
Molecular phylogeny and systematics of the pseudoxyrhophiine snake genus *Liopholidophis* (Reptilia, Colubridae): evolution of its exceptional sexual dimorphism and descriptions of new taxa

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Glaw, F., Nagy, Z. T., Franzen, M. & Vences, M. (2007). Molecular phylogeny and systematics of the pseudoxyrhophiine snake genus *Liopholidophis* (Reptilia, Colubridae): evolution of its exceptional sexual dimorphism and descriptions of new taxa. — *Zoologica Scripta*, 36, 291–300. The pseudoxyrhophiine snake genus *Liopholidophis* Mocquard, 1904 is endemic to Madagascar and consists of two distinct species groups. We performed molecular phylogenetic analyses using nucleotide sequences of c. 2200 bp from two mitochondrial genes (16S rRNA, *cyt b*) and one nuclear gene (*c-mos*) to test the monophyly of the genus *Liopholidophis* and to investigate the relationships of the known species and an unidentified *Liopholidophis* population. Our phylogeny strongly supports the polyphyly of the genus *Liopholidophis*, confirms the monophyly of both species groups, and reveals that the unidentified population belongs to a new species. We therefore transfer the species of the former *L. stumppffi* group (*L. epistibes*, *L. infrasignatus*, *L. lateralis*, *L. martaetae*, and *L. stumppffi*) to a new genus *Bibilava* gen. n. and describe *Liopholidophis dimorphus* sp. n. from the rainforests of Montagne d'Ambre National Park in northern Madagascar. Finally, we compare our phylogeny with previous hypotheses and discuss the evolution of the extreme sexual dimorphism in tail length of *Liopholidophis* s. str.

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Introduction

The genus *Liopholidophis*, established by Mocquard (1904), is part of a large and diverse radiation of colubrid snakes, the Pseudoxyrhophiinae (Nagy *et al.* 2003) and endemic to Madagascar (Guibé 1954; Domergue 1973). The genus was revised by Cadle (1996, 1998) and a further new species was added by Glaw *et al.* (2005). Accordingly, a total of 10 species in two species groups are currently recognized. The *Liopholidophis sexlineatus* group contains five species: *L. sexlineatus* (Günther 1882), *L. varius* (Fischer 1884), *L. doliocercus* (Peracca 1892), *L. grandidieri* (Mocquard 1904) and *L. rhadinaea* (Cadle 1996). These species have 17 rows of dorsal scales and exhibit an extreme sexual dimorphism in tail length, tails being much longer in males than in females. Correspondingly, the number of subcaudals is much higher and the total length is longer in males than in females (Cadle 1996). The species in this group

mainly occur in mid- and high-altitude habitats of eastern and central Madagascar. Presently, the *L. stumppffi* group also contains five species: *L. epistibes* (Cadle 1996), *L. infrasignatus* (Günther 1882), *L. lateralis* (Duméril & Bibron 1854), *L. martaetae* (Glaw, Franzen & Vences 2005) and *L. stumppffi* (Boettger 1881). All these species are characterized by the absence of strong sexual dimorphism in tail length and by 19 rows of dorsal scales at midbody (Cadle 1996; Glaw *et al.* 2005).

In his review of *Liopholidophis*, Cadle (1996) confirmed the two species groups already recognized by Parker (1925), but he was not able to confirm or reject the monophyly of *Liopholidophis* as a genus. *Liopholidophis* is still considered as of uncertain monophyly because no unequivocal characters are shared by all species currently placed in the genus (Cadle 2003). Moreover, the *L. sexlineatus* group (especially *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 (Cadle 1996).

A recent molecular phylogenetic analysis of Madagascan colubrids (Nagy *et al.* 2003) included only *L. sexlineatus*, but no representative of the *L. stumpffi* group, and therefore could not resolve the question about the monophyly of *Liopholidophis*. The aim of the present study is to clarify the systematics of the snakes currently assigned to the two species groups of *Liopholidophis*, to describe a new species recently collected by us in far northern Madagascar, and to gain new insights into the evolution of the extreme sexual dimorphism in tail length found in one of the species groups.

Materials and methods

The snakes were generally anaesthetized by injection with chlorobutanol, fixed in formalin, 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 and tail length were measured to the nearest millimetre with a caliper. We follow Cadle (1996) regarding the terminology of meristic and mensural data. Ventral scales were counted without preentrals. Museum acronyms are: Museo Regionale di Scienze Naturali, Torino (MRSN); Université d'Antananarivo, Département de Biologie Animale (UADBA); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); Zoological Museum, University of Amsterdam (ZMA); Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB); Zoologische Staatssammlung München (ZSM). FAZC, FGMV, FGZC, RJS and ZCMV are field numbers of specimens that will be catalogued in one of the mentioned museum collections. DNA was extracted using standard protocols (Sambrook *et al.* 1989). The complete mitochondrial gene cytochrome *b*, as well as fragments of the mitochondrial gene 16S rRNA and the nuclear *c-mos* were amplified in PCRs using the same primers

as Nagy *et al.* (2003). The PCR products were directly sequenced on different ABI Prism Genetic Analyser automated sequencers (Applied Biosystems, Foster City, USA). The sequences were checked for quality and aligned either by hand (*cyt b* and *c-mos*) or by CLUSTALX 1.83 (16S rRNA, Thompson *et al.* 1997). The concatenated data set consisted of 2201 nucleotide positions (regarding complete sequences only). The incongruence length difference (ILD) test was used to check the 'combinability' of the sequences. This and the subsequent phylogenetic analyses were carried out using the computer program PAUP*, version 4b10 (Swofford 2002). We performed parsimony analyses with 2000 bootstrap replicates. Maximum likelihood heuristic searches were performed under substitution model regimes selected by the hierarchical likelihood ratio tests in MODELTEST 3.7 (Posada & Crandall 1998) in order to find the appropriate nucleotide substitution model and using 100 (sequence data set of three genes) or 500 (cytochrome *b* sequences only) bootstrap replicates.

DNA sequences were deposited in GenBank; voucher specimens and accession numbers are listed in Table 1.

Results

Molecular phylogeny

The dataset of DNA sequences consisted of 2201 characters of which 520 were parsimony-informative. Maximum likelihood analysis recovered from the trees is shown in Figs 1 and 2. The respective monophyly of the two species groups in *Liopholidophis* was recovered with almost maximum support. However, the genus *Liopholidophis* turned out to be polyphyletic, the *L. sexlineatus* group placed sister to the genus *Liophidium* and the *L. stumpffi* group sister to the genus *Dromicodryas*. The new species from northern Madagascar (shown as *L. dimorphus* in Figs 1 and 2) which resembles *L. sexlineatus* in morphology is the sister group of the clade (*sexlineatus* + *dolicocercus*).

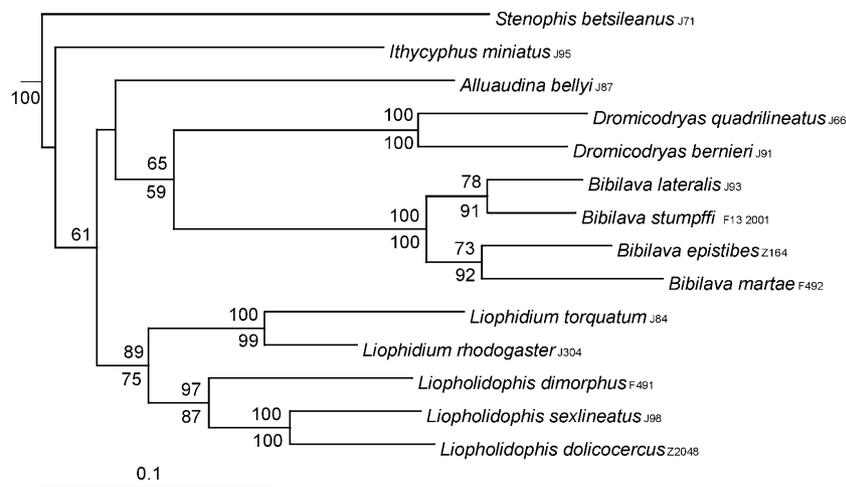


Fig. 1 Phylogenetic tree of *Liopholidophis* and *Bibilava*, based on 2201 nucleotide positions of two mitochondrial (16S rRNA, *cyt b*) and one nuclear gene (*c-mos*). Only complete sequences were included. Maximum likelihood bootstrap values (100 replicates) are given above branches, parsimony bootstrap values (2000 replicates) below branches. Only values over 50 are shown.

Table 1 Voucher specimens and GenBank accession numbers.

Species	Sample ID	Locality	Voucher specimen	GenBank accession no. c-mos	GenBank accession no. cytochrome <i>b</i>	GenBank accession no. 16S rRNA
<i>Mimophis mahfalensis</i>	J68	Kirindy	not collected	AY187993	AY188032	AY188071
<i>Alluaudina bellyi</i>	J87	Berara	MRSN (FAZC 10622)	AY187966	AY188005	AY188044
<i>Dromicodryas bernieri</i>	J91	Ifaty	UADBA (FGMV 2000-517)	AY187975	AY188014	AY188053
<i>Dromicodryas bernieri</i>	J372	Toliara	not collected	—	DQ979987	—
<i>Dromicodryas quadrilineatus</i>	J66	Sambava	not collected	AY187976	AY188015	AY188054
<i>Dromicodryas quadrilineatus</i>	F2743	Marojejy, Camp Mantella	ZSM 76/2005	—	DQ979989	—
<i>Ithycyphus miniatus</i>	J95	Berara	MRSN (FAZC 10680)	AY187980	AY188019	AY188058
<i>Stenophis betsileanus</i>	J71	Marojejy	ZFMK 60500	AY187998	AY188037	AY188076
<i>Liophidium torquatum</i>	J84	Montagne d'Ambre	not collected	AY187984	AY188023	AY188062
<i>Liophidium torquatum</i>	J307	Ranomafana (Vohiparara)	ZSM 691/2003	—	DQ979984	—
<i>Liophidium rhodogaster</i>	J304	Ranomafana National Park	ZSM 784/2003	DQ979971	DQ979978	DQ979964
<i>Liophidium rhodogaster</i>	F467	Montagne d'Ambre	UADBA (FGZC 467)	—	DQ979992	—
<i>Liophidium vaillanti</i>	B32	Kirindy	not collected	—	DQ979995	—
<i>Bibilava infrasignatus</i>	F207	Andohahela	UADBA (FGZC 207)	—	DQ979993	—
<i>Bibilava infrasignatus</i>	F208	Andohahela	ZSM 118/2004	—	DQ979994	—
<i>Bibilava lateralis</i>	J93	near Mantasoa	UADBA (FGMV 2000-36)	DQ979970	DQ979977	DQ979963
<i>Bibilava epistibes</i>	Z164	Ranomafana	UADBA 24506	DQ979972	DQ979979	DQ979965
<i>Bibilava martae</i>	F492	Montagne des Francais	ZSM 253/2004	DQ979974	DQ979981	DQ979967
<i>Bibilava stumpffi</i>	F13–2001	Nosy Be	ZSM 579/2001	DQ979976	DQ979983	DQ979969
<i>Bibilava stumpffi</i>	J331	Nosy Be	ZSM 579/2001	—	DQ979986	—
<i>Liopholidophis dimorphus</i>	F491	Montagne d'Ambre	ZSM 252/2004	DQ979973	DQ979980	DQ979966
<i>Liopholidophis dimorphus</i>	F529	Montagne d'Ambre	ZSM 276/2004	—	DQ979991	—
<i>Liopholidophis doliocercus</i>	Z2048	Marojejy, Camp Simpona	ZSM 60/2005	DQ979975	DQ979982	DQ979968
<i>Liopholidophis doliocercus</i>	Z2049	Marojejy, Camp Simpona	UADBA (ZCMV 2049)	—	DQ979990	—
<i>Liopholidophis sexlineatus</i>	J98	Mandraka	UADBA (FGMV 2000-38)	AY187985	AY188024	AY188063
<i>Liopholidophis sexlineatus</i>	J308	Antoetra	ZMA 19546 (FGMV 2002-68)	—	DQ979985	—
<i>Liopholidophis sexlineatus</i>	Z163	Ranomafana	UADBA 24498	—	DQ979988	—

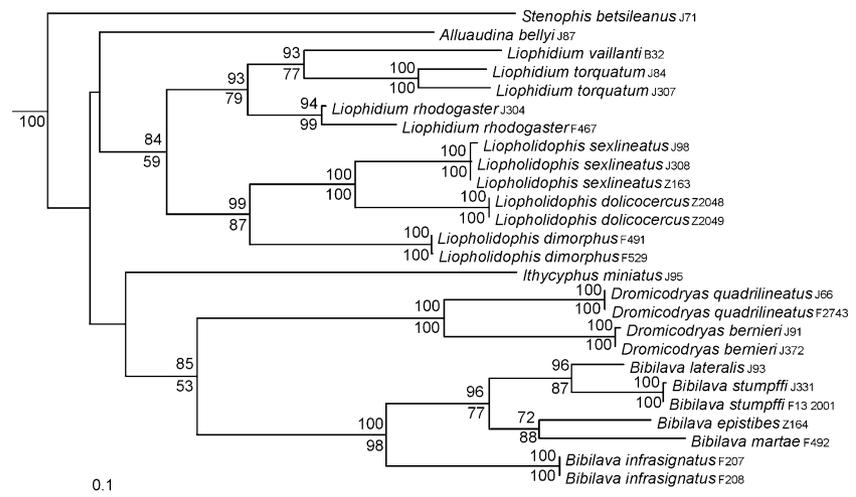


Fig. 2 Phylogenetic tree of *Liopholidophis* and *Bibilava*, based on cytochrome *b* sequences only, including also incomplete sequences. Maximum likelihood bootstrap values (500 replicates) are given above branches, parsimony bootstrap values (2000 replicates) below branches. Only values over 50 are shown.

Description of a new genus

Our phylogenetic trees (Figs 1 and 2) strongly support that the two *Liopholidophis* species groups represent distinct clades that are not sister to each other and therefore are best classified as different genera. Since *L. grandidieri*, a member of the *L. sex-*

lineatus group, was designated as type species of *Liopholidophis* (Williams & Wallach 1989) the species in this group are retained in their genus whereas the species of the *L. stumpffi* group require a new genus name. Alternatively, these species would have to be included in the genus *Dromicodryas*. Although

there is superficial external similarity in the habitus and pholidosis of *Dromicodryas* and the species of the *L. stumpffi* group, the latter option is, however, contradicted by several differences in dentition, pholidosis and the presence of apical pits. These differences led to the continued recognition of *Dromicodryas* with its current two species *D. bernieri* and *D. quadrilineatus* ever since the catalogue of Boulenger (1893). In addition, there is a high genetic divergence between the *L. stumpffi* group and *Dromicodryas* (Figs 1 and 2). We therefore suggest the recognition of a new genus which is described in the following.

***Bibilava*, gen. n.**

Type species. *Leptophis lateralis* Duméril, Bibron & Duméril, 1854.

Etymology. *Bibilava* is the Malagasy word for snake (biby = animal, lava = long) and is often used for the terrestrial snakes included in this genus which are common in open habitats and therefore regularly encountered by locals in Madagascar. The gender is defined as masculine.

Content. Five valid species, *Bibilava lateralis* (Duméril, Bibron & Duméril 1854), *B. stumpffi* (Boettger 1881), *B. infrasignatus* (Günther 1882), *B. epistibes* (Cadle 1996), and *B. martae* (Glaw, Franzen & Vences 2005), including their respective synonyms (*Dromicus baroni* Boulenger, 1888, *Dromicus madagascariensis* Günther, 1872, *Liophidium gracile* Mocquard, 1908).

Definition and diagnosis. *Bibilava* is defined as follows (mensural and meristic data according to Cadle 1996; Glaw et al. 2005 and Table 2): pupil round; 8 upper labials (4 and 5 touching eye); usually 10 lower labials; one loreal; apical pits usually present; 19–19–17 rows of dorsal scales; 141–185 ventral scales; anal plate divided; 62–109 subcaudals; maximum total length 920 mm; maximum snout-vent length 712 mm; female superiority in body size; tail length/total length 0.21–0.34; not strongly dimorphic relative tail length; posterior maxillary teeth longest and ungrooved; mandibular teeth subequal. For further characters see Cadle (1996: 450–452). *Bibilava* can be distinguished from all other Malagasy colubrids as follows: from *Langaba*, *Stenophis* and *Madagascarophis* by a round pupil (vs. vertical); from *Mimophis*, *Micropisthodon*, *Liopholidophis*, *Liophidium*, *Heteroliodon*, *Pararhadinaea* and *Exallodontophis* by 19 rows of dorsal scales (vs. 17) and from *Alluaudina*, *Leioheterodon*, and most *Pseudoxyrhopus* by a lower number of dorsal scale rows (19 vs. 21–25); from the two *Pseudoxyrhopus* species with 19 dorsal scale rows (*P. kely* and *P. imerinae*) by a higher number of subcaudals (37–43 vs. 62–109); from *Geodipsas*, *Compsophis*, *Brygophis*, *Alluaudina* and *Leioheterodon* by a divided anal scale (vs. undivided); from *Ithyocyphus* by a lower number of subcaudals (62–109 vs. 140–179). *Bibilava* is externally most similar to

Dromicodryas, but differs from this genus by the following characters: last two or three posterior maxillary teeth abruptly enlarged (not enlarged in *Dromicodryas*); not enlarged anterior mandibular teeth (distinctly enlarged in *Dromicodryas*); presence of apical pits (absent in *Dromicodryas*); lower number of ventral scale rows (141–185 vs. 195–219).

Distribution. Species included in *Bibilava* are distributed throughout humid eastern Madagascar from Montagne d'Ambre in the north to Andohahela in the south, ranging from sea level to about 1600 m altitude (Glaw & Vences 1994; Raxworthy & Nussbaum 1994; Cadle 1996; Andreone & Randriamahazo 1997; pers. obs.). In addition, *B. lateralis*, *B. stumpffi*, *B. epistibes* and *B. martae* are also known from less humid localities in western or northern Madagascar (e.g., Cadle 1996; Andreone et al. 2001; Glaw et al. 2005).

Description of a new species of *Liopholidophis*

After the transfer of the species of the former *L. stumpffi* group to the new genus *Bibilava* the genus *Liopholidophis* sensu stricto now consists only of the following five species: *L. sexlineatus*, *L. varius*, *L. doliocercus*, *L. grandidieri* and *L. rhadinaea*. Two specimens recently collected by us in northern Madagascar do not agree in morphology with any of these species and are grouped apart from *L. sexlineatus* and *L. doliocercus* in the molecular analysis.

Genus *Liopholidophis* Mocquard, 1904

***Liopholidophis dimorphus* sp. n.** (Figs 3 and 4)

Holotype. ZSM 252/2004 (field number FGZC 0491; Figs 3 and 4), adult male (hemipenes not extruded), collected at Montagne d'Ambre, northern MADAGASCAR, 12°30'S, 49°10'E, c. 800 m above sea level, by F. Glaw, M. Puente, R. D. Randrianiaina & A. Razafimanantsoa on 21 February 2004.

Paratype. ZSM 276/2004 (field number FGZC 0529), adult female, collected at Montagne d'Ambre, northern MADAGASCAR, c. 800–1000 m above sea level, by A. Razafimanantsoa on 24 February 2004.

Etymology. The species name 'dimorphus' refers to the unusual sexual dimorphism in tail length which is typical for the new species and most other species of *Liopholidophis* but exceptional among colubrid snakes.

Diagnosis. Among the species of *Liopholidophis*, *L. dimorphus* differs from *L. doliocercus* and *L. grandidieri* by the immaculate whitish venter (vs. black), and from *L. rhadinaea* by colouration (e.g., presence of light nape spots and dorsal lines in *L. rhadinaea*). Furthermore, *L. dimorphus* differs from *rhadinaea*, *dolicocercus*,

Table 2 Meristic and mensural data of comparative *Liopholidophis* and hitherto unstudied *Bibilava* specimens. Total length followed by snout-vent length [SVL] is given in millimetre. Specimens marked with (+) have incomplete tails.

	Sex	Locality	Total length [SVL]	Tail length/total length	Ventrals	Subcaudals	Eye diameter/eye-nostril distance	Loreal height/width	Preoculars (l/r)
<i>L. sexlineatus</i>									
ZSM 576/2001	♂	Andohariana (Andringitra)	595 [352]	0.41	153	129	1.0	1.0	1/1
ZSM 696/2003	♂	Samalaoatra	652 [372]	0.43	155	146	1.1	1.6	1/1
ZFMK 14364	♂	Perinet (= Andasibe)	686 + [404]	—	152	123+	1.0	1.1	1/1
ZSM 168/2006 (ZCMV 2560)	♂	Ankaratra	833 [451]	0.46	147	137	1.0	1.0	1/1
ZMB 34145	♂	Central-Madagascar	841 [442]	0.47	150	151	1.0	1.0	2/1
ZMB 34147	♂	Central-Madagascar	938 [505]	0.46	156	150	1.0	1.3	1/1
ZMB 34153	♂	Central-Madagascar	960 [480]	0.50	148	154	1.0	1.4	1/2
ZMB 34159	♂	Central-Madagascar	1385 [650]	0.53	154	151	0.9	1.1	2/1
ZMB 15828	♂	Sirabe (= Antsirabe?)	867 [462]	0.47	153	154	0.9	1.1	1/1
Mean ± SD			—	0.47 ± 0.04	152 ± 3	147 ± 9	1.0 ± 0.1	1.2 ± 0.2	—
Range			—	0.41–0.53	147–156	129–154	0.9–1.1	1.0–1.6	—
ZSM 377/2000	♀	Mandraka	547 [384]	0.30	138	76	1.1	1.6	1/1
ZFMK 62894	♀	Antananarivo	585 [415]	0.29	136	69	0.9	1.0	2/2
ZFMK 62334	♀	Ankaratra	408 [297]	0.27	139	76	0.9	1.4	1/1
ZFMK 62895	♀	Antananarivo	174 + [136]	—	140	55+	1.0	1.2	2/2
ZMA 19546	♀	Antoetra	505 [369]	0.27	139	70	1.0	1.1	1/1
ZSM 169/2006 (ZCMV 2561)	♀	Ankaratra	440 [325]	0.26	135	74	1.0	1.0	1/1
ZMB 34154	♀	Central-Madagascar	647 [455]	0.30	139	74	1.0	1.2	1/1
ZMB 34160	♀	Central-Madagascar	495 [364]	0.26	142	71	1.1	1.6	1/1
Mean ± SD			—	0.28 ± 0.02	139 ± 2	73 ± 3	1.0 ± 0.1	1.2 ± 0.2	—
Range			—	0.26–0.30	135–142	69–76	0.9–1.1	1.0–1.6	—
<i>L. dimorphus</i>									
ZSM 252/2004	♂	Montagne d'Ambre	1072 [615]	0.43	163	134	1.1	1.0	2/2
ZSM 276/2004	♀	Montagne d'Ambre	760 [536]	0.29	146	79	1.0	1.0	2/2
<i>L. dolicoecercus</i>									
UADBA (ZCMV 2049)	♂	Marojejy	1395 [770]	0.45	155	152	1.3	—	—
ZSM 60/2005	♂	Marojejy	1426 [728]	0.49	155	152	1.3	—	—
ZFMK 62245	♂	Mantadia	694 [494]	0.29	140	79	1.2	—	—
<i>L. varius</i>									
ZSM 233/2002	♀	Fierenana	474 [359]	0.24	144	67	1.0	—	—
<i>B. stumpffi</i>									
ZMB 9981	♂	Nosy Be	704 [470]	0.33	150	100	1.2	—	—
ZMB 69370	♂	Nosy Be	628 [423]	0.33	155	88	1.1	—	—
ZMB 23810	♂	Madagascar	696 [482]	0.31	159	95	1.2	—	—
ZMB 19224	♀?	Nosy Be	628 + [475]	—	152	59+	1.1	—	—
<i>B. epistibes</i>									
ZMB 14400	♂	Madagascar	753 [514]	0.32	165	92	1.4	—	—
ZMB 69369	♂	Madagascar	607 [406]	0.33	159	97	1.3	—	—
ZSM 58/2005	♂	Ste. Luce	520 [359]	0.31	162	101	1.7	—	—
ZMB 69368	♂?	Madagascar	613 [425]	0.31	165	98	1.2	—	—
ZMB 15829	♀?	Sirabe (= Antsirabe?)	722 [502]	0.30	156	93	1.2	—	—
ZMB 14297	♀	Madagascar	577 [405]	0.30	154	90	1.1	—	—
ZMB 14290	♀	Madagascar	730 [515]	0.29	162	88	1.1	—	—
<i>B. infrasinatus</i>									
ZSM 171/2006 (RJS 1000)	♀	Anosibeana'ala	736 [576]	0.22	149	65	1.2	—	—
ZSM 170/2006 (ZCMV 2987)	♂	Samalaoatra?	496 [374]	0.25	150	75	1.3	—	—
ZMB 34162	♂	Central-Madagascar	854 [652]	0.24	155	73	1.1	—	—

grandidieri and *varius* by meristic data, especially by the number of ventrals and subcaudals in males, and maximum total length of both sexes (see Tables 2 and 3). *Liopholidophis dimorphus* mostly resembles *L. sexlineatus* (Fig. 5) by scale counts just

reaching its upper range in the number of ventral scale rows in males (163 vs. 147–163) and the number of subcaudals in females (79 vs. 67–79). *Liopholidophis dimorphus* differs from *L. sexlineatus* in having two preoculars (vs. preoculars mostly

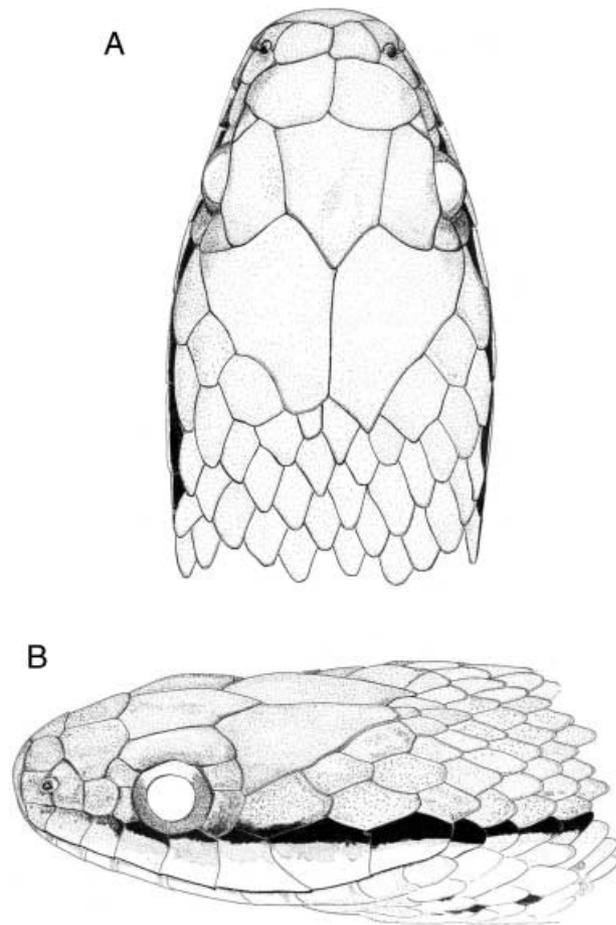


Fig. 3 A, B. Head drawings of *Liopholidophis dimorphus* sp. n. (holotype). —A. Dorsal view. —B. Lateral view.

fused; Table 2), in having the loreal as high as wide (ratio height/width 1.0 in *L. dimorphus* vs. > 1.0 in *L. sexlineatus*; Table 2), apparently by a larger maximum size of females (total length 760 mm vs. 649 mm, snout-vent length 536 mm vs. 475 mm), and by colouration. *Liopholidophis dimorphus* has an overall lighter, reddish brown dorsal colouration (vs. olive brown to blackish in *L. sexlineatus*), an immaculate venter (vs. mostly mottled), and only two distinct narrow lateral stripes, one starting on the posterior half of the body (vs. a system of continuous, partly diffuse, narrow to broad stripes; Figs 4 and 5). Furthermore, the male of *L. dimorphus* has mat dorsal scales (shiny in males of *L. sexlineatus*) and strongly differs from *L. sexlineatus* genetically (16.1–16.4% uncorrected pairwise sequence divergence in the cytochrome *b* gene).

Description of the holotype. Adult male, in good state of preservation, but has partly lost the outermost layer of the scales for unknown reasons. Total length 1072 mm, tail length 457 mm (43% of total length). Dorsal scales smooth, mat, without apical



Fig. 4 Holotype of *Liopholidophis dimorphus* sp. n. in life (ZSM 252/2004).

pits. Dorsals in 17-17-15 rows. Scale row reduction from 17 to 15 rows at the level of ventral 115. One preventral, 163 ventrals. Anal plate divided. Subcaudal pairs 134. Upper labials 8/8 (left/right), with 4–5 touching the eye. Lower labials 10/10, the first pair in contact behind the mental, 1–5 touching an anterior genial, 5–6 touching a posterior genial. Anterior genials slightly shorter than posterior. Two preoculars. Loreal present, as high as wide (ratio height/width 1.0). Rostral wider than high (ratio height/width 0.61). Temporals 1 + 2 + 3. Greatest head width (parietal region) 10.5 mm, head length (tip of snout to end of mandibles) 20.5 mm. Head wider than neck. Pupil round. Eye moderately large, diameter 3.2 mm, equal to the distance between eye and posterior edge of nostril. Body higher than wide.

Life colouration of the holotype (based on slides taken in the field, see also Fig. 4). Dorsal ground colouration reddish brown. A narrow black stripe covers the suture of the ventrals and the dorsals and extends from the first ventral to the tip of the tail. A second narrow lateral stripe starts posteriorly at ventral 103 and extends to the cloaca. It covers the upper portions of dorsal scale row 2 and the lower portions of dorsal scale row 3. A third, facial stripe on the upper supralabial edges begins on labial 3 and continues onto the posterior third of the body as an indistinct and disintegrated lateral to dorso-lateral row of black mottlings. The mottled area is 1–3 scales wide and covers scale rows 4–7. The lower portions of the supralabials are immaculate white. A diffuse orange coloured longitudinal stripe on the lowermost dorsal scale rows extends from the mouth angle onto the first third of the body and then gradually becomes darker.

Ventral surfaces of head, neck, body and tail immaculate cream-white to pale orange, except for the outer edges of the ventrals which are dusted with black, iridescent. During approximately 10 months of preservation in alcohol the overall colouration faded only slightly, with the exception of the

Table 3 Variation in basic meristic and mensural data of the species of the genus *Liopholidophis* (former *L. sexlineatus* group), based on Cadle (1996, 1998), Thomas *et al.* (2001) and Table 2. Data are given as ranges followed by the number of specimens in parentheses. Total length followed by snout-vent length [SVL].

	<i>rhadinaea</i>	<i>dolicocercus</i>	<i>grandidieri</i>	<i>varius</i>	<i>sexlineatus</i>	<i>dimorphus</i>
Dorsals	17-17-15	17-17-15	17-17-15	17-17-15	17-17-15	17-17-15
Ventrals						
♂♂	170–179 (7)	152–160 (7)	169–171 (2)	146–154 (7)	147–163 (24)	163
♀♀	150–160 (11)	140–150 (5)	147–161 (2)	139–150 (7)	135–148 (22)	146
Subcaudals						
♂♂	126–137 (6)	140–164 (7)	215–221 (2)	88–103 (7)	127–160 (19)	134
♀♀	69–88 (11)	79–88 (5)	>98–113 (2)	67–71 (4)	67–79 (21)	79
Maximum total length [snout-vent length] (mm)						
♂♂	749 [429]	1426 [770]	1636 [732]	889 [591]	1385 [675]	1072 [615]
♀♀	424 [309]	992 [705]	674 [436]	664 + [578]	649 [475]	760 [536]
Tail length/total length						
♂♂	0.37–0.43 (6)	0.38–0.49 (7)	0.54–0.55 (2)	0.30–0.42 (7)	0.41–0.53 (20)	0.43
♀♀	0.24–0.28 (11)	0.29–0.30 (4)	0.35 (2)	0.24–0.26 (4)	0.24–0.30 (20)	0.29
Eye diameter/eye–nostril distance						
	1.05–1.45 (13)	0.96–1.31 (9)	1.16–1.38 (3)	0.77–1.0 (6)	0.87–1.44 (33)	1.03, 1.0

orange coloured stripe on the anterior lowermost dorsals, which completely faded to light brown.

Variation. The paratype is an adult female, in mediocre state of preservation (slightly macerated). Total length 760 mm, tail length 224 mm (29% of total length). Dorsal scales smooth, shiny, without apical pits. Dorsals in 17-17-15 rows. Scale row reduction from 17 to 15 rows at the level of ventral 88. One preventral, 146 ventrals. Anal plate split into three scales, two on left side. Subcaudal pairs 79. Upper labials 8/8, with 4–5 touching the eye. Lower labials 10/10, the first pair in contact behind the mental, 1–5 touching an anterior genial, 5–6 touching a posterior genial. Anterior genials slightly shorter than posterior. Two preoculars. Loreal present, as high as wide (ratio height/width 1.0). Rostral wider than high (ratio height/width 0.74). Temporals 1 + 2 + 3. Greatest head width (parietal region) 13.5 mm, head length (tip of snout to end of mandibles) 23.0 mm. Head wider than neck. Pupil round. Eye moderately large, diameter 3.3 mm, equal to the distance between eye and posterior edge of nostril. Body wider than high.

Habitat, natural history and distribution. The male holotype was collected on the ground during the day when it was crossing a trail in primary rainforest. No water body was recognized around this locality. This observation could be considered as a first indication that the species has terrestrial rather than semiaquatic habits (in contrast to *L. sexlineatus*, e.g., Cadle 1996: 410–411). The female paratype was found in rain forest as well (A. Razafimanantsoa, pers. comm.). The latter specimen contained two food items, the left hind foot of a large microhylid frog (probably *Plethodontohyla laevipes*, length of hind foot 42 mm, including calcaneum of tarsus) and the remains



Fig. 5 *Liopholidophis sexlineatus* (from Andringitra) in life.

of a large milliped (Diplopoda) with more than 44 mm length. However, it is unclear if the milliped has been consumed by the snake itself or has arrived there via the frog's stomach. The *Plethodontohyla* remains confirm the observation of Cadle (2003) who noted already that forest species of *Liopholidophis* eat a high proportion of microhylid frogs (*Platypelis*, *Plethodontohyla*).

Liopholidophis dimorphus is only known from Montagne d'Ambre National Park (= Ambohitra) and is possibly endemic to this volcanic massif, which is covered by primary rain forest. The reserve appears to be well protected and might ensure the survival of the species for the near future. The new *Liopholidophis* species from Montagne d'Ambre, listed by Raxworthy & Nussbaum (1994), might refer either to *L. epistibes*, which was described by Cadle (1996; also based on material from Montagne d'Ambre, p. 385) or to *L. dimorphus* described herein, or to another undescribed species.

Remarks. The available names in *Liopholidophis* include: *Dromicus macrocerus* (Günther 1882) (type locality ‘eastern Betsileo’). This taxon is considered to be a junior synonym of *L. sexlineatus* (Cadle 1996: 408). This author writes (Cadle 1996: 412): ‘Günther (1882) described females and males of *L. sexlineatus* (as *Dromicus sexlineatus* and *D. macrocerus*, respectively) in the same paper, failing to realize that the extraordinary differences in tail length and subcaudal counts manifested sexual dimorphism (of a nature hitherto unknown in snakes). The error was caught by Boulenger (1893: 246), who correctly identified types of *sexlineatus* as females and those of *macrocerus* as males.’ Regarding this situation it seems clear that *D. macrocerus* is not a senior synonym of *L. dimorphus*. Recently, Thomas *et al.* (2001) placed *Philodryas pallidus* Werner, 1926 (type locality ‘Montevideo, Uruguay’, in error) in the synonymy of *L. varius*. However, the number of ventrals (146) and subcaudals (103) of the holotype strongly differ from those of *L. dimorphus*.

Discussion

Distribution and habitat of Liopholidophis and Bibilava

Beside the morphological and genetic differences between *Liopholidophis* and *Bibilava*, also the pattern of distribution seems to be different between both genera. The discovery of *L. dimorphus* is the first record of a *Liopholidophis* s. str. species from far northern Madagascar and it seems even likely that this species is endemic to the north. *Liopholidophis dimorphus* was found at about 800 m above sea level in the rainforest which is in concordance with the altitudinal distribution and the wet habitats of the other *Liopholidophis* species (mid- and high altitude rainforests or wet mountain habitats). In contrast, *Bibilava* species are all known to occur also at low altitude and even on offshore islands (Nosy Be, Nosy Boraha) and four of the five species (*B. epistibes*, *B. lateralis*, *B. martae* and *B. stumpffi*) are not restricted to humid habitats but also occur in the relatively dry western and northern regions of Madagascar (Cadle 1996; Andreone *et al.* 2001; Glaw *et al.* 2005).

Phylogenetic relationships in Bibilava

Concerning the phylogenetic relationships within *Bibilava* (where our sampling is complete at the species level) Cadle (1996) hypothesized a sister group relationship between *B. stumpffi* and *B. epistibes*, based on similar habitus and the extremely bilobed hemipenes. Our data suggest a sister group relationships between *stumpffi* and *lateralis* on one hand and *epistibes* and *martae* on the other hand, indicating that the distinctly striped pattern of *B. lateralis* is derived. The molecular analysis further indicates that *B. infrasignatus* is the most basal species (see Fig. 2). Among *Bibilava*, this species is characterized by the lowest number of subcaudals, the shortest relative tail length, and the largest known female size.

Phylogenetic relationships and evolution of sexual dimorphism in Liopholidophis

Cadle (1996) demonstrated male superiority in body size (snout-vent length and total length) for all species of *Liopholidophis* except for *dolicocercus*. Our data indicate male superiority also for this species and *L. dimorphus*, showing that this character is a consistent synapomorphy of all *Liopholidophis*. Male superiority in colubrids is exceptional (Shine 1991) as is the extreme sexual dimorphism in tail length shown by *Liopholidophis* (Cadle 1996). Our molecular trees offer a robust *Liopholidophis* phylogeny with high support for each node, but unfortunately, only three out of six *Liopholidophis* species were available for the molecular analysis. However, the fourth species, *L. grandidieri*, is almost certainly the sister species to *L. dolicocercus*, as was already suggested by Cadle (1996) and is clearly indicated by the synapomorphic black ventral side and by similar dorsal colouration and meristic data (see Table 3). Concerning the position of *rhadinaea*, a preliminary hypothesis is possible as well. Cadle (1996) already noticed that *L. rhadinaea* shares important synapomorphies of *Liopholidophis* (especially the extreme sexual dimorphism in tail length, and dentitional characters), but on the other hand is superficially very similar to several species of *Liophidium* (pink ventral side, light nape spots, small size). Our discovery of the sister group relationship of *Liopholidophis* and *Liophidium* offers the possibility to reconcile this mosaic character distribution of *rhadinaea* by placing it as the most basal *Liopholidophis* (or much less likely as basal *Liophidium*) rather than deeply nested within *Liopholidophis* as suggested by Cadle (1996; Fig. 4). Using this plausible assumption on the position of *rhadinaea*, which is apparently not contradicted by any known morphological character, allows to present the following, almost complete phylogenetic hypothesis for the *Liopholidophis* species, leaving only *L. varius* apart: (*rhadinaea*- (*dimorphus*- (*sexlineatus*- (*dolicocercus* — *grandidieri*))))). Using this topology as a working hypothesis allows to hypothetically reconstruct the evolution of sexual dimorphism in the genus based on data of 81 specimens of these five species. As is evident from Table 3 there is a consistent trend of increasing maximum total length and maximum snout-vent length of males from *rhadinaea* to *grandidieri*. In contrast, females show at most a poorly recognizable increase of maximum total length but no clear trend concerning maximum snout-vent length. A second trend is that the ratio of tail length/total length is slightly increasing from the small *rhadinaea* to the large *grandidieri* in males and females (Table 3 and Fig. 6A). Interestingly, the same trend is even more pronounced intraspecifically within *L. sexlineatus* males where larger males consistently have proportionally longer tails (Table 2 and Fig. 6B). These data indicate an allometric coevolution of snout-vent length and tail length that started early in the evolution of *Liopholidophis* and might have led from a small *Liophidium*-like ancestor without extreme

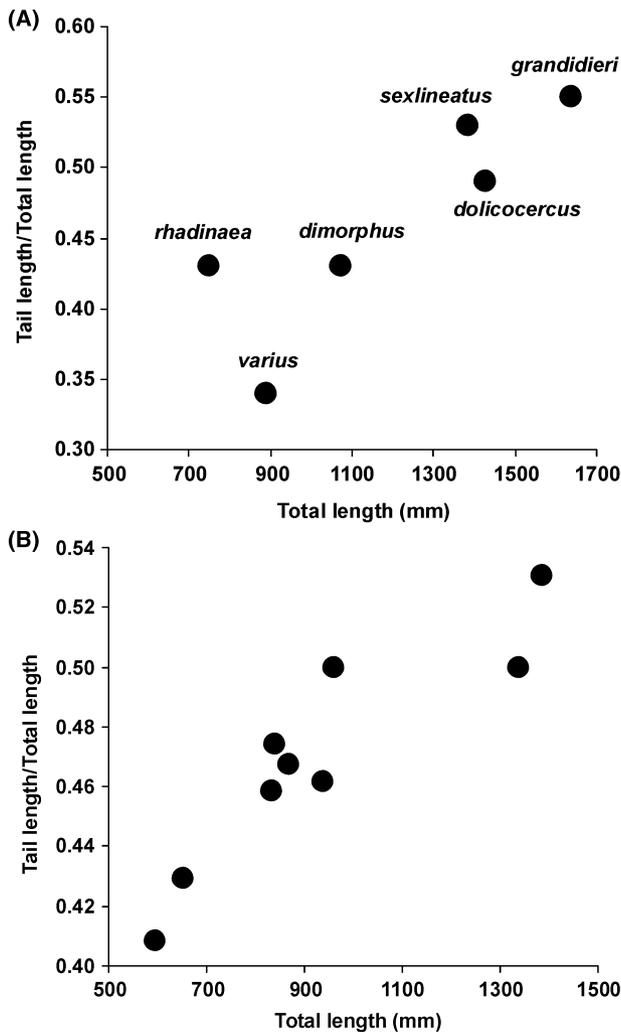


Fig. 6 A, B. Correlation of relative tail length and total length (only specimens with complete tails were considered). —A. In the largest known males of the six *Liopholidophis* species (*dimorphus* ZSM 252/2004; *dolicocercus* ZSM 60/2005; *grandidieri* MNHN 021-03, data from Cadle 1996; *rhadinaea* MCZ 180399, data from Cadle 1996; *sexlineatus* ZMB 34159; *varius* BMNH 1946.1.7.66, data from Cadle 1998). —B. Within *L. sexlineatus* males (MCZ 11604 from Cadle 1996; ZMB 15828, 34145, 34147, 34153, and 34159; ZSM 576/2001, 696/2003, and 168/2006).

dimorphism in tail length (and probably without male superiority) to the large *grandidieri* with a tail length that even exceeds body length. The selective force driving this body size increase is unknown, but it is usually considered as likely that larger males obtain a disproportionately high number of matings either due to female choice, success in male–male rivalry or even due to the ability of larger males to coercively inseminate females (Shine & Mason 2005). In contrast, the extremely elongated tails of *Liopholidophis* males (which are

rather thin and not very muscular) are unlikely to confer significant advantages in male–male rivalry or in the ability to coercively inseminate females. Hence, female choice remains as the most probable main selective force for the allometric increase of the male’s tail length.

Differentiation between *Liopholidium* and *Liopholidophis*

Despite the significant progress in understanding the relationships between *Liopholidophis* and *Liopholidium*, their early diversification remains enigmatic. Cadle (1996) discussed the striking similarities of *L. rhadinaea* with several species of *Liopholidium*. Strong sexual dimorphism in tail length, an unusual and unquestionably derived character within colubrids, is the most obvious characteristic indicating the relationships of *rhadinaea* to *Liopholidophis* (Cadle 1996: 381). The problem to distinguish *Liopholidophis* and *Liopholidium* becomes even more obvious when including an undescribed dwarf species that was hitherto known by only a single adult male collected at Andasibe in 1966. This specimen was considered as *Liopholidium* incertae sedis by Domergue (1988) and as ‘genus and species inquirenda’ by Cadle (1996). In 1996, we found a second male of this enigmatic species at Andasibe, indicating that it represents a new species rather than an aberrant specimen. The difficulties to allude this species either to *Liopholidophis* or to *Liopholidium* might confirm that *Liopholidophis* evolved from a small *Liopholidium*-like ancestor. This species needs further study and will certainly affect the definition and delimitation of *Liopholidophis* and *Liopholidium*.

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