

Phylogenetic relationships of a new species of pseudoxyrhophiine snake (Reptilia: Lamprophiidae: *Thamnosophis*) suggest a biogeographical link between western and northern Madagascar

Frank Glaw^{a,*}, Zoltán T. Nagy^b, Jörn Köhler^c, Michael Franzen^a, Miguel Vences^d

^aZoologische Staatssammlung München, Münchhausenstrasse 21, 81247 München, Germany

^bRoyal Belgian Institute of Natural Sciences, JEMU, rue Vautier 29, 1000 Brussels, Belgium

^cDepartment of Natural History – Zoology, Hessisches Landesmuseum Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany

^dDivision of Evolutionary Biology, Zoological Institute, Technical University of Braunschweig, Spielmannstr. 8, 38106 Braunschweig, Germany

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Abstract

We describe a new species of the pseudoxyrhophiine snake genus *Thamnosophis* from a dry forest of the karstic massif Tsingy de Bemaraha in central western Madagascar. *Thamnosophis mavotenda* sp. n. is characterised by 19 dorsal scale rows, 188 ventrals, 110 subcaudals, and by colouration (e.g. yellow head sides). Morphological and molecular phylogenetic data indicate that the species is most closely related to the recently described *Thamnosophis martae* from the far north of the island which inhabits dry karstic forest and subhumid lowland rainforest. This species pair represents a well-supported example of a sister-group relationship in snakes between northern Madagascar and the Tsingy de Bemaraha plateau, and corroborates preliminary observations in other reptile species. We discuss this finding in the light of recent hypotheses on the biogeographic zonation of Madagascar.

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Introduction

Madagascar's biodiversity is famous for its extraordinary species richness and its endemism at several taxonomic levels. Although the distribution of species is still poorly known in most cases, it is evident that the geographic range of many species, including amphibians and reptiles, is restricted to small areas. Despite several historical attempts to reflect the observed patterns of endemism by biogeographic zonations of the island

(e.g. Angel 1942 for reptiles), comprehensive hypotheses explaining the evolution of this microendemism have yet to be developed (Wilmé et al. 2006). Even the primary bioclimatic east–west (wet–dry) vicariance tenet has been challenged by Yoder and Heckman (2006), who showed that in mouse lemurs (*Microcebus*) the primary phylogenetic split is between a northern and a southern clade. Although large-scale modelling, including thousands of species, is increasingly used to identify centers of endemism and to draw conclusions for conservation prioritization (e.g. Kremen et al. 2008), a more detailed analysis of the phylogeny and distribution of smaller test groups is still crucial to gain more specific insights into the biogeography of certain species.

*Corresponding author.

E-mail address: frank.glaw@zsm.mwn.de (F. Glaw).

The genus *Thamnosophis* Jan, 1863 is part of a larger radiation of Malagasy pseudoxyrhophiine snakes (Nagy et al. 2003) that is now included in the family Lamprophiidae (Vidal et al. 2007). Currently, five species are included in the genus (Cadle and Ineich 2008): *Thamnosophis stumpffi* (Boettger, 1881), *T. lateralis* (Duméril, Bibron & Duméril, 1854), *T. infrasignatus* (Günther, 1882), *T. epistibes* (Cadle, 1996), and *T. martae* (Glaw, Franzen & Vences, 2005). Members of these species have 19 rows of dorsal scales and no strong sexual dimorphism in tail length (Domergue 1973; Cadle 1996, 1998). During a recent survey in the Tsingy de Bemaraha in western Madagascar we discovered a single individual of a new *Thamnosophis* species which strongly resembles *T. martae* in pholidosis but *T. epistibes* in live colouration. In the following we describe the new species, investigate its phylogenetic position, and discuss the biogeographic implications of our findings.

Material and methods

Specimens were fixed in formalin or 90% 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 (TL) were measured to the nearest millimeter. We follow Cadle (1996) in the terminology of meristic and mensural

data. Counts of ventral scales include ventrals but no preentrals. Geographical coordinates of localities were determined by global positioning receivers (GPS). Institutional abbreviations: MNHN = Museum National d'Histoire Naturelle, Paris; UADBA = Université d'Antananarivo, Département de Biologie Animale; ZSM = Zoologische Staatssammlung München. FGZC and ZCMV refer to field numbers assigned by F. Glaw and M. Vences, respectively.

DNA was extracted using standard protocols (Sambrook et al. 1989). The complete mitochondrial cytochrome *b* gene was amplified in PCRs using the same primers as Nagy et al. (2003). The PCR products were sequenced directly on ABI Prism Genetic Analyzer automatic sequencers (Applied Biosystems, Foster City, USA). The sequences were checked for quality and aligned by hand. Phylogenetic analyses were carried out using 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 AIC implemented in MrModeltest 2.2 (Nylander 2004) in order to find the appropriate nucleotide substitution model, and validated by 200 full bootstrap replicates. Bayesian trees were calculated using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), running 2×10^6 generations. The new DNA sequences have been deposited in GenBank. For accession numbers and data on voucher specimens, see Table 1.

Table 1. Collecting data, voucher specimens, and GenBank accession numbers for the snakes included in the molecular and morphological analyses.

| Species | Locality information | Voucher specimen | Accession no. |
|--------------------------|--|-----------------------|---------------|
| <i>D. bernieri</i> | Ifaty | UADBA (FGMV 2000-517) | AY188014 |
| <i>D. quadrilineatus</i> | Sambava | Not collected | AY188015 |
| <i>T. epistibes</i> | Ranomafana | UADBA 24506 | DQ979979 |
| <i>T. infrasignatus</i> | Imaloka, 21°14.527'S, 47°27.909'E, 1020 m | UADBA (ZCMV 2934) | FJ403475 |
| <i>T. lateralis</i> | Near Mantasoa | UADBA (FGMV 2000-36) | DQ979977 |
| <i>T. lateralis</i> | Isalo, Namazaha | M5546 | FJ403476 |
| <i>T. martae</i> | Montagne des Français, 12°19'34"S, 49°20'09"E, c. 300 m | ZSM 253/2004 (HT) | DQ979981 |
| <i>T. martae</i> | Montagne des Français, without exact locality data | ZSM 1596/2008 | FJ403480 |
| <i>T. martae</i> | Montagne des Français, c. 1.8 km SW Andavakoera, 12°20.24'S, 49°21.26'E, 200 m | ZSM 1595/2008 | FJ403479 |
| <i>T. martae</i> | Forêt d'Ambre, c. 6 km NW Sakaramy, 12°25.17'S, 49°13.01'E, 514 m | ZSM 1597/2008 | FJ403481 |
| <i>T. martae</i> | Forêt d'Ambre, c. 6 km NW Sakaramy, 12°27'33"S, 49°13'39"E, 470 m | ZSM 2062/2007 | FJ403477 |
| <i>T. mavotenda</i> | Bendrao forest, Bemaraha NP, 18°47'04"S, 44°51'37"E, 427 m | ZSM 127/2006 (HT) | FJ403478 |
| <i>T. stumpffi</i> | Nosy Be | ZSM 579/2001 | DQ979983 |

D. = *Dromicodryas*; *T.* = *Thamnosophis*; HT = holotype.

Results

Molecular phylogenetic relationships within *Thamnosophis*

The molecular tree (Fig. 1) confirms *T. infrasignatus* as the most basal species in *Thamnosophis* (see Glaw et al. 2007b), as well as close relationships between *T. stumpffi* and *T. lateralis* in one sublineage and between *T. epistibes* and *T. martae* in another. The specimen from Bemaraha is placed in this second lineage, as sister to *T. martae*. Pairwise sequence divergence in the cytochrome *b* gene was 10.9–11.2% between *T. martae* and the Bemaraha specimen, 13.3% between *T. epistibes* and the Bemaraha specimen, and 13.7–14.0% between *T. martae* and *T. epistibes*. These divergence values are higher than that between *T. lateralis* and *T. stumpffi* (9.3–9.5%). Sequences of all *T. martae* specimens were very similar to each other; individuals from the same locality shared the same haplotype. The pairwise sequence divergence in the cytochrome *b* gene was 0.0–0.5%. Although distinctly different mitochondrial haplotypes can occur even within populations of pseudoxyrhophiine snakes (Nagy et al. 2007), we are confident that the strong genetic differentiation between *T. martae* and the Bemaraha specimen,

together with various non-molecular characteristics (see below), is indicative of specific distinctness of the two forms. We therefore describe the Bemaraha specimen as a new species.

Thamnosophis mavotenda sp. n. (Figs. 2–4, 5A, 6)

Etymology

The specific epithet is derived from the Malagasy words “mavo” (yellow) and “tenda” (throat) and refers to the yellow throat of the holotype. It is to be treated as a noun in apposition for the purposes of nomenclature.

Type material

Holotype (ZSM 127/2006; field number FGZC 0922): Adult male; western Madagascar, Mahajanga Province, Tsingy de Bemaraha National Park, Bendrao forest, 18°47'04"S, 44°51'37"E, 427 m a.s.l., 26 March 2006, leg. F. Glaw, J. Köhler, P. Bora & H. Enting.

Diagnosis

The male holotype of *Thamnosophis mavotenda* sp. n. differs from males of *T. stumpffi*, *T. epistibes*, *T. lateralis*, and *T. infrasignatus* by a higher number of ventrals (188 vs. 141–166) and subcaudals (110 vs.

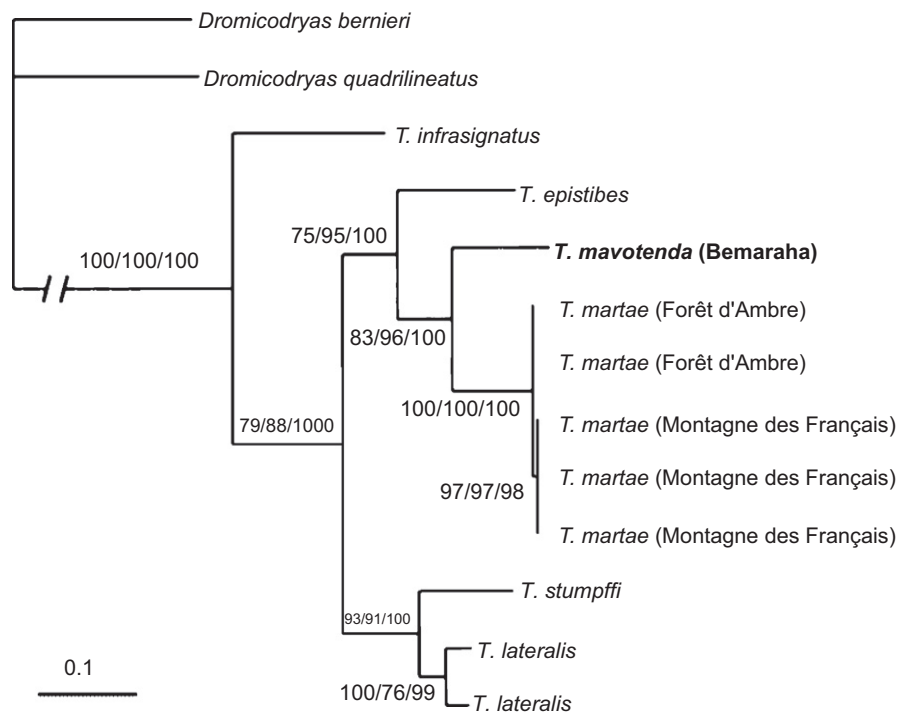


Fig. 1. Phylogenetic relationships of the six *Thamnosophis* species. Maximum likelihood phylogram based on complete cytochrome *b* sequences (1111–1114 bp), except for *T. infrasignatus* (partial sequence of 1006 bp). Numbers at nodes are parsimony bootstraps/maximum likelihood bootstraps/Bayesian posterior probabilities (2000 replicates, 200 replicates, 2×10^6 generations, respectively). *Dromicodryas* species served as outgroup.



Fig. 2. Male holotype of *Thamnosophis mavotenda* sp. n., dorsolateral view in life.



Fig. 3. Male holotype of *Thamnosophis mavotenda* sp. n., preserved, ventral view.

66–104) (see Table 2 in Glaw et al. 2005). In addition, it differs from *T. stumpffi* by its extensive dark spots and stripes on the venter (vs. venter immaculate). The new species is virtually identical to its presumed sister

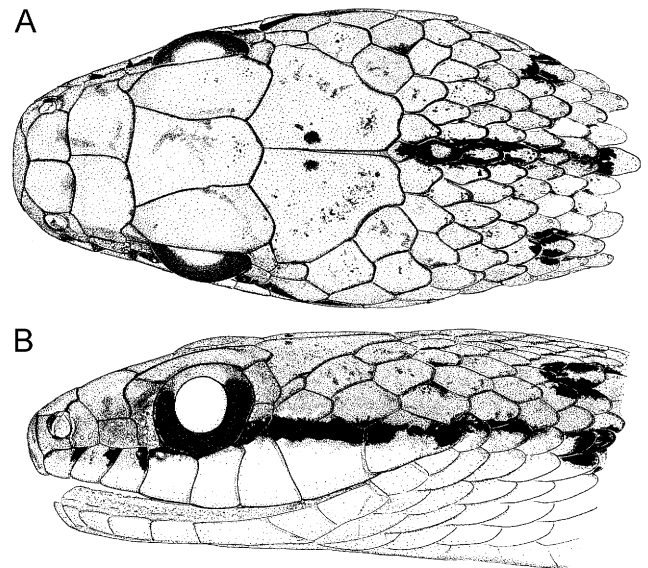


Fig. 4. Male holotype of *Thamnosophis mavotenda* sp. n., head: (A) Dorsal view. (B) Lateral view. Drawings by Ruth Kühbandner.

species, *T. martaë*, with regard to standard scale counts. For better comparisons, we were able to examine five additional individuals of *T. martaë* (previously known

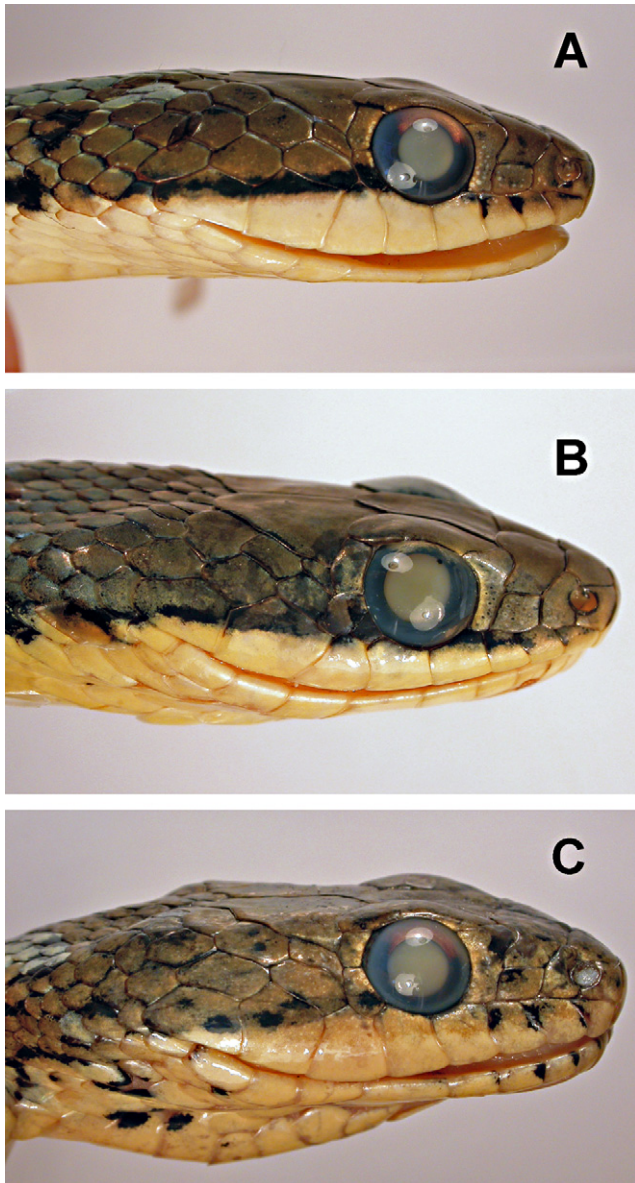


Fig. 5. Lateral views of heads. (A) *Thamnosophis mavotenda* sp. n. (holotype, ZSM 127/2006). (B) *T. epistibes* (ZSM 230/2002 from Vohidrazana). (C) *T. martae* (holotype, ZSM 253/2004 from Montagne des Français).

from the holotype only; Table 2) which had been obtained during recent field surveys in Forêt d'Ambre and Montagne des Français of northern Madagascar (see also D'Cruze et al. 2007, 2008). Morphometric data for these specimens are presented in Table 2; for collection data see Table 1. The holotype of *T. mavotenda* sp. n. differs from the adult specimens of *T. martae* by a more slender head (relative head width 1.9% of SVL vs. 2.0–2.5% in *T. martae*), by yellow colouration of labials and lateral neck (vs. greyish in life), a long postocular bar that is nearly confluent with the lateral markings (Figs. 4B, 5A; vs. postocular



Fig. 6. Male holotype of *Thamnosophis mavotenda* sp. n., preserved, dorsal view.

bar and lateral markings separated, Fig. 5C), a broad median dorsal stripe covering 5–6 dorsals (vs. 2–3 dorsals, if present), a greenish-brown ground colouration (vs. brown), a heavily blotched ventral side without distinct lateral rows of spots (vs. dusted with tiny markings and distinct lateral spots), and a pale-coloured ventral side of the tail with isolated dark blotches (vs. intensive dark dusting). Since only a single specimen of *T. mavotenda* was available, the significance of all described colour differences and of the minor differences in head proportions requires confirmation from additional specimens, which might show some degree of intraspecific variability (see Cadle 1996). On the other hand, *T. martae* and *T. mavotenda* show substantial genetic differentiation as well (Fig. 1).

Description

Adult male, left hemipenis partially extruded, in good state of preservation, but has partly lost the outermost layer of scales for unknown reasons.

Total length 846 mm, tail length 256 mm (30% of total length). Dorsal scales smooth, with two apical pits (Fig. 4). Dorsals in 19-19-17 rows. Scale row reduction from 19 to 17 rows at level of ventral 109. Three preventrals, 188 ventrals. Cloacal plate divided. Subcaudal pairs 110. Upper labials 8/8, with 4–5 touching the eye. Lower labials 10/10, first pair in contact behind mental, 1–5 touching an anterior genial, 5–6 touching a posterior genial. Anterior genials shorter than posterior ones. Preocular single, two postoculars. Loreal present, wider than high (height/width ratio 0.82). Temporals 2+2+3. Body approximately as high as wide. Greatest head width (parietal region) 11.2 mm, head length (tip of snout to end of mandibles) 21.7 mm. Head wider than neck. Pupil round. Eye large, diameter 4.3 mm. Distance between eye and posterior edge of nostril 3.7 mm.

Table 2. Morphometric data of *Thamnosophis mavotenda* sp. n. and *T. martaе*.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|----------------------------|----------|-----|-----|-----|------|------|-------|-----|-----|
| <i>T. mavotenda</i> sp. n. | | | | | | | | | |
| ZSM 127/2006 (HT) | Male | 846 | 590 | 256 | 0.30 | 11.2 | 0.019 | 188 | 110 |
| <i>T. martaе</i> | | | | | | | | | |
| ZSM 253/2004 (HT) | Male | 847 | 575 | 272 | 0.32 | 14.5 | 0.025 | 185 | 109 |
| UADBA (FGZC 1777) | Male | 893 | 598 | 295 | 0.33 | 12.7 | 0.021 | 184 | 117 |
| ZSM 1597/2008 | Male | 628 | 435 | 193 | 0.31 | 8.8 | 0.020 | 186 | 116 |
| ZSM 1596/2008 | Female | 794 | 545 | 249 | 0.31 | 11.3 | 0.021 | 188 | 105 |
| ZSM 1595/2008 | Female | 682 | 472 | 210 | 0.31 | 10.9 | 0.023 | 187 | 106 |
| ZSM 2062/2007 | Juvenile | 321 | 230 | 91 | 0.28 | 6.6 | 0.029 | 188 | 106 |

HT = holotype; 1 = life stage or sex; 2 = total length (mm); 3 = snout-vent length (mm); 4 = tail length (mm); 5 = tail length/total length; 6 = head width (mm); 7 = head width/snout-vent length; 8 = number of ventrals; 9 = number of subcaudal pairs.

Colouration in life (based on digital photographs taken in the field; see Fig. 2 and Glaw and Vences 2007, p. 448 under *Liopholidophis* cf. *martaе*): Ground colouration of head medium brown to greenish-brown. Dorsal side of head almost immaculate, but with slightly darker sutures of scales and two small roundish dark spots near inner margins of parietals. Upper labials, lower labials and lateral side of neck below postocular bar mostly yellow. Upper labials 1–3 with dark upper posterior corners. A dark postocular bar extends from lower half of lower postocular into angle of jaws, where it is confluent with dark lateral markings; bar covers lower half of lower primary temporal, upper half of supralabial 7, and center of supralabial 8.

Ground colouration of dorsal scale rows 1–2 (neck and anterior body) and 1–3 (posterior body) medium to dark greenish-brown, of dorsal scale rows 3–4 (neck and anterior body) and 4–6 (posterior body) light brown. This light lateral band greyish brown on anterior quarter of body, changing to greenish-brown posteriorly. Mid-dorsals 5–6 dark greenish-brown. Longitudinal stripes most distinctive on anterior quarter of body, becoming more diffuse posteriorly. A series of large roundish black blotches on lower flanks, starting anteriorly behind postocular bar and extending onto posterior half of body. Blotches most distinctive on anterior quarter of body, becoming much narrower in midsection, posteriorly reduced to a diffuse series of narrow vertical bars. Dorsals of anterior half of body partly with dark markings at margins, forming diffuse reticulation; the latter most distinctive on anterior quarter of body, gradually fading posteriorly. Posterior quarter of body and tail without dark markings or reticulation. Light ground colouration gradually suffused with large dark grey blotches and mottling, especially on posterior thirds of body and tail. Ventral surface of head immaculate. Anterior quarter of venter with three irregular rows of dark spots (starting

on ventral 15), which midventrally form one and ventrolaterally two more or less distinct lines (Fig. 3). Spots fuse posteriorly and form a more or less continuous broad midventral line and two indistinct ventrolateral bands. Ventral surface of tail whitish, mottled with large irregular dark grey blotches.

After approximately 20 months of preservation and due to the loss of the outermost layer of head scales and dorsals, the dorsal ground colouration has faded considerably and changed to a more or less homogeneous grey-brown, making the alternating light and dark longitudinal zones nearly invisible (Fig. 6). The intensive yellow colouration of labials and lateral neck has also faded completely and changed to cream-whitish.

Habitat and habits

The holotype was captured during the day, swimming in a river of c. 6–8 m width and c. 50 cm depth. The adjacent vegetation was disturbed dry forest on calcareous ground. The snake probably tried to escape by swimming, having been disturbed by people walking in the river.

Distribution and conservation

Thamnosophis mavotenda is only known from a single individual captured in the Tsingy de Bemaraha National Park. Thus, any statements on the species' distribution and conservation status must remain tentative. Several Malagasy reptile and amphibian species are known only from this nature reserve (e.g. Schimmenti and Jesu 1996; Puente et al. 2005; Glaw et al. 2007a; Köhler et al. 2007), suggesting its importance as a center of endemism. It is therefore possible that *T. mavotenda* is endemic to the Tsingy de Bemaraha as well. We did not notice any obvious threat to the species, and its occurrence in a relatively large, protected area seems to indicate that it is not severely threatened, although it is remarkable that intensive surveys in this park (Bora et al. in press)

did not reveal further specimens. Using the same rationale and IUCN criteria as applied during the Global Amphibian Assessment for Malagasy amphibians (Andreone et al. 2005), we classify *T. mavotenda* as “Data Deficient”.

Remarks

Glaw et al. (2005) discussed available names in the genus *Thamnosophis* (then: *Liopholidophis stumpffi* group) in their description of *T. martaë*. Since pholidosis in *T. mavotenda* sp. n. is very similar to that in *T. martaë*, all names predating the latter can be excluded for the same reasons. Nevertheless, we re-examined the two syntypes of *Liophidium gracile* Mocquard, 1908 (a synonym of *T. stumpffi* according to Cadle 1996) in order to exclude the possibility that these syntypes are not conspecific. Morphometric data of these two specimens are as follows: (1) MNHN 1893.211 (Montagne d’Ambre): male, snout-vent length 345 mm, tail length 154 mm (total length 499 mm), 150 ventrals, 90 subcaudal pairs; (2) MNHN 1884.595 (Nosy Be): juvenile, snout-vent length 176 mm, tail length 89 mm (total length 265 mm), 145 ventrals, 99 subcaudal pairs. These data confirm that both syntypes of *Liophidium gracile* belong to *Thamnosophis stumpffi* and clearly are not referable to *T. martaë*, which was discovered recently in Forêt d’Ambre (Table 1). Remarkably, neither *T. stumpffi* nor *T. epistibes* (recorded from this massif by Cadle 1996, p. 385, based on two specimens collected in 1963) could be found in Montagne d’Ambre during intensive herpetological surveys over the past two decades (D’Cruze et al. 2008).

Usage of the genus name *Thamnosophis* instead of *Bibilava* follows Cadle and Ineich (2008). *Thamnosophis* Jan, 1863 originally included snake species from different continents, and remained poorly defined until Wall (1923) designated *Leptophis lateralis* from Madagascar as the type species. Unfortunately, this designation was apparently overlooked by Parker (1925) and all subsequent authors who published accounts on the Malagasy snake genus *Liopholidophis* Mocquard, 1904. None of them quoted the work of Wall (1923), nor discussed or drew the necessary conclusions from his designation. Although Williams and Wallach (1989) had already correctly listed *T. lateralis* as the type species of *Thamnosophis*, it took another two decades until Cadle and Ineich (2008) finally clarified the entire issue. Thus, *Liopholidophis* was used incorrectly for more than 80 years. Nevertheless, this name does remain valid for several species, because *Liopholidophis* in the earlier, wider sense has turned out to be non-monophyletic, hence was partitioned into two monophyletic genera by Glaw et al. (2007b). For one of these, the latter authors coined the genus name *Bibilava* which, however, is an objective junior synonym of *Thamnosophis* (Cadle and Ineich 2008).

Discussion

A recent proposal for biogeographic zonation in Madagascar (Wilmé et al. 2006) has emphasised the role of watersheds as an alternative to earlier hypotheses that had largely relied on bioclimatic zones (e.g. Angel 1942). Based on the complete molecular sampling of *Thamnosophis* and the relatively numerous distribution records of the species (see maps in Glaw and Vences 2007), we here use these snakes as a model to discuss the hypothesis of endemism outlined by Wilmé et al. (2006).

Thamnosophis lateralis is exceptionally widespread in Madagascar, hence is not informative for testing any biogeographic zonation hypothesis. Its close molecular relationships to *T. stumpffi* suggest that it is a phylogenetically young species that might have evolved allopatrically in the subhumid north before very successfully invading the rest of Madagascar. This hypothesis will be testable in future studies, as it predicts the most basal phylogeographic lineages within *T. lateralis* to occur in northern Madagascar, as in other widespread Malagasy reptiles (Boumans et al. 2007).

Thamnosophis stumpffi occurs in two different bioclimatic and vegetational zones (rainforest and dry forest) and in at least two different centers of endemism (Wilmé et al. 2006), therefore does not clearly support any model. *Thamnosophis infrasignatus*, the most basal species, occurs along the rainforest of the east and in the Sambirano region, supporting bioclimatic zonations.

A distinct biogeographic pattern is evident for the clade *T. epistibes-martaë-mavotenda*, supporting a primary east–west vicariance followed by secondary speciation between *T. martaë* and *T. mavotenda* in the west. Morphologically, the east–west split was accompanied by significant morphological changes in the western/northern lineage, i.e. by an increase in the number of ventrals, subcaudals, and total length of males (data for females missing or insufficient), and perhaps by adaptation to the drier climate or the limestone habitats.

The presence of *T. epistibes* at Mahajanga in the west (Cadle 1996) at first glance does not seem to agree with this primary east–west vicariance. However, Mahajanga is located at the mouth of the Betsiboka river, and the presence of *T. epistibes* here can be explained by the Wilmé et al. (2006) hypothesis, in which the Betsiboka forms a retreat-dispersion watershed facilitating dispersals between eastern and western Madagascar. The Betsiboka watershed also slices the west into different centers of endemism, each of which contains only smaller rivers with headwaters at lower elevations. One of these, bordered by the Betsiboka and Tsiribihina rivers, includes the Tsingy de Bemaraha plateau and the distribution range of *T. mavotenda*. Known records of the presumed sister species, *T. martaë*, are restricted to a

small area in one center of endemism in the extreme north of the island (Wilmé et al. 2006). This center of endemism also includes other areas such as Daraina. However, although *T. martae* is common at Montagne des Français (D’Cruze et al. 2007), it has not been discovered in the Daraina region (Rakotondravony 2007) nor elsewhere in northwestern Madagascar (Ankarana, Sambirano, Berara: Rakotomalala 2002; Andreone et al. 2001, 2003; authors’ pers. obs.), which suggests local endemism in the Montagne des Français/Forêt d’Ambre region. Similarly, *T. mavotenda* has not been recorded elsewhere in the northwest (e.g. Ankara-fantsika: Ramanamanjato and Rabibisoa 2002; Mori et al. 2006). Further data are necessary to clarify whether the apparently disjunct distribution of *T. martae* and *T. mavotenda* indicates relict ranges of both species in karstic habitats or is an artifact due to insufficient sampling and/or cryptic habits of these snakes.

In contrast, the data for the entire genus *Thamnosophis* do not clearly support any single biogeographic zonation hypothesis. Instead, each species or clade appears to be a unique case, suggesting a mosaic of complex biogeographic patterns. A large number of factors might have influenced the present-day distribution of species, including bioclimate, watersheds, geological, historical and stochastic events, ecological competition, predation, dispersal abilities, and many others. Despite this complexity, remarkable differences in the origin of the Bemaraha fauna are evident between amphibians and reptiles: Recent studies on the amphibians of the Tsingy de Bemaraha (Vences et al. 2000; Glaw et al. 2007a; Köhler et al. 2007) found close molecular relationships to eastern Madagascar and hypothesized that rivers may provide sufficient biogeographic corridors from central Madagascar to the west. In contrast, there is no obvious example of clear eastern relationships of Bemaraha reptiles. Instead, they appear to show a very different pattern suggesting close relationships to northern Madagascar, as indicated by the presence of *Alluaudina bellyi*, *Amphiglossus reticulatus*, *Heteroliodon lava*, *Lygodactylus heterurus*, *Furcifer* cf. *petteri*, *Paroedura* cf. *homalorhina*, *Uroplatus* cf. *ebenai* and *U.* cf. *henkeli* (Bora et al. in press). Further examples may be the closely related species pair *Zonosaurus boettgeri* (north) and *Z. maramaintso* (Bemaraha region) (Raselimanana et al. 2006), as well as *Z. bemaraha* which has close relationships with specimens from Daraina in the north (Raselimanana et al. in press). Although their taxonomy and phylogenetic relationships have usually not been studied in detail, all these northern and northwestern species or species complexes have their southernmost localities in Bemaraha. A first study by Greenbaum et al. (2007) demonstrated that the large *Uroplatus* from Bemaraha is sister to *U. henkeli* from Nosy Be. Our analysis of

the phylogenetic position of *Thamnosophis mavotenda* reveals a similar, though even more disjunct pattern.

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