the left/right order if they are unequal. All teeth counts were done on the left side only. Whenever the data ascertained by our own differ from the literature, we give the data from the literature in brackets.

DNA was extracted using standard phenol-chloroform protocols (modified after Sambrook et al. 1989) or by using commercial DNA extraction kits following the manufacturer's protocol. The complete mitochondrial gene cytochrome *b* (cytb), fragments of the mitochondrial genes 16S rRNA (16S) and cytochrome oxidase I (COI) as well as the nuclear oocyte maturation factor Mos (c-mos) were amplified in PCRs using the same primers as Nagy et al. (2003) and Nagy et al. (2012). PCR products were directly sequenced on different ABI capillary sequencers (Life Technologies). The sequences were checked for quality and aligned either by hand (cytb, COI and c-mos) or in MAFFT 6 (16S rRNA, Katoh et al. 2002; Katoh and Toh 2008). The concatenated data set consisted of 2,860 nucleotide positions (regarding complete sequences only). Parsimony analyses with 2,000 bootstrap replicates were carried out using the computer program PAUP*, version 4b10 (Swofford 2002). Subsequently, the concatenated data set was partitioned according to codon positions and genetic markers; hence a total of ten data partitions were set (i.e. three partitions each for the protein-coding genes cytb, COI and c-mos, and one partition for the 16S data). Best-fit nucleotide substitution models for each partition were selected by jModeltest v0.1.1 (Posada 2008) under the Bayesian information criterion (BIC). The Bayesian analysis of phylogenetic inference was performed with MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). Two parallel runs, each including four Markov chains, were run for 10 million generations, and every 1,000$^{th}$ tree was sampled. Convergence was checked by Tracer v1.5 (Rambaut and Drummond 2009), and the first 10% of the trees was discarded as burn-in. In all phylogenetic analyses, *Alluaudina bellyi* was used as outgroup taxon. DNA sequences were deposited in GenBank; voucher specimens and accession numbers are listed in Table 1.

To trace the evolution of sexual dimorphism in *Liopholidophis*, we reconstructed ancestral states of the relation between mean tail length and mean snout-vent length, each separately for males and females. We used the parsimony reconstruction method in Mesquite 2.72 (Maddison and Maddison 2009) and two different maximum likelihood algorithms, as implemented in the packages APE (Paradis et al. 2004) and GEIGER (Harmon et al. 2008) of the R 2.14.1 software (R Development Core Team 2011). In addition to our own data, we used data from Cadle (2009). Additionally, we added measurement data from *Liophidium torquatum* to account for the most closely related genus. Only data of two male specimens were available from *L. baderi*, and only of a single female of *L. oligolepis*, so we treated the values of the opposite sex as missing data in the parsimony analysis. This was not possible in the maximum likelihood analyses because these algorithms do not accept missing data. We took two different approaches to solve this problem. In the first approach, we inserted the measured values of male *L. baderi* for the (missing) male *L. oligolepis* and those of female *L. oligolepis* for the (missing) female *L. baderi*. We believe that this is a feasible approach because both species are closely related and very similar. In the second approach, we removed the species whose data are missing completely from the tree, each for the calculation of male and female values. Finally, we compared the results that were yielded by both approaches.

## Results

### Molecular phylogeny and ancestral character state reconstructions

The data set of DNA sequences consisted of 2,860 characters, of which 538 were parsimony-informative. The Bayesian analysis recovered the tree shown in Fig. 1. All species of *Liopholidophis* belong to a monophylum that is clearly distinct from the genus *Liophidium* (which is represented by one species of each major intrageneric clade). The monophyly of *Liopholidophis* received relatively high support, whereas each of its two major subclades is recovered with maximal support. One of these major subclades, here called clade A, includes *L. dimorphus*, *L. rhadinaea* and the two dwarf species *L. baderi* sp. nov. and *L. oligolepis* sp. nov. described below. The two new species are recovered as sister taxa with high support, whereas the relationships of *L. rhadinaea* and *L. dimorphus*,

**Table 1** Samples used in the current study with GenBank accession numbers (AN)

| Species | Sample ID | Locality | Voucher specimen | GenBank AN c-mos | GenBank AN cytochrome *b* | GenBank AN 16S rRNA | GenBank AN COI |
|---|---|---|---|---|---|---|---|
| *Alluaudina bellyi* | J87 | Berara | MRSN (FAZC 10622) | AY187966 | AY188005 | AY188044 | JQ909245 |
| *Liophidium torquatum* | J84 | Mt. d'Ambre | Not collected | AY187984 | AY188023 | AY188062 | JQ909410 |
| *Liophidium rhodogaster* | J304 | Ranomafana NP | ZSM 784/2003 | DQ979971 | DQ979978 | DQ979964 | JQ909405 |
| *Liopholidophis dimorphus* | FGZC 491 | Mt. d'Ambre | ZSM 252/2004 | DQ979973 | DQ979980 | DQ979966 | JQ909414 |
| *Liopholidophis dolicocercus* | ZCMV 2048 | Marojejy NP | ZSM 60/2005 | DQ979975 | DQ979982 | DQ979968 | JQ909415 |
| *Liopholidophis sexlineatus* | J98 | Mandraka | UADBA (FGMV 2000–38) | AY187985 | AY188024 | AY188063 | JQ909421[1] |
| *Liopholidophis baderi* | 62235 | Andasibe | ZFMK 62235 | KC988269 | KC988264 | - | JQ909423 |
| *Liopholidophis oligolepis* | FGZC 2796 | Marojejy NP | ZSM 153/2005 | KC988270 | KC988265 | KC988274 | JQ909422 |
| *Liopholidophis rhadinaea* | ZCMV 2921 | Ambatolahy river | ZSM 894/2006 | KC988271 | KC988266 | KC988275 | JQ909418 |
| *Liopholidophis varius* | DRV 5679 | Ambatodisakoana | Uncatalogued | KC988272 | KC988267 | KC988276 | JQ909424 |
| *Liopholidophis grandidieri* | FGZC 4686 | Tsinjoarivo | ZSM 345/2010 | KC988273 | KC988268 | KC988277 | JQ909417 |

[1] *Liopholidophis sexlineatus*: COI sequence from ZCMV 2560 (Ankaratra)

shown as sister species in Fig. 1, are poorly resolved. The second major subclade, here called clade B, comprises *L. dolicocercus*, *L. grandidieri*, *L. varius* and *L. sexlineatus* with a strongly supported sister relationship between *L. sexlineatus* and *L. varius* and a less well-supported relationship between *L. dolicocercus* and *L. grandidieri*. Uncorrected pairwise sequence divergences in the cytochrome *b* gene were 7.7% between *L. baderi* and *L. oligolepis*; 13.0% between *L. baderi* and *L. rhadinaea*; 12.2% between *L. oligolepis* and *L. rhadinaea*; and 7.2% between *L. sexlineatus* and *L. varius*. Distances between species from the two major clades ('interclade divergence') range from 15.9–17.3%. Sequence divergence in the nuclear c-mos gene is rather low between the species of the *Liopholidophis rhadinaea* group (clade A). Only six of 570 bp were variable and no heterozygous sequences were observed in the c-mos data set. The highest divergences were found between *L. dimorphus-L. rhadinaea* (5 bp) and *L. rhadinaea-oligolepis* (5 bp), followed by *L. rhadinaea-L. baderi* (4 bp), *L. dimorphus-oligolepis* (2 bp), *L. dimorphus-L. baderi* (1 bp) and *L. baderi-L. oligolepis* (1 bp).

Figure 1 also shows the results of the ancestral character state reconstruction for the relative tail length (i.e. the relation tail length/snout-vent length). Relative tail length in males is generally higher in the species of clade B than in those of clade A, with *L. varius* as the only exception. The values between the closely related sister species *L. varius* (0.48) and *L. sexlineatus* (0.90) show the highest difference compared with the other species pairs, suggesting a strong reduction of relative male tail length in the former species. The longest relative male tail length is found in *L. grandidieri* (1.18) and *L. sexlineatus* (0.90), the shortest in *L. baderi* (0.40) and *L. varius* (0.48). According to the maximum likelihood reconstruction, relative male tail length was 0.79 in the ancestor of clade B, 0.57 in the ancestor of clade A and 0.64 in the ancestor of all *Liopholidophis* species.

In all cases, the differences in absolute values between the two methods of maximum likelihood reconstruction (APE vs. GEIGER) were less than 0.01. The differences between the results of our two maximum likelihood approaches (replace missing values with values from a sister taxon vs. cropping the branch of the taxon with missing values) were also very small, with a mean difference in absolute values of less than 0.02. All values differed by less than 0.08 between the two approaches. Notably, ancestral state reconstruction using parsimony yields lower relative male tail length values: 0.53 for the ancestor of clade A, 0.60 for the ancestor of clade B and 0.55 for the ancestor of all *Liopholidophis* species.

Differences among species in the relative tail length of females (Fig. 1) are generally much lower than in males, ranging from 0.30-0.55. Reconstructed values using maximum likelihood and parsimony are very similar, and the differences between them are never larger than 0.03. The lowest values are found in *L. oligolepis* (0.30) and *L. varius* (0.33), confirming a significant tail length decrease during the evolution of these species.

Quantifying sexual dimorphism in tail length as the ratio between relative tail lengths of males and females per species results in the lowest values in *L. sexlineatus* (0.43) and *L. grandidieri* (0.47). In both these species, female relative tail length is less than half the respective male value. If arbitrarily defining extreme tail length dimorphism as cases where relative female length is around or below half the relative female tail length (values 0.53-0.43), then this applies to four species belonging to both clade A (*L. rhadinaea*) and clade B (*L. dolicocercus, L. grandidieri, L. sexlineatus*). According to the ratios of the reconstructed values using ML (Fig. 1), two independent origins of this extreme dimorphism are hypothesised

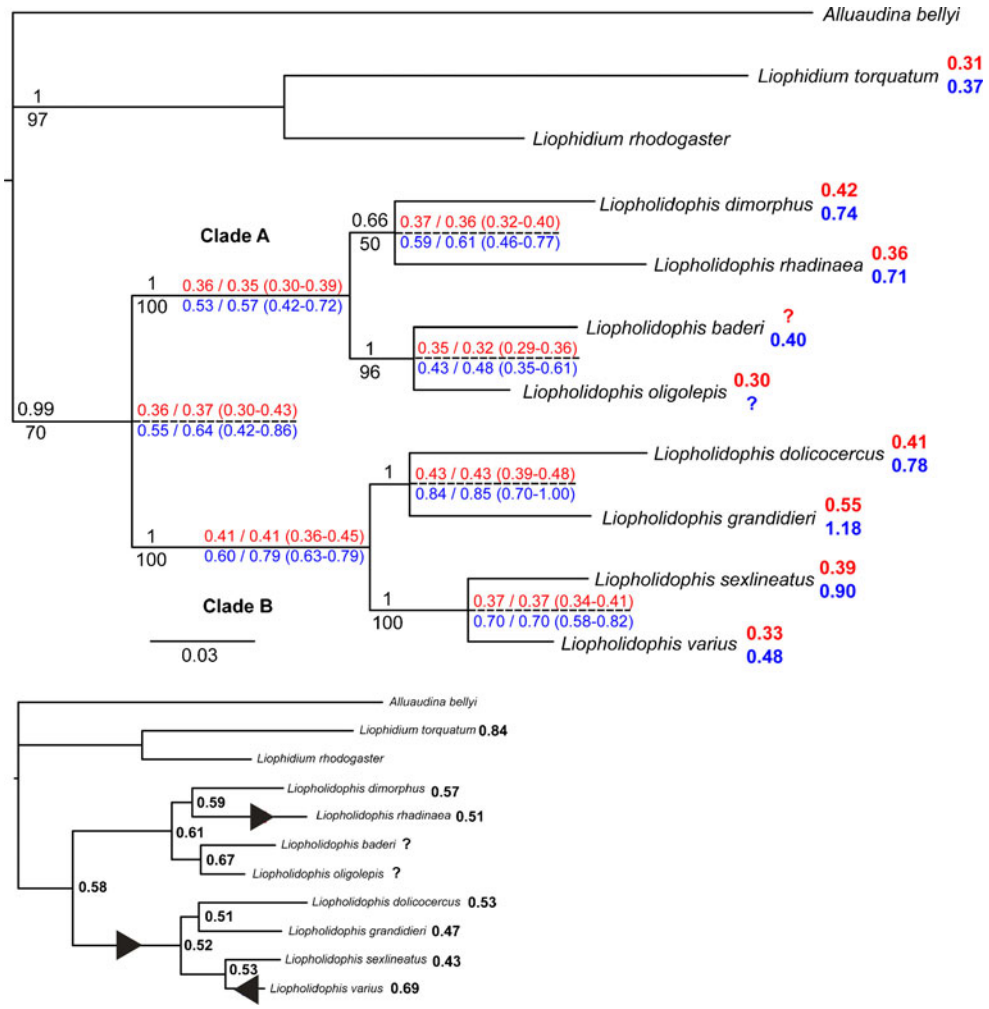


**Fig. 1** Phylogenetic tree of all *Liopholidophis* species based on sequences of three mitochondrial and one nuclear gene (16S rRNA, cytb, COI and c-mos). For *L. baderi* no 16S sequence was available. Bayesian posterior probabilities (10 million generations) are given above branches, parsimony bootstrap values (2,000 replicates) below branches. The relation of tail length/snout-vent length (red: female, blue: male) is given for all species of *Liopholidophis*, and for *Liophidium torquatum*, on the right of the species names. Reconstructed values for nodes are given at the branches, as results of parsimony/maximum likelihood (95% confidence interval). The lower figure shows the same tree with sexual dimorphism in relative tail length plotted on taxa (expressed as ratio of relative tail length of males/females). Ancestral values calculated on ML-reconstructed values for males and females. Symbols show origin (>) and reversal (<) of extreme dimorphism (values 0.43-0.53, i.e. females having relative tail lengths roughly half that of males or lower)

(in *L. rhadinaea,* and in the ancestor of clade B), as well as one reversal (in *L. varius*).

## Systematic accounts

*Liopholidophis baderi* sp. nov. (Fig. 2)
*Liophidium* sp. (Domergue 1988)
"genus and species inquirenda" (Cadle 1996a)

*Holotype* ZFMK 62235, probably adult male (right hemipenis partially everted), collected dead on a trail near Hotel Feon'ny Ala (18° 56.845'S, 48° 25.078'E, ca. 940 m a. s. l.), at ca. 2.5 km distance from the village of Andasibe, central eastern Madagascar, on 31 January 1996 by F. Glaw.

*Paratype* MNHN 1988.331, probably adult male (hemipenes fully everted), collected at Perinet [=Andasibe], central eastern Madagascar, on 19 December 1966 by E. R. Brygoo (according to Domergue 1988), but see Cadle (1996a: 455).

*Diagnosis* A species attributed to the genus *Liopholidophis* because of its general morphology and its position in the

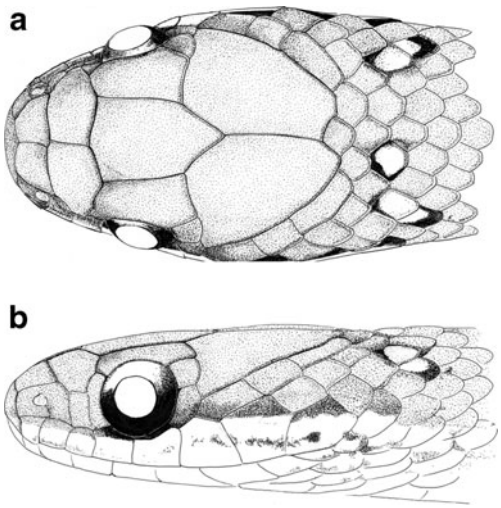


**Fig. 2** Head drawings of *Liopholidophis baderi* sp. nov. (holotype, ZFMK 62235) in (**a**) dorsal and (**b**) lateral view

molecular phylogenetic tree (Fig. 1). The new species differs from all species of *Liopholidophis*, the superficially similar *Liophidium*, and all other Madagascan lamprophiid snakes by the presence of only 15 dorsal scale rows around the midbody (versus at least 17 scale rows at midbody in all other advanced Malagasy snakes). In addition it differs from all other species of *Liopholidophis* except *L. rhadinaea* by much smaller size of males (maximum total length 312.5 mm versus 889–1636 mm), lower number of subcaudals in males (71–77 versus 88–221), short relative tail length (male tail length/total length 0.28–0.29 versus 0.30–0.55), presence of three light spots in the neck (versus absence) and a uniformly red belly in life that fades in preservative (never red in all other species). The new species is similar in general habitus and colouration (red belly in life, light spots in the neck) to *Liopholidophis rhadinaea* (Fig. 5) but differs from this species by having fewer ventrals in males (149–158 versus 170–179), fewer subcaudals in males (71–77 versus 126–137), and smaller size (maximum total length of males 312.5 mm versus 749 mm, maximum snout-vent length of males 221.5 mm versus 429 mm). *L. baderi* is the sister species and most similar to *L. oligolepis* sp. nov., which will be described and diagnosed below. *L. baderi* differs furthermore from all other *Liopholidophis* species by substantial genetic differentiation.

*Description of the holotype* Adult male, in good state of preservation. Total length 283.0 mm, snout-vent-length 205.0 mm, tail length 78.0 mm (28% of total length). Greatest head width (temporal region) 5.1 mm, head length (tip of snout to end of mandibles) 8.4 mm. Distance between tip of snout and the posterior edge of the parietals 7.0 mm. Body dorsoventrally depressed (probably according to the finding situation dead on a road). Head only little wider than neck. Pupil round. Eye large, diameter horizontally 1.7 mm, larger than the distance between anterior margin of eye and posterior edge of nostril (1.1 mm). Dorsal scales smooth, without apical pits in 15–15–15 rows, but 17 scale rows directly behind the head. Scale row reduction from 17 to 15 rows at the level of ventral 5. Two preventrals, 158 rounded, not angulated ventrals. One gular scale between the posterior inframaxillaries and the first preventral. Anal scute divided. Subcaudals 71/72 all divided plus terminal spine. Reduction of dorsocaudal rows from 8 to 6 at the level of subcaudals 9–12, from 6 to 4 at the level of subcaudals 33–36 and from 4 to 2 at the level of subcaudals 69–70.

Supralabials 8, with $4^{th}$–$5^{th}$ touching the eye. Infralabials 9, the first pair in contact behind the mental, $1^{st}$–$4^{th}$ touching the anterior inframaxillary, $4^{th}$–$5^{th}$ touching the posterior inframaxillary, the posteriormost infralabial reaches slightly beyond the posterior margin of the last supralabial. Two pairs of inframaxillaries both the same width, but the anterior (2.0 mm) pair slightly shorter than the posterior (2.4 mm). Rostral wider (1.8 mm) than high (0.9 mm) and visible from above. Nasal semi-divided (undivided above the nostril, divided below), touching first and second supralabial. One loreal present, higher (0.6 mm) than wide (0.4 mm), touching second and third supralabial. One preocular, scarely visible from above, not in contact with frontal, touching third and fourth supralabial. Two postoculars, lower one slightly larger than upper one, upper postocular in contact with parietal, lower postocular touching parietal, anterior temporal, fifth and sixth supralabial. Temporals 1+2+3. Dorsal surface of head shows the typical lamprophiid scalation consisting of nine shields. Frontal longer (2.8 mm) than wide (1.8 mm), longer than the distance to the posterior margin of rostral (1.5 mm). Parietals longer (3.3 mm) than the frontal.

Dentition: Maxillary teeth 25+2 without diastema, nearly same size, the last two teeth distinctly enlarged and ungrooved. Maxillary reaching beyond the palatine. Dentary teeth ca. 30, small, equal in size.

Colouration in preservative: General dorsal ground colouration brown. Dorsal rows 1–4 light brown become gradually darker vertebrally. Lower part of scale row five dark brown followed by a narrow pale stripe, situated in the middle of the scale and vertebrally bordered by very fine darker pigment. Upper part of row 5 and row 6 light brown. Rows 7+8 a little darker than rows before creating the appearance of a broad, indistinctly darker vertebral stripe. The pale lateral stripe starts six scales behind the posterior margin of the parietal and runs continuously on the fifth row on the body and on the second scale row on the tail nearly until the tip of tail. On the neck there are three distinct white spots. These ocelli occupy 1–1.5 scales and are bordered by a thin dark ring. Ground colour of dorsal side of head reddish brown. Lower part of the supralabials pale. A white stripe runs from the rostral across the supralabials until the neck. This stripe is indistinctly lighter than the pale colour of the supralabials and irregularly bordered ventrally by dark pigment from the sixth supralabial until the neck and dorsally from a weakly developed dark postocular strip, which starts at the lower margin of the eye and runs until the level of the third ventral. Underside of head, body and tail uniform pale in preservative, except the extreme outer margins of ventrals and subcaudals, which show the same light brown colouration as the first dorsal scale row. Photographs of the preserved holotype will be made publically available via the Reptile Database (http://www.reptile-database.org/). Details of life colouration unknown, but still with reddish venter when found shortly after death, fading in preservative into whitish.

*Description of the paratype* A detailed description of the paratype was already provided by Domergue (1988) and Cadle (1996a).

Adult male. Total length 312.5 mm, snout-vent length 221.5 mm, tail length 91.0 mm (29% of total length). Greatest head width (temporal region) 4.8 mm, head length (tip of snout to end of mandibles) 9.1 mm. Distance between tip of snout and

the posterior edge of the parietals 7.3 mm. Body slightly compressed laterally. Head only a little wider than neck. Pupil round. Eye large, diameter horizontally 1.6 mm, larger than the distance between anterior margin of eye and posterior edge of nostril (1.2 mm). Dorsal scales smooth, without apical pits in 15–15–15 rows, but 17 scale rows directly behind the head, scale row reduction from 17 to 15 rows at the level of ventral 4. Two preventrals, 149 rounded, not angulated ventrals. One gular scale between posterior inframaxillaries and the first preventral. Anal scute divided. Subcaudals 77/77 all divided plus terminal spine. Reduction of dorsocaudal rows from 8 to 6 at the level of subcaudal 11, from 6 to 4 at the level of subcaudals 31–33 and from 4 to 2 at the level of subcaudal 71.

Supralabials 8, with $4^{th}$–$5^{th}$ touching the eye. Infralabials 9, the first pair in contact behind the mental, $1^{st}$–$4^{th}$ touching the anterior inframaxillary, $4^{th}$–$5^{th}$ touching the posterior inframaxillary. Two pairs of inframaxillaries both the same width, but the anterior (2.3 mm) pair slightly shorter than the posterior (2.6 mm). Rostral wider (1.8 mm) than high (1.0 mm), visible from above. Nasal semi-divided (undivided above the nostril, divided below), touching first and second supralabial. One loreal present, higher (0.7 mm) than wide (0.4 mm), touching second and third supralabial. One preocular, scarely visible from above, not in contact with frontal, touching third and fourth supralabial. Two postoculars, lower one slightly larger than upper one, upper postocular in contact with parietal, lower postocular touching parietal, anterior temporal, fifth and sixth supralabial. Temporals 1+1+2/1+1+3. Dorsal surface of head shows the typical lamprophiid scalation consisting of nine large shields. Frontal longer (2.7 mm) than wide (2.1 mm), longer than the distance to the posterior margin of rostral (1.5 mm). Parietals longer (3.8. mm) than the frontal.

Dentition: Maxillary teeth 26+2 [27+2 on the right side, Cadle 1996a] without diastema, the last two teeth distinctly enlarged and ungrooved. Maxillary reaching beyond the palatine. Dentary teeth ca. 31, small, equal in size.

Colouration in preservative: In comparison with Figure 42 in Cadle (1996a) the specimen has significantly faded, especially the three light spots on the neck. Nevertheless, the colouration and pattern of the paratype generally correspond with the holotype. The white lateral stripe starts seven scales behind the parietal and runs on the lower part of the fifth scale row.

*Habitat, natural history, and conservation status* The male holotype was collected dead on a trail near the hotel "Feon' ny Ala", at ca. 2.5 km distance from the village Andasibe. This locality was largely surrounded by secondary forest, but was very close to the Reserve Speciale Analamazoatra, which appears well protected. *L. baderi* is only known from a single location (Andasibe) in central eastern Madagascar. Although the area around this village has been extensively surveyed by herpetologists, local guides and tourists, only two specimens are known so far, one collected in 1966 and the other collected 30 years later in 1996, suggesting that this snake is rather secretive or rare at least around the type locality. Regular surveys of snake roadkills between the village of Andasibe and the Hotel Feon' ny Ala did not reveal the snake either (R. Dolch, pers. comm.). Due to the very limited knowledge we suggest considering this species as "Data Deficient" according to the IUCN criteria used for the recent assessment of Malagasy reptiles.

*Etymology* The specific name is a patronym for Frank Bader (Germany) in recognition of his support of research and nature conservation through the BIOPAT initiative.

*Liopholidophis oligolepis* sp. nov. (Figs. 3–4)

*Holotype* ZSM 153/2005 (field number FGZC 2796), probably adult female, Marojejy National Park, near a campsite locally known as "Camp Mantella" (14°26.260'S, 49°46.533'E; 481 m a.s.l.), northeastern Madagascar, collected on 15 February 2005 by F. Glaw, M. Vences & R. D. Randrianiaina.

*Diagnosis* A species attributed to *Liopholidophis* because of its general morphology and its position in the molecular phylogenetic tree. *Liopholidophis oligolepis* differs from all other lamprophiid snakes of Madagascar except *L. baderi* by the presence of only 15 dorsal scale rows around midbody. In addition it differs from all other species of *Liopholidophis* except *L. rhadinaea* and *L. baderi* by a uniformly red belly in life that fades in preservative (never red in all other species) and by the presence of a light marking in the neck (versus absence). The new species differs from *L. rhadinaea* by having fewer ventrals in the female (137 versus 170–179), fewer subcaudals in the female (54 versus 69–88) and probably smaller size. *L. oligolepis* is most similar in morphology and small size to its sister species *L. baderi* but differs by having fewer ventrals (137 versus 149–158), fewer subcaudals (54 versus 71–77) and probably details of colouration (neck with two light spots connected to a light band versus three isolated light spots), smaller SVL (179.5 mm versus 205–221.5 mm) and smaller tail length (54.5 mm versus 78–91 mm). *L. oligolepis* differs furthermore from all other *Liopholidophis* species by substantial genetic differentiation.

*Description of the holotype* Female (sex determined by incision at the base of tail). Total length 234.0 mm, snout-vent length 179.5 mm, tail length 54.5 mm (23% of total length). Greatest head width (temporal region) 5.7 mm, head length (tip of snout to end of mandibles) 8.9 mm. Distance between tip of snout and the posterior edge of the parietals 7.2 mm.

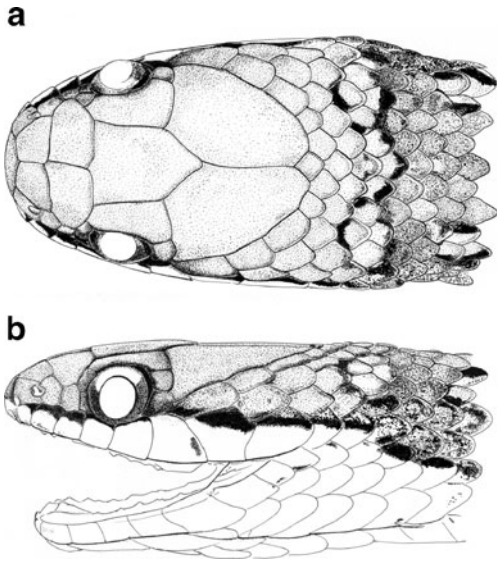


**Fig. 3** Head drawings of *Liopholidophis oligolepis* sp. nov. (holotype, ZSM 153/2005) in (**a**) dorsal and (**b**) lateral view

Body slightly compressed laterally. Head only a little wider than neck. Pupil round. Eye large, diameter horizontally 1.7 mm, larger than the distance between anterior margin of eye and posterior edge of nostril (1.1 mm). Dorsal scales smooth, without apical pits in 15–15–15 rows, but 17 scale rows directly behind the head, scale row reduction from 17 to 15 rows at the level of ventral 7 (left side) and ventral 6 (right side), respectively. Two preventrals, 137 rounded, not angulated ventrals [inserted half ventrals not counted: (1) between ventrals 92–93 on the right side; (2) before the anal scute on the left side]. One gular scale between the posterior inframaxillaries and the first preventral. Anal scute divided. Subcaudals 54/54 all divided plus terminal spine. Reduction of dorsocaudal rows from 8 to 6 at the level of subcaudals 7–8, from 6 to 4 at the level of subcaudals 18–19 and from 4 to 2 at the level of subcaudals 46–47.


**Fig. 4** Holotype of *Liopholidophis oligolepis* sp. nov. in (**a**) dorsal and (**b**) ventral view

Supralabials 8, with $4^{th}$–$5^{th}$ touching the eye. Infralabials 9, the first pair in contact behind the mental, $1^{st}$–$4^{th}$ touching the anterior inframaxillary, $4^{th}$–$5^{th}$ touching the posterior inframaxillary. Two pairs of inframaxillaries both the same width, but the anterior (2.2 mm) pair slightly shorter than the posterior (2.5 mm). Rostral wider (1.8 mm) than high (0.9 mm) and visible from above. Nasal semi-divided (undivided above the nostril, divided below), touching first and second supralabial. One loreal present, higher (0.7 mm) than wide (0.5 mm), touching second and third supralabial. One preocular, scarely visible from above, not in contact with frontal, touching third and fourth supralabial. Two postoculars, lower one slightly larger than upper one, upper postocular in contact with parietal, lower postocular touching parietal, anterior temporal, fifth and sixth supralabial. Temporals 1+2+3. Dorsal surface of head shows the typical lamprophiid scalation consisting of nine shields. Frontal longer (2.8 mm) than wide (2.2 mm), longer than the distance to the posterior margin of rostral (1.6 mm). Parietals longer (3.6 mm) than the frontal.

Dentition: Maxillary teeth 24+2 without diastema, the last two teeth distinctly enlarged and ungrooved. Maxillary reaching beyond the palatine. 16 palatine teeth. Dentary teeth ca. 30, small, equal in size.

Colour in preservative: General dorsal ground colouration entirely dark brown. Lower part of scale row four distinctly darker. At the upper part is a pale dot, situated at the upper basal edge of that scale. Row 5 bears a pale dot at the lower basal edge. These two rows of pale dots appear as a continuous lateral stripe, which starts six scales behind the posterior margin of the parietal and runs continuously on the fourth and fifth row on the body and on the second scale row on the tail nearly until the tip of tail. On the neck there are two distinct white ocelli occupying 4 scales and bordered by a dark ring. Both ocelli were connected by a pale "v"-shaped band, which is also dark bordered. Ground colour of dorsal side of head a little lighter than body. Supralabials whitish, bordered dorsally by a dark brown stripe. This stripe starts at the first supralabial, touches the lower margin of the eye and the lower postocular, running until the angle of the jaws, and then turns transversally on the first dorsal scale row and fades within the body's ground colour. A second "stripe" created by little dark spots on the outer edges of the anterior ventrals runs along the whitish throat and becomes the dark outer edge of the subsequent ventrals. Underside of head, body and tail uniform pale in preservative, except the outer margins of ventrals and subcaudals, which show the same dark brown

**Fig. 5** *Liopholidophis rhadinaea* in life, from Talatakely, Ranomafana National Park (ZSM 1602/2008)

colouration as the first dorsal scale row in sharp contrast to the whitish ventral ground colour. Colouration in life (see Figure 5 and photograph in Glaw and Vences 2007: 448 "*Liophidium* sp.") dorsally similar to that in preservative. Ventral side of body and tail red in life, beige on throat; ventral colours fading into whitish after preservation.

*Habitat, natural history, and conservation status* The holotype, so far the only known individual of this species, was collected in a pitfall bucket in a largely undisturbed primary rainforest of the Marojejy National Park. Due to the very limited knowledge we suggest considering this species as "Data Deficient" according to the IUCN criteria used for the recent assessment of Malagasy reptiles.

*Etymology* The species name *oligolepis* is derived from the two Greek words, "oligo" meaning "few" and "lepis" meaning "scale," and refers to the very low scale counts of this species (15 dorsal scale rows, 137 ventrals, 54 subcaudals), which are unique among Malagasy snakes. It is used as a noun in apposition.

*Remarks* The available names in the genera *Liopholidophis* and *Liophidium* were discussed by Glaw et al. (2007) and Franzen et al. (2009) indicating that no earlier names are available for *L. baderi* or *L. oligolepis*.

## Discussion

### Phylogenetic relationships among *Liopholidophis*

Due to its importance for understanding the evolution of the unusual sexual dimorphism seen in *Liopholidophis*, its intrageneric phylogeny and systematics received comparatively much attention in the past 15 years (Cadle 1996a, 2009; Glaw et al. 2007) leading to a re-definition of the genus, the description of two new species (*L. rhadinaea* and *L. dimorphus*) and competing hypotheses about their phylogeny. Our present study provides the first molecular phylogeny that includes all six previously recognised species (for the former molecular study only three species were available), and in addition the two new species described herein, thereby changing former hypotheses significantly.

One unexpected result is the presence of two deeply separated clades within *Liopholidophis* indicating the existence of two distinct species groups and suggesting that sexual size dimorphism has evolved not in a linear but in a complex pattern including at least one reversal in *L. varius* and perhaps a second in the clade containing the two new species. This also suggests that even highly apomorphic and distinct morphological characters like extreme male tail length are of limited value to reconstruct the phylogenetic history of a certain group if not accompanied by a robust molecular phylogeny. Similar discrepancies between expected phylogenetic relationships based on morphological data and molecular phylogenies have commonly been observed among other Malagasy reptiles and amphibians, including skinks (Schmitz et al. 2005; Crottini et al. 2009), chameleons (Townsend et al. 2011) and frogs (Andreone et al. 2005). Three species in the *L. rhadinaea* group (clade A), *L. rhadinaea*, *L. baderi* and *L. oligolepis,* share several characters that are unique in the genus: a uniformly reddish ventral surface in life (fading entirely in preservative), light colour in the neck (three well-defined light spots in *L. rhadinaea* and *L. baderi*, two light spots connected to a light band in *L. oligolepis*) and a small to very small snout-vent length. Furthermore, the hemipenis of *L. baderi* is nearly identical to that of *L. rhadinaea* (Cadle 1996a) and the dark morph of *L. rhadinaea* is rather similar in dorsal colouration to *L. oligolepis*, suggesting that *L. rhadinaea* is the closest relative to the two new species. However, our molecular phylogeny neither supports nor excludes this hypothesis, although single gene trees of the COI gene (shown in Nagy et al. 2012) favour this relationship with relatively high support, leaving *L. dimorphus* as basal species in the *L. rhadinaea* group.

As is shown in Fig. 1, *L. baderi* and *L. oligolepis* clearly belong to *Liopholidophis* and not to the genus *Liophidium*. Due to its similarities with other *Liophidium*, Domergue (1988) identified the paratype of *L. baderi* as *Liophidium* sp. and Cadle (1996a) as "genus et species inquirenda". *L. baderi* and *L. oligolepis* share even more characters, so that their sister group relationship was expected. They are the only Malagasy snakes with 15 dorsal scale rows at midbody; they are very small (234–312.5 mm total length) and, as is evident from the low numbers of subcaudal scales, apparently lack a strong sexual dimorphism in tail length compared to the other species. *L. oligolepis* differs from *L. baderi* by having even fewer ventrals (137 versus 149–158), fewer subcaudals (54 versus 71–77) and probably smaller SVL and tail length. Although these differences appear to be quite distinct, they

might be partly due to the fact that both specimens of *L. baderi* are males whereas the only specimen of *L. oligolepis* is a female. Males generally have more ventrals, more subcaudals, larger SVLs and larger tail lengths than females in all species of *Liopholidophis* (see Glaw et al. 2007; Cadle 2009). However, substantial genetic differentiation between the two dwarf species surpassing the level between *L. sexlineatus* and *L. varius* as well as the known intraspecific variation in other lamprophiid snakes (see Nagy et al. 2007, 2010, 2012; Hawlitschek et al. 2012) suggests that both forms are taxonomically distinct. We expect that the discovery of new specimens will reveal more reliable differences between these two species.

The phylogeny in the *Liopholidophis sexlineatus* group (clade B) is well resolved in our molecular tree (Fig. 1) and these relationships are also supported by non-molecular data. All four species in this clade are large-sized and all except *L. varius* share an extremely long tail length in males. The two largest (SVL of males up to 732 mm and 770 mm respectively) black-bellied species *L. dolicocercus* and *L. grandidieri* are recovered as sister species. *L. sexlineatus* is sister to *L. varius* and these similar species (which differ mainly by the tail length of males and are hardly distinguishable as females) have the lowest genetic divergence (7.2% in the cytochrome *b* fragment; additional sequences of *L. sexlineatus* not shown) between any *Liopholidophis* species.

## Reversals of sexual size dimorphism

The ancestral character state reconstructions based on the phylogeny presented in Fig. 1 revealed a strong and rapid relative tail length reduction in both males and females of *L. varius*. Although our molecular phylogeny does not fully resolve the relationships in the *L. rhadinaea* group, and despite the partial absence of data, a reduction of relative tail length is likely also in the two new dwarf species. This trend would be even more evident if the relationships in the *rhadinaea* group would turn out to be (*dimorphus* (*rhadinaea* (*baderi* - *oligolepis*))), as is suggested by COI single gene trees (Nagy et al. 2012) and by morphological and chromatic data.

*L. varius* is closely related to *L. sexlineatus* and both species are similar in size and general morphology. Distinct sexual size dimorphism in tail length is evident in both species, but is much less developed in *L. varius* compared to the other three species of the *L. sexlineatus* group (male tail length 185–300 mm versus 243–904 mm, number of subcaudals 88–103 versus 127–221), leading Cadle (1996a) to consider *L. varius* the basal species of *Liopholidophis*. However, its position in our molecular phylogeny (Fig. 1) strongly suggests that the relatively short male tail length in *L. varius,* and in general its weakly expressed sexual tail length dimorphism, is a reversal that might have occurred rather rapidly in this case given the relatively low genetic distance between both species. The reduction of male tail length is not accompanied by miniaturisation in this case and thereby might be mainly the result of sexual selection. The ecology of both species is poorly known but ecological differences are evident in altitudinal distribution and habitat. *L. varius* is only known from mid-altitude rainforests and swamps, whereas *L. sexlineatus* is more common in mountainous habitats where it occurs as high as 2,498 m (Chiari et al. 2006). The adaptation to cold, high altitude habitats might also explain the viviparity of this species, although the reproductive mode is only known for three additional *Liopholidophis* species (*L. rhadinaea*, *L. dolicocercus* and *L. grandidieri*), which are all oviparous (Cadle 2009).

*L. baderi* and *L. oligolepis* are most likely among the smallest advanced snakes in Madagascar, and their reduction in tail length is accompanied by a significant miniaturisation of the body, suggesting that the primary force for these changes might be due to changes in natural selection (e.g., caused by shifts in the ecological niche), which might have been accompanied by changes in sexual selection.

## Morphological constraint hypothesis and antipredator defence

One hypothesis to explain extreme tail length in snakes refers to the Morphological Constraint Hypothesis (King 1989), proposing that males have relatively longer tails to accommodate hemipenes and retractor muscles. However, hemipenis length is rather short in *Liopholidophis* males (Cadle 2009, pers. obs.), even more in those with extreme tail length, strongly confirming the finding of Cadle (2009) that the extreme tail length in male *Liopholidophis* is unlikely to be explained by the Morphological Constraint Hypothesis. Hemipenes and associated anatomy are expected to expose greater constraints on minimal tail length of short-tailed snakes (King 1989; Cadle 2009) although even in the short-tailed *L. baderi*, the fully everted hemipenis is small (5 mm length in MNHN 1988.331 according to Cadle 1996a) compared to the 91.0 mm of tail length. With 6.5 mm length, the fully everted hemipenis of one adult male of the long-tailed *L. rhadinaea* (MCZ 180394) is only slightly longer (Cadle 1996a) indicating that tail length and hemipenis length are probably not strongly correlated in these snakes.

Antipredator defence (as reviewed by Arnold 1988) remains as an alternative hypothesis to explain the extraordinary long tails in *Liopholidophis*. Cadle (2009) discussed the potential role of long tails in *Liopholidophis* in antipredator defence as is known from some other snakes, especially those with breakable tails. He concluded that antipredator defence plays an insignificant or no role in the evolution of long tails in *Liopholidophis*. However, indications of a defence display exist for two species with very long tails in males: *Liopholidophis rhadinaea* occasionally becomes immobile when disturbed (Cadle 2003: 999) and a strange freezing

behaviour including presentation of the aposematically coloured ventral side was recently observed in three individuals of *L. grandidieri* (unpublished pers. obs.), which is the species with longest relative tail length in the genus. Furthermore, most *Liopholidophis* species have a colourful ventral colouration in life, being either red or purple (*L. rhadinaea*, *L. baderi*, *L. oligolepis*) or showing an aposematic pattern of black and yellow (*L. dolicocercus*, *L. grandidieri*). These data suggest that the antipredator defence hypothesis should not be ruled out and is at least more plausible than the Morphological Constraint hypothesis, emphasising the need for further studies.

Small snakes on islands

Islands like Hispaniola, Cuba, New Guinea or Madagascar are well known to harbour many extremely miniaturised dwarf species including the smallest vertebrates and amniotes (Hedges and Thomas 2001; Rittmeyer et al. 2012; Glaw et al. 2012). This fact suggests that further study of island faunas may help to reveal the evolutionary constraints of body size (Hedges 2008) although it is unclear if the principles of island biogeography really affect Malagasy snakes as this island is massive and often considered a micro-continent. The smallest snakes on earth are worm snakes (Scolecophidia) where the smallest species, *Leptotyphlops carlae*, has a total adult length of approximately 100 mm (Hedges 2008). Advanced (alethinophidian) snakes are substantially larger, and the smallest species range in total length between 20–30 cm (Bauchot 1997). *Liopholidophis baderi* and especially *L. oligolepis* (total length of the holotype 234 mm) belong into this size range as well and are the only advanced snakes of Madagascar with only 15 dorsal scale rows at midbody, and the holotype of *L. oligolepis* has a low number of ventral scales (137). Only four other advanced snake species from Madagascar have fewer than 140 ventrals, a character shared only by *Compsophis boulengeri* (131–137 ventrals, total length up to 353 mm; Cadle 1996b), *Compsophis zeny* (132–137 ventrals, total length up to 281 mm; Cadle 1996b), *Heteroliodon fohy* (133–136 ventrals, total length 252–280 mm; Glaw et al. 2005; Megson et al. 2009) and *Pseudoxyrhopus kely* (134–139 ventrals, snout-vent length 170–228 mm; Raxworthy and Nussbaum 1994; Ramanamanjato et al. 2007). All these four species are terrestrial and among the smallest advanced Malagasy snakes. The same is true for *Liopholidophis oligolepis*, suggesting that this species is a good candidate for being among the smallest Malagasy alethinophidian snakes although morphological variation and especially sexual dimorphism of this species is still entirely unknown. In any case the low number of ventral scale counts in these small species confirms the results of previous studies that found correlations between the body vertebrae number—which in advanced snakes equals the number of ventrals (Alexander and Gans 1966) —and body size (e.g. Lindell 1994).

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