

---

# NATURAL HISTORY AND TAXONOMIC NOTES ON *LIOPHOLIDOPHIS GRANDIDIERI* MOCQUARD, AN UPLAND RAIN FOREST SNAKE FROM MADAGASCAR (SERPENTES: LAMPROPHIIDAE: PSEUDOXYRHOPHIINAE)

JOHN E. CADLE<sup>1,2</sup>

<sup>1</sup>Centre ValBio, B.P. 33, 312 Ranomafana-Ifanadiana, Madagascar

<sup>2</sup>Department of Herpetology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA, e-mail: jcadle@calacademy.org

**Abstract.**—Few observations on living specimens of the Malagasy snake *Liopholidophis grandidieri* Mocquard have been previously reported. New field observations and specimens from Ranomafana National Park amplify knowledge of the natural history of this species. *Liopholidophis grandidieri* is known from above 1200 m elevation in pristine rain forests with a high diversity of hardwoods and bamboo. In some areas of occurrence, the forests are of short stature (15–18 m) as a result of lying atop well-drained boulder fields with a thin soil layer. Dietary data show that this species consumes relatively small mantellid and microhylid frogs obtained on the ground or in phytotelms close to the ground. A female collected in late December contained four oviductal eggs with leathery shells. One specimen formed a rigid, loose set of coils and body loops, and hid the head as presumed defensive behaviors; otherwise, all individuals were complacent when handled and showed no tendency to bite. I describe coloration and present photographs of living specimens from Ranomafana National Park. The ventral colors of *L. grandidieri* were recently said to be aposematic, but I discuss other plausible alternatives.

**Key Words.**—conservation; diet; habitat; reproduction; snakes; systematics

---

## INTRODUCTION

The natural history and systematics of many snake species from Madagascar remain poorly documented. In some cases, morphological characters, geographic ranges, natural history, and colors in life are poorly documented because observations on living snakes are unavailable and few specimens may exist in museum collections. Among these is *Liopholidophis grandidieri* Mocquard (1904), which was known only from the holotype until the mid-1990s, by which time one additional specimen had been collected and two others were identified in old museum materials (Cadle 1996a). *Liopholidophis grandidieri* is still known from few specimens and few observations on its behavior or natural history have been reported.

Eight species of *Liopholidophis* are currently recognized (Cadle 1996a; Glaw et al. 2007, 2014). Five species (*L. dimorphus*, *L. doliocercus*, *L. grandidieri*, *L. rhadinaea*, and *L. sexlineatus*) are characterized by remarkable sexual dimorphism in tail length and exceptionally long tails in males (Cadle 1996a, 2009; Glaw et al. 2007, 2014). *Liopholidophis varius* is less exceptional in both characters (Cadle 2009) and these features are unknown in *L. oligolepis* and *L. baderi* because specimens of only one sex are known for these species (Glaw et al. 2014). *Liopholidophis grandidieri*

exhibits the greatest sexual dimorphism in tail length and the greatest reported relative tail length of any snake (tails average 18% longer than body length in males; Cadle 2009). Several hypotheses that might explain these extraordinary characteristics have been considered (morphological constraint, antipredator defense, sexual selection) but no explanation is yet entirely satisfactory (Cadle 2009, Glaw et al. 2014). A recent molecular phylogeny of all species of *Liopholidophis* indicated a sister relationship between *L. grandidieri* and the species most similar to it in external characters, *L. doliocercus* (Glaw et al. 2014).

At the time of the previous review (Cadle 1996a), no observations on living specimens of *Liopholidophis grandidieri* were available. Yet detailed natural history data will ultimately be necessary to fully understand the significance of the exceptional morphology of these snakes. The data I report here are based on five specimens of *Liopholidophis grandidieri* obtained since the species was last reviewed (Cadle 1996a). All of the new observations are from Ranomafana National Park (RNP) and vicinity, obtained in January 2001 and December 2003 during 17 days at two field sites. The main purpose of this report is to present new data on the natural history and behavior of *L. grandidieri* based on field observations and specimens obtained since the previous character summaries (Cadle 1996a). I put into broader context here data on four specimens of *L.*

*grandidieri* previously examined (Cadle 1996a: 460), update basic taxonomic data for the species, and provide for the first time color descriptions and photographs of *L. grandidieri* in life from RNP.

## MATERIALS AND METHODS

A field team of three logged on average eight hours per day during daylight hours and four to six hours at night while making a general faunal inventory (herpetofauna, birds, and mammals); streambeds and existing footpaths allowed access to the forest. *Liopholidophis grandidieri* were encountered opportunistically and captured by hand (none were captured by pitfall trap lines set at each site). I recorded snout-vent length (SVL, in mm), measured from the tip of the snout to the posterior edge of the anal plate, and tail length, measured from the posterior edge of the anal plate to the tip of the tail. Relative tail length (RTL) is here defined as tail length divided by SVL. I recorded mass (g) using Pesola® scales (Pesola AG, Baar, Switzerland). I acquired stomach contents of snakes by regurgitation after capture. I prepared vouchers as standard museum specimens by fixation in 10% formalin for approximately one month, followed by storage in 70–75% ethanol. Specimens discussed herein were deposited in the California Academy of Sciences (CAS, San Francisco), The Field Museum (FMNH, Chicago), the Museum of Comparative Zoology (MCZ, Cambridge), the Muséum National d'Histoire Naturelle (MNHN, Paris), The Natural History Museum (BMNH, London), and the Université d'Antananarivo Département de Biologie Animale (UADBA, Antananarivo).

## RESULTS

**Habitats and environments.**—I found five new specimens of *Liopholidophis grandidieri* at three sites from upland rain forests (1200–1250 m; Fig. 1). Details of the collection sites are as follows (specimen vouchers from each locality follow the coordinates): 4 January 2001 on a trail between the villages of Ambendrana and Amindrabe, about 1200 m elevation (21.3833°S, 47.3600°E; FMNH 261185); 8 and 11 January 2001 near a field camp approximately 4 km (Euclidean distance) east of Amindrabe village, 1200–1250 m elevation (21.3833°S, 47.4000°E; FMNH 261186–87); and 20 and 27 December 2003 near a field camp 9 km (Euclidean distance) east of Anjamba village, 1200 m elevation (21.3255°S, 47.4027°E; CAS 250594, UADBA–JE Cadle 15035). The localities are just within the western boundary of RNP, or just outside the park near its western boundary (4 January 2001 only). Hereafter, I refer to the 2001 localities as “Amindrabe” (total of eight

days field work) and the 2003 locality as “Anjamba” (nine days).

The following describes habitats at localities within RNP where *L. grandidieri* was observed in 2001 and 2003; local Malagasy names for the trees and bamboos are given.

**Amindrabe.**—Between the villages of Ambendrana and Amindrabe a trail passes through rice fields and secondary forest, with patches of what seem to be relatively undisturbed stunted forest mainly along ridge tops; one specimen of *Liopholidophis grandidieri* was found in these ridge-top forests. In the vicinity of the Amindrabe field camp (Fig. 1), terrain varies from 1200–1250 m elevation and much of it is characterized by ravines separating sharp ridges. A small river, the Apepina River, occasionally disappears under boulder jumbles for tens of meters at a stretch and then reappears on the surface. Boulders within the riverbed are covered with a thin to moderately thick layer of moss on exposed portions. The forest canopy is 15–18 m in higher parts but patches within the forest are sometimes less, especially on ridge tops. I attribute the short stature of the forest to its growth on top of an extensive boulder field. Soil may also be of poor quality and thin. Bamboos are especially dense, including large stands of the giant species known locally as *volotsangana* (*Bambusa madagascariensis*; Poaceae). Prominent large hardwood trees in this forest were *tavolo* (*Cryptocarya* sp.; Lauraceae), *ramy* (*Carnarium madagascariensis*; Burseraceae), and *hazondrano* (*Ilex mitis*; Aquifoliaceae).

**Anjamba.**—The terrain in the vicinity of the field camp was a series of ridges separated by valleys with small streams. The streams have substrates of rocks and boulders toward headwaters and sand or gravel downstream. Uncommonly, the streams have cut to bedrock and sometimes flow over steep precipices, forming small waterfalls. The Iarena River at the campsite has a streambed 3–4 m wide, low current velocity, and was fairly shallow (300–500 mm) during the fieldwork because no substantial rain had fallen for several days. The river had a sand and gravel substrate at the camp but contained boulders upstream ~75 m. Jumbles of huge boulders were present in some areas, with small caves present among some of these. A trail heading east from camp passed over several low ridges and arrived at a somewhat larger stream, the Ambohibory River. All of the local streams ultimately flow into the Andranaroa River to the west according to a local informant.

At Anjamba the forest is dominated by four tree species: *tapia* (*Uapaca louvelii*; Euphorbiaceae), the dominant tree, *rotra* (*Syzygium* sp.; Myrtaceae), *shandramy* (*Abrahamia* sp.; Anacardiaceae), and



FIGURE 1. Representative views of the habitat of *Liopholidophis grandidieri* in Ranomafana National Park, Madagascar. Photographs, taken in January 2001, are from the southwestern edge of the park near the village of Amindrabe. (Photographed by John Cadle).

*vatsilana* (*Polyscias ornifolia*; Araliaceae). The canopy height is approximately 15–18 m. The understory, very dense in some places and more open in others, has many kinds of bamboos, tree ferns, palms, and a diverse array of *Pandanus* species. Trees are moss-covered on the lower several meters. Other epiphytes are not abundant, consisting of a few orchids and ferns on some trees. Lianas are moderately common. Bamboos are apparently highly diverse and with a variety of growth forms – low herbaceous ground cover, long vines extending into the subcanopy (probably *Cephalostachyum viguieri* [*tsimbolovolo*]), and more typical cane-like forms, including the large *Bambusa madagascariensis*. Swampy areas are present in flats with poor drainage; these often have emergent *Pandanus* and are covered with a dense layer of *Pandanus* leaf litter.

**Behavior and natural history.**—All *Liopholidophis grandidieri* reported here were active during morning hours (0945–1155). Four individuals were actively moving in sunny areas when found, whereas the other (CAS 250594) was coiled in a sunny patch on a trail at 1000 (apparently sunning) on a cool, partly cloudy morning (it had food in its stomach, as discussed below).

I observed all other individuals on clear and relatively hot days. One individual was crossing a trail in a ridge-top forest, but all the others were in forests along valley floors. Despite extensive work at night at all field sites, I found no snakes asleep on vegetation at night. Other snakes obtained in sympatry with *L. grandidieri* at Amindrabe were *Compsophis infralineatus* and *Thamnosophis infrasignatus*; and at Anjamba, *C. infralineatus*, *Pseudoxyrhopus oblectator*, and *T. infrasignatus*. At Anjamba, a steady soaking rain fell for several hours during the approach to the camp on 19 December 2003, but afterward no rain fell until 26 December 2003, when a steady rain began mid-afternoon and continued until 2200. Regular, but relatively brief, rain showers occurred most afternoons during fieldwork at Anjamba.

I obtained dietary data for two specimens, which had small frogs in their stomachs. FMNH 261186 (442 mm SVL) was active at 1050 on a *Pandanus* emergent from the edge of a small river. The snake was moving when first seen about 700 mm above the level of the river on the *Pandanus* fronds, where it may have been sunning. It retreated to a cavity in the ground at the base of the *Pandanus*. Regurgitated stomach contents of FMNH 261186 included one *Guibemantis pulcher* (26 mm SVL; Mantellidae), one microhylid (cf. *Platypelis*, 14 mm SVL), and the remains of one or perhaps two well digested frogs, which clearly had been in the gut much longer (one of them about 20 mm SVL). The *Guibemantis* and the microhylid were very recently swallowed, as no digestion was evident on them; thus, the snake was apparently actively foraging when encountered. *Guibemantis pulcher* and *Platypelis* spp. are commonly found in phytotelms such as leaf axils of *Pandanus*. CAS 250594 (402 mm SVL) regurgitated three small *Mantidactylus* (cf. subgenera *Brygoomantis* and/or *Gephyromantis*; Fig. 2), whose SVLs were 12.3–16.2 mm. Thus, *L. grandidieri* probably forages for frogs terrestrially and in low phytotelms accessible from the ground (e.g., *Pandanus* axils as shown here). Notably, in these two instances, the prey items are small relative to the sizes of the snakes. One female (UADBA–JEC 15035) I obtained 20 December 2003 contained four leathery-shelled oviductal eggs (SVL measurements of this specimen are not available but its mass, including the clutch, was 31 g).

*Liopholidophis grandidieri* is docile when captured and no specimens attempted defensive bites. Field notes describe the behavior of FMNH 261185, which was actively moving when captured, as “rather lethargic.” Later, when gently prodded, this specimen coiled into a compact, but loose, set of coils and body loops with the bright yellow ventral surface of the tail exposed on top and the head hidden beneath (Fig. 3). The body was very rigid during this posturing and the snake maintained rigidity while manipulated in the hand. Even when the



**FIGURE 2.** Stomach contents of *Liopholidophis grandidieri* from CAS 250594 (402 mm SVL). Known prey items are small frogs (Mantellidae, shown here, and Microhylidae). Scale bar is 10 mm. (Photographed by Noel Graham).

loose mass was turned over, the snake did not attempt to reposition or right itself, and it maintained rigid posture when placed on a surface to photograph.

**Taxonomic notes and metric data.**—I obtained metric data for four specimens of *Liopholidophis grandidieri* (measurements not available for UADBA-JEC15035). All reported specimens are possibly adults, but CAS 250594 and FMNH 261185 are the two smallest individuals (female and male, respectively; Table 1). Two females were sexually mature (containing oviductal eggs) at 412–456 mm SVL (Cadle 1996a) but there are no data on size at sexual maturation for males.

Variation in basic taxonomic characters for *Liopholidophis grandidieri* are somewhat expanded by adding data for specimens reported here to that previously documented (Cadle 1996a), as follows, presented as (male range, female range): ventrals (161–171, 147–161); subcaudals (211–221, 113–122); SVL (390–732 mm, 402–436 mm); tail length/total length (0.51–0.56, 0.34–0.38); tail length/SVL (1.04–1.28, 0.51–0.60). One specimen (FMNH 261187) had 10/10 infralabials instead of the 9/9 found in all others. All other basic scale counts for the new specimens were identical to those presented in Cadle (1996a: table 1). The female reported here (CAS 250594) and one of the males (FMNH 261187) have the greatest reported relative tail lengths for their respective sexes of *L. grandidieri*, 0.60 and 1.28, respectively (Table 1).

**Coloration in life.**—The coloration of living specimens of *Liopholidophis grandidieri* has not been described and few portrayals of living specimens are available (Figs. 3 and 4; see Discussion). Color notes for FMNH 261185–86 follow. FMNH 261185 is a male, 390 mm SVL (Fig. 3). The dorsum has an irregular black pattern consisting of paired, slightly offset, mid-dorsal squarish to rectangular blotches anteriorly, merging gradually into an obscure checkered or chevron pattern at one-third the body length. Areas between the blotches are bright yellow anteriorly, dull yellow posteriorly. Anteriorly, most dorsal scale edges, but especially the anteriolateral edges, are bright yellow. The yellow edges are more frequent on the mid-dorsal six to eight scale rows and some yellow pigment spills onto the adjacent skin between the dorsal scales. The posterior body is similar, except dull rather than bright

**TABLE 1.** Metric data (body proportions and mass) for specimens of *Liopholidophis grandidieri* from Ranomafana National Park, Madagascar. Measurements are in mm. (CAS = California Academy of Sciences, FMNH = Field Museum Natural History Collection).

	CAS 250594 Female	FMNH 261185 Male	FMNH 261186 Male	FMNH 261187 Male
Total length	645	772	903	1204
Tail length	243	382+tip	461	677
SVL	402	390	442	527
RTL	0.60	0.98+	1.04	1.28
Mass (g)	20	22	n/a	46

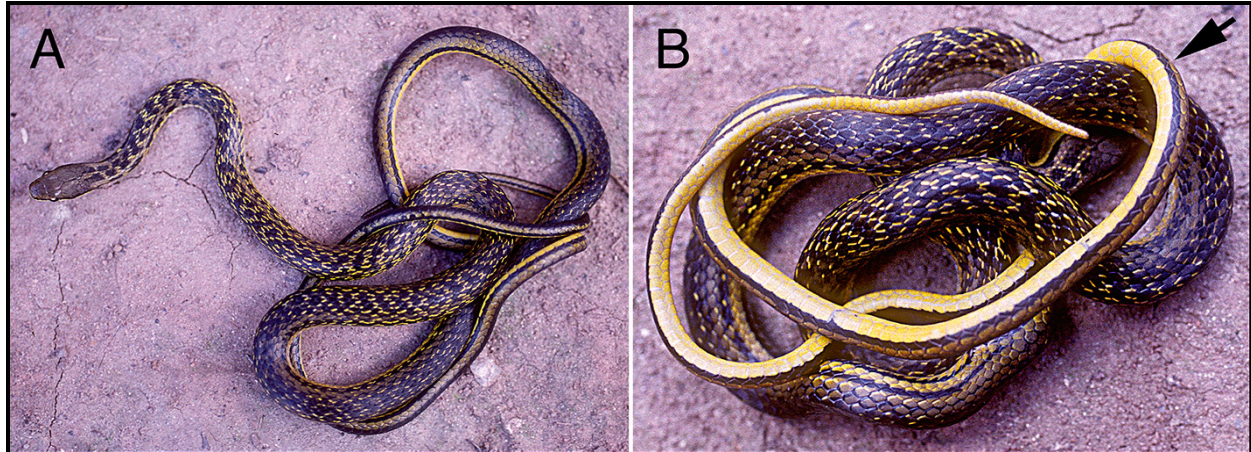


FIGURE 3. Defensive coiling and head hiding behavior of a male *Liopholidophis grandidieri*. The photographs show two stages in the formation of a loose mass in FMNH 261185. A: the snake has begun to ball up the posterior part of the body. B: complete formation of the mass, with the head hidden underneath the coils on the right (arrow). (Photographed by John Cadle).

yellow.

Dorsal row 1 is bright yellow the whole body length. A lateral series of elongate black blotches is on scale rows 2 and 3 on the neck. These merge gradually to form a well-defined black lateral line on dorsal rows 2 and 3 that abruptly ends at the vent. A similar black ventrolateral line at the subcaudal-dorsocaudal border begins at the vent and continues to the tail tip. The tail is blackish on top, dirty yellow laterally. The top of the head is medium brown and unpatterned. A dense black postocular line extends from the eye and merges with the elongate lateral blotches on the neck. The tongue is black.

The upper and lower labials, chin, throat, and anterior ventrals are immaculate bright yellow, which becomes paler after about the tenth ventral. A median series of fine dark gray spots begins at about ventral 15 and eventually merges with a dense array of black flecks on the gray ground color laterally on the ventral scales. The central part of most ventrals is solid black (Fig. 5B). The lateral edges of 10–15 ventrals anterior to the vent are bright yellow, merging into dull gray anteriorly. The subcaudals are immaculate bright yellow except for a median irregular dark line proximally. The coloration of FMNH 261186 (male, 442 mm SVL; Fig. 4) is essentially identical to that just described except that its venter is more completely black (less gray anteriorly), and the ventrals anterior to the vent have only a few small yellow flecks.

**Coloration in preservative.**—Preserved specimens are brown to yellowish brown with extensive black dorsal markings (Fig. 5A; Cadle 1996a). The bright yellow scale borders present in life and yellow wash on the venter become white, strongly contrasting with the rest of the scales. The black postocular line varies in width. It usually covers the lower postocular scale, anterior

temporal, lower posterior temporal, and the upper edges of the last two supralabials; in some specimens (e.g., CAS 250594) it is broader, covering portions of the upper posterior temporal and lateral edges of the parietal scales. Some black pigment is present in the loreal region of all specimens, usually forming a border along

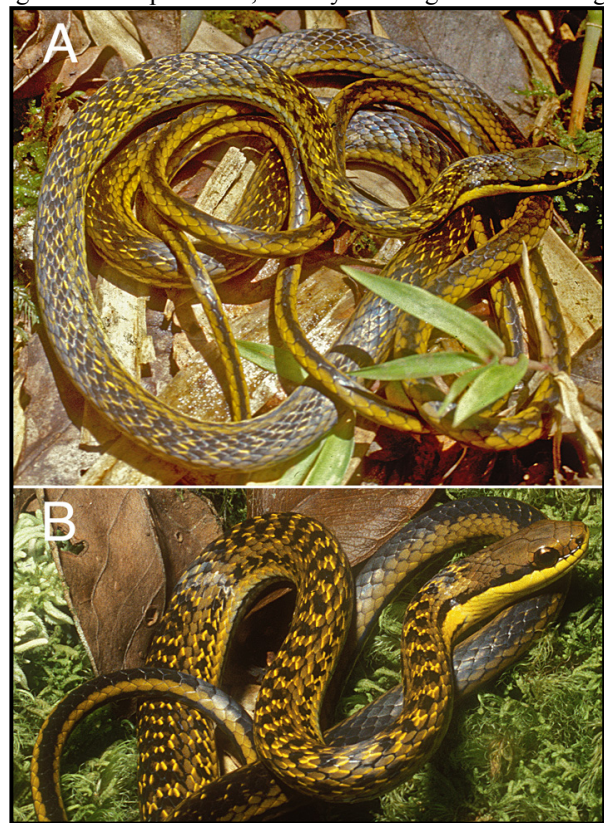


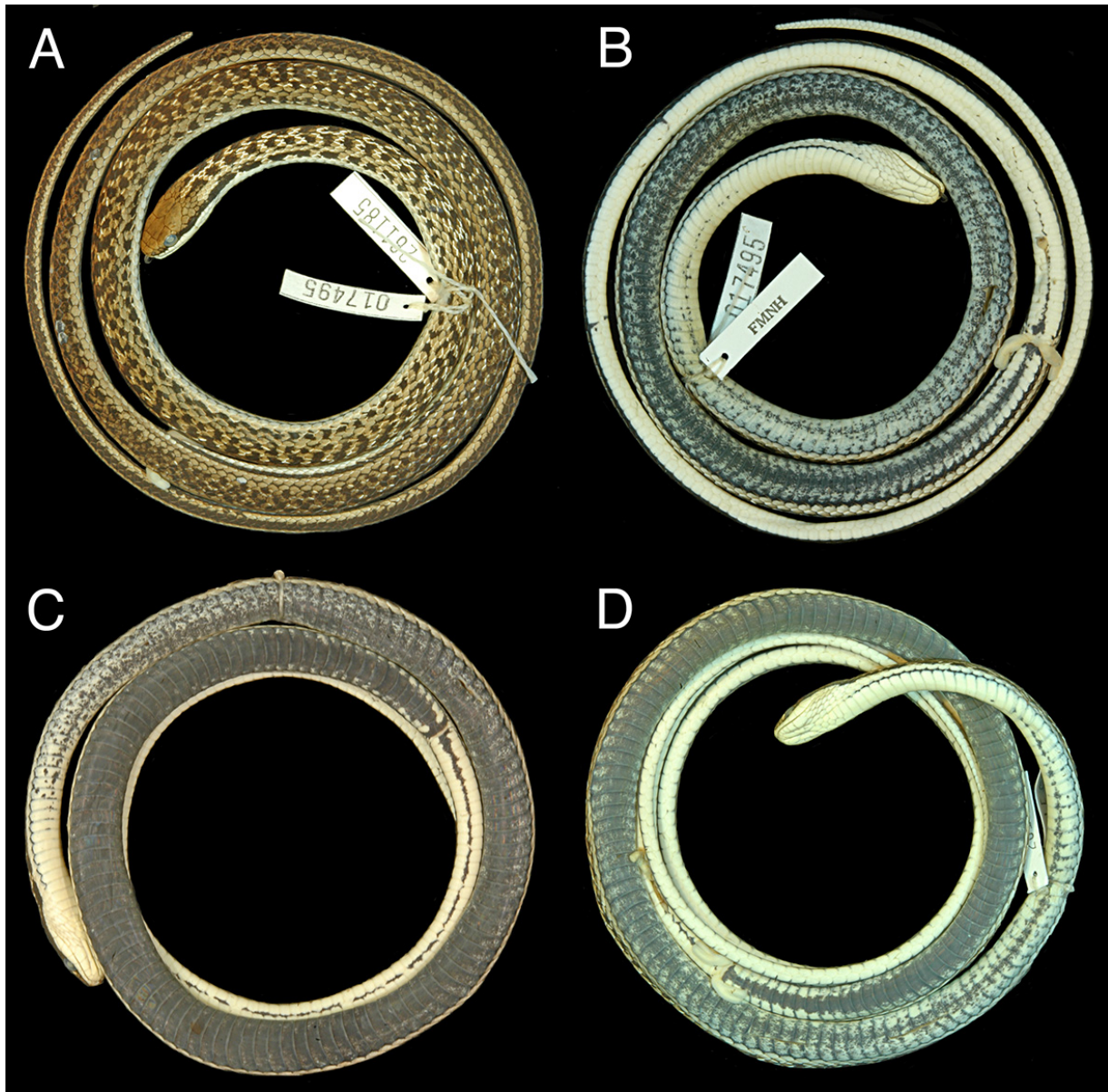
FIGURE 4. Photographs of *Liopholidophis grandidieri* in life. A: FMNH 261187. B: FMNH 261186. Both specimens from near Amindrabe, Ranomafana National Park. (Photographed by John Cadle).

the upper edges of the supralabials but occasionally present on the preocular, loreal, and nasal scales.

The amount of black ventral pigmentation varies (Fig. 5; see also Cadle 1996a: figs. 18, 20). In all specimens the anterior-most ventrals lack black pigment and there is usually some reduction in black pigment just anterior to the vent. Irregular white flecking and spotting is present at the lateral edges of the ventral scales in some individuals. Extensive black ventral pigmentation ends at the vent, although black pigment usually occurs on the median subcaudal suture for a variable distance along the tail; MCZ 180297 has a thick mid-ventral black line on the subcaudals for most of the tail length. In all

specimens there is a definitive black line covering the lateral edges of the subcaudals and the inferior edge of the dorsocaudals.

The extent of black pigmentation on the venter may be, in part, size-related (Fig. 5). The two smallest specimens (FMNH 261185 and CAS 250594, male and female, respectively; Fig. 5A-C) have the most extensive pale areas on the venter. In larger specimens the correspondence of the extent of pale areas with size seems less clear. For example, FMNH 261187 (527 mm SVL) has extensive pale coloration on the anterior one-third of the venter and lateral pale flecking the length of the body (Fig. 5D), whereas some smaller specimens,



**FIGURE 5.** Preserved specimens of *Liopholidophis grandidieri* to emphasize differences in ventral black pigmentation. A-B: Dorsal and ventral views of FMNH 261185 (390 mm SVL, male). C: CAS 250594 ventral (402 mm SVL, female). D: FMNH 261187 ventral (527 mm SVL, male). (Photographed by John Cadle).

e.g., BMNH 95.7.4.32, 456 mm SVL (Cadle 1996a: fig. 20), have more extensive black pigment on the venter. The largest specimen of *Liopholidophis grandidieri* is the male holotype (MNHN 02-103, 732 mm SVL) and it has the most solidly black venter of all specimens (Cadle 1996a: fig. 18). The number of known specimens is too few to evaluate whether sexes differ in the pattern of black ventral pigmentation.

#### DISCUSSION

**Locality records and distributional comments.**—*Liopholidophis grandidieri* has been formally reported only from three definite localities on the eastern escarpment of Madagascar: RNP, Ambohimombo Forest, and Tsinjoarivo (Cadle 1996a, Goodman et al. 2000, Glaw et al. 2014); geographic coordinates are given in Cadle (1996a) and Goodman et al. (2000). Additional records include the indefinite locality “eastern Imerina” and the questionable type locality in southwestern Madagascar (Cadle 1996a). Other than several unsubstantiated records from “the eastern forests” (UICN/PNUE/ WWF 1990: 223; see Cadle 1996a), only one other published locality for “*Liopholidophis grandidieri*” exists: a record from the Andringitra Massif (Raxworthy and Nussbaum 1996). This record apparently is based on UMMZ 209474, which has been subsequently reidentified as *L. sexlineatus* (Gregory E. Schneider, pers. comm.). I have not independently verified its identity, but a more recent summary of the Andringitra herpetofauna (Raselimanana 1999) did not include *L. grandidieri* in its faunal list. The source of the ‘Andringitra’ record of *L. grandidieri* reported by Glaw and Vences (2007) also is seemingly based on Raxworthy and Nussbaum (1996). Thus, apart from the probably erroneous type locality, RNP is the southernmost documented locality for this species.

**Occurrence and biology.**—All records of *Liopholidophis grandidieri* from RNP are from higher elevations (1200–1375 m) in the western and southern sectors of the park (five records, this paper; one previous record reported in Cadle 1996a). Rain forests in these areas are pristine, but vary in species composition and forest structure according to soil depth and quality, terrain relief, and other factors such as the presence of boulder fields or white sand areas. For example, there exist extensive areas of forest growing atop boulder fields in which soil depth is minimal and soil water availability is low due to deep crevices among the boulders. Such forests are short in stature compared to adjacent patches of forest on deeper, richer soils, and they often differ in species composition and the relative abundance of dominant plants. Similarly, forests growing along ridge tops also have lower canopies, probably in part due to edaphic conditions. The granitic

massif referred to as Mount Maharira, from which the first RNP specimen of *L. grandidieri* came (Cadle 1996a), has expanses of open granite with sparse grasses and short stature trees where sufficient soil accumulates within crevices or depressions.

All sightings of *L. grandidieri* in RNP are from these mixed forest types, including one record from open granitic expanses with scattered grasses, shrubs, and open canopy (Cadle 1996a). Extensive areas with these habitats occur on the western side of RNP and thus are probably suitable for this species. I have sampled at many locations from 600–1200 m elevation within RNP over a period of years and have failed to record *L. grandidieri* below 1200 m (unpubl. data); thus, the species seems likely to be restricted to higher elevations within the park. The elevational distribution in RNP is consistent with other reported locales for the species: Tsinjoarivo at 1400 m (Goodman et al. 2000) and Ambohimombo at 1200 m (Cadle 1996a).

I encountered no *Liopholidophis grandidieri* asleep on vegetation during night surveys. Although sleeping diurnal snakes are encountered on vegetation at night in many tropical rain forests (e.g., Martins 1993), in my experience diurnal snakes are almost never found asleep in vegetation in upland rain forests in Madagascar. In contrast, in lowland rain forests in Madagascar, diurnal arboreal snakes such as *Langaha madagascariensis* and *Micropisthodon ochraceus* do sleep in vegetation at night at least occasionally (pers. obs.).

The reproductive and diet data reported herein are similar to previous data on this and other species of *Liopholidophis*. Seven reported specimens of *L. grandidieri* with associated dates of collection were obtained December–April (Cadle 1996a, Goodman et al. 2000), which corresponds to the rainy season in southeastern Madagascar (Wright and Andriamihaja 2003). Gravid females with clutch sizes of four or five ( $n = 3$ ) were obtained in December and January (Cadle 1996a and herein). Thus, as for most Malagasy snakes (Cadle 2009), oviposition in *L. grandidieri* apparently takes place during the rainy season. Prey comprising small mantellid and microhylid frogs, documented herein for *L. grandidieri*, is similar to other species of *Liopholidophis*, for which recorded prey are frogs and/or their eggs. Microhylids predominate among known prey for species of *Liopholidophis* (Cadle 1996a, 2003; Glaw et al. 2007). The only non-frog stomach contents was a millipede from *L. dimorphus* (Glaw et al. 2007), which probably was secondarily ingested.

*Liopholidophis grandidieri* is known by local Betsileo people in the Ranomafana region, who refer to it as *mandotrala* (pronounced roughly *man – doo –tra –la*, with ‘a’ sounded as ‘ah’). This name is also occasionally used for other diurnal terrestrial forest snakes in the region. *Mandotrala* is a compound word derived from the words *manditra* (the name used in the

RNP region by the Tanala ethnic group for the boa, *Sanzinia madagascariensis*), and *ala* (forest), hence “forest snake” (*manditra* seems to be commonly combined with other words to form compound names for snakes having no resemblance or relationship to the boa).

**Defensive behavior and coloration.**—Head hiding and body rigidity, such as described here for *Liopholidophis grandidieri*, are widespread defensive behaviors in snakes (Greene 1988). However, the loose coils described herein lack the form of a cylindrical or compact ball, as seen in some other snakes of diverse lineages (Bustard 1969; Greene 1988; Cadle and Myers 2003). Glaw et al. (2014) reported a “freezing behavior, including presentation of the aposematically colored ventral side” in three individuals of *L. grandidieri*. These behaviors are perhaps similar to the behavior reported here, although balling and head hiding were not specifically mentioned. Tonic immobility is known in one other species of *Liopholidophis*, *L. rhadinaea*, but in that species balling or coiling behavior accompanying immobility was not observed and the individual exhibiting this behavior did not display the ventral reddish coloration (Cadle 1996a, 2003).

As pointed out by Glaw et al. (2014), most species of *Liopholidophis* have bright and/or contrasting colors on the venter (exceptions are *L. sexlineatus*, *L. dimorphus*, and *L. varius*, which are generally dull-colored ventrally). *Liopholidophis rhadinaea*, *L. baderi*, and *L. oligolepis* have reddish, pinkish, or purplish hues. In *L. grandidieri* and *L. doliocercus* the venters are mostly black, but with contrasting white or yellow stripes (*L. doliocercus*) or yellow patches (*L. grandidieri*; Cadle 1996a, this paper; Glaw et al. 2014). The ventral surfaces of the tails in *L. grandidieri* and *L. doliocercus* are a predominantly pale color (white or yellow). Without presenting evidence, Glaw et al. (2014) asserted that the ventral colors in the last two species were aposematic signals. However, aposematic colorations function as warnings to potential predators of noxious, venomous, or otherwise dangerous qualities (Cott 1940; Greene 1988; Ruxton et al. 2004); such colors also occur as deceptive signals in mimics of dangerous animals to deceive visually oriented predators.

Nearly all reports of behavior for species of *Liopholidophis* comment on their docility or complacency, with many individuals not even resorting to defensive bites (Cadle 1996a and herein). Likewise, neither mimicry complexes nor poisonous, venomous, or noxious properties involving *Liopholidophis* species have been documented. All available evidence indicates that *Liopholidophis* spp. do not represent ‘high cost’ prey to potential visual predators. Lacking such evidence of ‘cost’ or experimental evidence of predator responses, it is inappropriate to refer to their bright or

contrasting ventral colors as aposematic signals (Glaw et al. 2014). Moreover, tail coloration (whether bright or dull) and tail displays in snakes have many potential functions that require detailed natural history data to distinguish, even though none are necessarily mutually exclusive (Greene 1973, 1988).

Some other potential functions of the ventral colorations of *Liopholidophis* are consistent with documented defensive behaviors. First, the bright colors on the ventral surface of the tail may divert predatory attacks toward this more expendable part of the body, a function often referred to as ‘diversion’ or ‘deflection’ (Ruxton et al. 2004). This function is a common defensive mechanism in snakes (Greene 1973, 1988), and is suggested most strongly in *Liopholidophis* by the balling and head hiding behavior described here for *L. grandidieri*. The posture adopted during this display presented the bright yellow ventral surface of the tail to a potential predator while the head was secluded beneath the body (Fig. 3). Thus, the tail was positioned and displayed such that it could be a target of predatory attacks. Secondly, bright ventral colors are possibly startle signals that suddenly present novel stimuli to potential predators, thus increasing their attack time and allowing prey to escape (Greene 1988, Ruxton et al. 2004). If the ventral colorations of *Liopholidophis* function in this manner, then the behavioral repertoires presenting them to predators (such as associated tail or body posturing and eventual flight) are yet to be documented. The bright yellow undersurface of the tail in the display of *L. grandidieri* described herein appeared only late in the sequence of balling behavior and was not accompanied by flight. Thus, it seems unlikely to function primarily as a startle display in this instance.

Whether the coloration in life for *Liopholidophis grandidieri* described here is typical of other populations is unclear, although all specimens are superficially similar. The only other color photograph generally available is a specimen from Tsinjoarivo portrayed on the internet at <http://www.arkive.org/grandidiers-water-snake/liopholidophis-grandidieri/> (Accessed 30 April 2014). In that specimen the pale lateral stripes on the body and tail are vivid orange rather than bright yellow, as in all specimens documented from RNP. According to the photographer, the colors portrayed in the web photo are artificially more orange than the snake was in life. Jörn Köhler (pers. comm.) reports that the stripes on this specimen were actually deep yellow with brown overtones, unlike the bright yellow in Ranomafana specimens.

**Rarity and conservation.**—*Liopholidophis grandidieri* has been considered one of the ‘rare’ snakes of Madagascar and the IUCN Red List account comments that the species is “very rare” (Raxworthy and



Vences 2010). However, rarity per se for tropical wet-forest snakes can be difficult to assess and potentially misleading for conservation relevance. Myers (2003) succinctly summarized the issues: “Biologists familiar with the great diversity of serpents in tropical rain forests know that rarity or the appearance of rarity is compounded by several factors, including: (1) many, indeed most, wet-forest snakes seem to have low population densities relative to temperate species; (2) many are hard to find because of secretive habits; and (3) some are less likely to be encountered because of small geographic ranges and/or specialized microhabitats.” Myers (2003) was concerned with truly rare snake species still known from only one or two specimens after many decades of intensive fieldwork on snakes in Panamanian rain forests.

The situation with *Liopholidophis grandidieri* is entirely different. Until definite localities and basic information on its occurrence became available, this species was, indeed, rare in museum collections (Cadle 1996a). However, *L. grandidieri* is likely to be common in upland rain forests above 1200 m in RNP. An encounter rate of five individuals over 17 days of field work would not be considered rare for a tropical rain forest snake by any standards; in fact, just the opposite. Several snakes known to occur at RNP have been seen far more seldom than *L. grandidieri*, and thus might thereby be considered rarer in some sense. For example, *Compsophis zeny* has been seen and reported only once over a period of 25 y in the most heavily researched and visited site within RNP, Talatakely (Cadle 1996b). Several other species are nearly as rare within the park, judged solely from the number of sightings (*Compsophis boulengeri*, *Langaha madagascariensis*, *Ithycyphus perineti*). Based on my surveys it seems likely that *L. grandidieri* is among the more common snakes within its area of occurrence at RNP (upland rain forests above 1200 m). Five of 15 total snakes (four species) obtained during the surveys at Amindrabe and Anjamba were *L. grandidieri*.

Few data are available at other locales in Madagascar, but few upland rain forests have been surveyed with any intensity. Several individuals of *Liopholidophis grandidieri* were encountered during recent fieldwork at Tsinjoarivo (Glaw et al. 2014); the species does not seem to be rare there, as it has also been encountered in other brief surveys (Goodman et al. 2000). Raxworthy and Vences (2010) assessed *L. grandidieri* as Vulnerable B1ab(iii) based on IUCN criteria of small geographic range, few localities, and potentially continued decline in habitat quality or extent. Nonetheless, wet forests above 1200 m occur along nearly the entire length of the eastern escarpment of Madagascar, and some protected areas (Andohahela, Andringitra, Ranomafana, and Marojejy) have extensive highland areas that may harbor appropriate environments for *L. grandidieri*.

Thus, *Liopholidophis grandidieri* may have a broader distribution than is presently documented. In this case it seems that rarity of sightings yield few clues as to its status in the wild, although more surveys of upland rain forests are needed. On the other hand, general deforestation in Madagascar could adversely affect snake populations in upland rain forests as humans encroach ever closer from the central plateau. Many snake species, including *L. grandidieri*, are endemic to relatively pristine mid- and upper elevation rain forests and thus are especially sensitive to deforestation effects. Forests at Tsinjoarivo and Ambohimombo, two of three documented localities for *L. grandidieri*, are highly fragmented and under local pressures.

A potentially grave threat to *Liopholidophis grandidieri* and the many other frog-eating snakes of Madagascar is the recent discovery of the amphibian fungal disease chytridiomycosis in frogs originating from Madagascar (Kolby 2014). Earlier studies failed to detect chytrid fungus in free-living Malagasy frogs, including samples collected in 2007 from RNP (Vredenburg et al. 2012; Crottini et al. 2013). However, chytrid fungi were detected in 2013 and 2014 at low prevalence in RNP frogs (Molly Bletz, pers. comm.). The virulence of the fungal strain(s) in Madagascar is yet to be determined. Nonetheless, because many snakes in Madagascar rely completely or significantly on frogs as prey (Cadle 2003), snake populations can be impacted if there are declines in frog populations. In the only quantitative data available on this problem, populations of nine species of frog-eating snakes collapsed following a chytridiomycosis epidemic at a protected cloud forest locality in Monteverde, Costa Rica (Pounds 2000). Thus, if recent reports (Kolby 2014; Molly Bletz, pers. comm.) are substantiated and chytrid strains in Madagascar are highly virulent, Madagascar may be poised to witness severe declines in its mega-diverse frog fauna and the predators that depend on them, such as *L. grandidieri*.

*Acknowledgments.*—Field work in Madagascar was supported by Madagascar National Parks and its predecessor, the Association National pour la Gestion des Aires Protégées (ANGAP); the Ministère des Eaux et Forêts; the Institute for the Conservation of Tropical Environments (ICTE, Stony Brook University), and its counterpart, the Madagascar Institut pour la Conservation des Environnements Tropicaux (MICET). Thanks especially to Patricia Wright and Benjamin Andriamihaja for support, and the collaboration of the local Ranomafana National Parks office and personnel. Permits for research and export were issued by ANGAP (263-MINENV.EF/SG/DGEF/EPB/SCBLF; 09ON-EA03/MGO4; 0990/EAL/MG00/CWN). Emile Rajeriarison and the late Pierre Talata, long-term friends and companions, assisted in the fieldwork; I owe both of

them more than I can express or repay. Several Malagasy colleagues provided special help: Rosette Ralisoamalala for field assistance, Paul Rakotonirina for help with plant names, and Florent Ravoavy for discussions on Malagasy snake names. The Chicago Zoological Society, through its Chicago Board of Trade Fund, funded fieldwork. Animals were handled in accordance with the Institutional Animal Care and Use Committee of the Chicago Zoological Society (03-2000). I thank the following museum personnel for information and other assistance: David C. Blackburn, Robert C. Drewes, Noel Graham, Lauren Scheinberg, and Jens Vindum (CAS); Ronald Nussbaum and Gregory E. Schneider (UMMZ); Alan Resetar (FMNH); and José Rosado (MCZ). Other museum personnel were previously acknowledged (Cadle 1996a, 2009). I thank Jörn Köhler for providing copies and information on his photographs of *L. grandidieri*. Jesse McKinney helped prepare photographs for the figures and Noel Graham photographed and measured the frogs for Fig. 2. For comments on the manuscript, I thank Harry W. Greene and Patricia C. Wright.

### LITERATURE CITED

- Bustard, H.R. 1969. Defensive behavior and locomotion of the Pacific Boa, *Candoia aspera*, with a brief review of head concealment in snakes. *Herpetologica* 25:164–170.
- Cadle, J.E. 1996a. Snakes of the genus *Liopholidophis* (Colubridae) from eastern Madagascar: new species, revisionary notes, and an estimate of phylogeny. *Bulletin of the Museum of Comparative Zoology* 154:369–464.
- Cadle, J.E. 1996b. Systematics of snakes of the genus *Geodipsas* (Colubridae) from Madagascar, with descriptions of new species and observations on natural history. *Bulletin of the Museum of Comparative Zoology* 155:33–87.
- Cadle, J.E. 2003. Colubridae, snakes. Pp. 997–1004 *In* The Natural History of Madagascar. Goodman, S.M., and J. Benstead (Eds.). University of Chicago Press, Chicago, Illinois, USA.
- Cadle, J.E. 2009. Sexual dimorphism and reproductive biology in the Malagasy snake genus *Liopholidophis* (Lamprophiidae: Pseudoxyrhophiinae). *Proceedings of the California Academy of Sciences* 60:461–502.
- Cadle, J.E., and C.W. Myers. 2003. Systematics of snakes referred to *Dipsas variegata* in Panama and western South America, with revalidation of two species and notes on defensive behaviors in the Dipsadini (Colubridae). *American Museum Novitates* 3409:1–47.
- Cott, H.B. 1940. Adaptive Coloration in Animals. Methuen and Co., London, UK.
- Crottini, A., A. Bollen, C. Weldon, D.L. Dalton, A. Kotzé, J. Noël, B. Iambana, and F. Andreone. 2013. Amphibian survey and current absence of *Batrachochytrium dendrobatidis* (Bd) in Ivoloina Park, Toamasina (eastern Madagascar). *African Journal of Herpetology* 63:70–78.
- Glaw, F., and M. Vences. 2007. A Field Guide to the Amphibians and Reptiles of Madagascar. 3<sup>rd</sup> Edition. Vences and Glaw Verlag, Köln, Germany.
- Glaw, F., C. Kucharzewski, Z.T. Nagy, O. Hawlitschek, and M. Vences. 2014. 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. *Organisms, Diversity, and Evolution* 14:121–132.
- Glaw, F., Z.T. Nagy, M. Franzen, and M. Vences. 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.
- Goodman, S.M., D. Rakotondravony, M.J. Raherilalao, D. Rakotomalala, A.P. Raselimanana, V. Soarimalala, J.-M. Duplantier, J.-B. Duchemin, and J. Rafanomezantsoa. 2000. Inventaire biologique de la forêt de Tsinjoarivo, Ambatolampy. Akon'ny Ala (Bulletin du Département des Eaux et Forêts de l'Essa) 27:18–27.
- Greene, H.W. 1973. Defensive tail display by snakes and amphisbaenians. *Journal of Herpetology* 7:143–161.
- Greene, H.W. 1988. Antipredator mechanisms in reptiles. Pp. 1–152 *In* Biology of the Reptilia, Vol. 16, Ecology B: Defense and Life History. Gans, C., and R.B. Huey (Eds.). Alan R. Liss, Inc., New York, New York, USA.
- Kolby, J.E. 2014. Presence of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* in native amphibians exported from Madagascar. *PLOS One* 9(3):e89660.
- Martins, M. 1993. Why do snakes sleep on the vegetation in central Amazonia? *Herpetological Review* 24:83–84.
- Mocquard, F. 1904. Description de quelques reptiles et d'un batracien nouveaux de la collection du Muséum. *Bulletin du Muséum National d'Histoire Naturelle*, Paris 10:301–309.
- Myers, C.W. 2003. Rare snakes – Five new species from eastern Panama: reviews of northern *Atractus* and southern *Geophis* (Colubridae: Dipsadinae). *American Museum Novitates* 3391:1–47.
- Pounds, J.A. 2000. Amphibians and reptiles. Pp. 150–177 *In* Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Nadkarni, N.M., and N.T. Wheelwright (Eds.). Oxford University Press, New York, New York, USA.
- Raselimanana, A.P. 1999. Le herpétofaune. Pp. 81–97 *In* Inventaire Biologique de la Réserve Spéciale du Pic

Cadle.—Natural history of *Liopholidophis grandidieri*.

- d'Ivohibe et du Couloir Forestier qui la relie au Parc National d'Andringitra (Recherches pour le Développement, série Sciences Biologiques no. 15). Goodman, S.M., and B.P.N. Rasolonandrasana (Eds.). Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, Madagascar.
- Raxworthy, C.J., and R.A. Nussbaum. 1996. Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: a study of elevational distribution and local endemism. *Fieldiana Zoology*, new series 85:158–170.
- Raxworthy, C.J., and M. Vences. 2010. *Liopholidophis grandidieri*. In IUCN 2013. IUCN Red List of Threatened Species, version 2013.2. Available at [www.iucnredlist.org](http://www.iucnredlist.org). (Accessed 15 April 2014).
- Ruxton, G.D., T.N. Sherratt, and M.P. Speed. 2004. Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals, and Mimicry. Oxford University Press, Oxford, UK.
- UICN, PNUE, and WWF. 1990. Madagascar: Profil de l'environnement. UICN, Gland, Switzerland and Cambridge, England.
- Vredenburg, V.T., L. du Preez, L. Raharivoloniaina, D.R. Vieites, M. Vences, and C. Weldon. 2012. A molecular survey across Madagascar does not yield positive records of the amphibian chytrid fungus *Batrachochytrium dendrobatidis*. *Herpetology Notes* 5:507–517.
- Wright, P.C., and B. Andriamihaja. 2003. The conservation value of long-term research: a case study from the Parc National de Ranomafana. Pp. 1485–1488 In *The Natural History of Madagascar*. Goodman, S.M., and J. Benstead (Eds.). University of Chicago Press, Chicago, Illinois, USA.



**JOHN E. CADLE** (on the right, pictured in the field with Ratatatasolo and the late Pierre Talata at 'Amindrabe') received a Bachelor of Science in Zoology from the University of Georgia and a Ph.D. in Zoology from the University of California at Berkeley. He conducted his postdoctoral work at the Smithsonian Institution's National Museum of Natural History and at LSU Medical Center in New Orleans. John has held faculty positions at the Academy of Natural Sciences (Philadelphia), the Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology at Harvard University, and the Chicago Zoological Society. He currently is the Senior Scientific Advisor for the Centre ValBio field station in Ranomafana, Madagascar, a Research Professor with the Institute for the Conservation of Tropical Environments at Stony Brook University, and a Research Associate with the California Academy of Sciences. His fieldwork on reptiles and amphibians has taken him all over the U.S., Central and South America, Africa, and Madagascar. John's research interests are systematics, morphology, and ecology of all amphibians and reptiles, with a primary focus on snakes. He is a member of the IUCN Amphibian Specialist Group and has participated in the Global Amphibian Assessment for Madagascar and conservation assessments for amphibians and reptiles in Ecuador, Peru, Bolivia, and Madagascar. (Photographed by Emile Rajeriarison)