

shared between Madagascar and Africa. To help clarify the relationships of the species, hemipenes of four species of Malagasy *Geodipsas* (*boulengeri*, *infralineata*, *laphystia*, *zeny*) and the three African species (*depressiceps*, *procterae*, *vauerocegae*) are described. Hemipenes of the four Malagasy species are similar in structure and ornamentation, including the derived characters of nonbilobation and distal division of the sulcus spermaticus. The sulcus spermaticus is centrolineal in orientation and the organs are entirely spinose. Although hemipenes of the African species of *Geodipsas* are nonbilobed and have a centrolineal sulcus, their hemipenes are otherwise dissimilar to the Malagasy species. Moreover, whereas hemipenes of the east African species, *G. procterae* and *G. vauerocegae*, share unusual apical structures and are otherwise extremely similar, the hemipenis of the central African *G. depressiceps* has unusual longitudinal ridges and bears little resemblance to that of the other African species. Incidental observations on the skull morphology and pupil form of *Geodipsas* are presented. The pupil is broadly elliptical (subcircular), as contrasted with a round or narrowly elliptical (slitlike) form, as has been reported in the literature.

Examination of the basis for including African species in *Geodipsas* (type species: *Geodipsas infralineata*) shows that conclusion to be based on little evidence of relationship. Thus, the monophyly of *Geodipsas* is questioned. Other than the derived character of loss of hemipenial bilobation, which has evolved many times within colubrids, few special similarities exist in known morphological characters of the African and Malagasy species. A nonbilobed hemipenis is present in at least one other Malagasy genus, *Alluaudina*, thus calling into question its relevance in defining a monophyletic *Geodipsas sensu lato*. *Alluaudina* also shares with Malagasy *Geodipsas* a broadly elliptical pupil, an unusual condition. These shared characters suggest that *Alluaudina* may be among the closest relatives of Malagasy species of *Geodipsas*. The conclusion that the three African species are monophyletic *inter se* is also questioned because of the morphological disparity between *G. depressiceps* and the other two species. On the other hand, Malagasy *Geodipsas* share basic and detailed similarities in hemipenial morphology that suggest their close relationship.

Among the Malagasy species of *Geodipsas*, *laphystia* and *infralineata* share putative derived characters associated with arboreality; *boulengeri* and a species of *Geodipsas* previously confused with "*heimi*" from the vicinity of Montagne d'Ambre share putative derived similarities of color pattern and sulcus spermaticus. The species of each of these pairs are presumed sister taxa. *Geodipsas zeny* and *G. vinckei* are of uncertain relationship to the other species.

INTRODUCTION

Geodipsas Boulenger is currently the only genus of colubrid snakes, and one of

few reptile genera, shared by Madagascar and the African mainland. Rasmussen et al. (1995) reviewed two of the three African species. Four Malagasy species are recognized in recent literature (Guibé, 1958; Brygoo, 1983; Glaw and Vences, 1994): *infralineata* (Günther, 1882), *boulengeri* (Peracca, 1892), *heimi* Angel (1936), and *vinckei* Domergue (1988). A survey of the herpetofauna of the Ranomafana National Park (referred to in the text simply as "Ranomafana" or **RNP**) in eastern Madagascar has revealed several new species of amphibians and reptiles and required partial revision or clarification of the status of some others (Cadle, 1995, 1996). During the RNP survey, four species of *Geodipsas* were collected, and this paper summarizes their taxonomy and natural history. One of the RNP snakes, *Geodipsas infralineata*, is the best known of all the Malagasy species of *Geodipsas*, although, as indicated later, an undescribed species has heretofore been confused with it. That undescribed species and another one are described as new herein. Determining the identity of the fourth RNP species required consideration of the status of *Tachymenis boulengeri* Peracca (1892) and *Geodipsas heimi* Angel (1936). Evidence is presented indicating that these names refer to the same taxon. As the oldest available name is *Tachymenis boulengeri* Peracca, *Geodipsas heimi* Angel is synonymized with it.

MATERIALS AND METHODS

My study of *Geodipsas* is based primarily on specimens collected during the RNP survey, but I have incorporated data from other specimens (see *Specimens Examined*) in connection with museum surveys. Most natural history observations are from the RNP, although for the widespread species *G. infralineata* I have included personal and published observations from other localities.

Hemipenial terminology follows Myers (1973, 1974) and Myers and Campbell (1981), and procedures for their descrip-

tion and illustration are described by Cadle (1996). All everted organs were inflated with colored jelly to enhance the surface ornamentation prior to description. For visualization of mineralized hemipenial spines in one instance (*Remarks* in the account for *Geodipsas laphystia*, new species), I hydrated the organs, placed them in 2% potassium hydroxide (KOH) containing several drops of saturated alizarin red S overnight, destained them in 2% KOH, and processed them through a graded series of glycerin/ethanol mixtures, finally storing them in 70% ethanol.

Head proportions were measured with dial calipers to the nearest 0.01 mm; other measurements were made to the nearest millimeter with a ruler. For descriptions of vertebral hypapophyses, I followed the terminology and general descriptive protocols of Malnate (1972).

Coordinates for localities were derived from maps (1:50,000, 1:100,000, or 1:1,000,000) published by the Foiben-Taosarintanin'i Madagasikara, Antananarivo (FTM), or from the Defense Mapping Agency (1989) gazetteer. Specific localities within the RNP (see *Specimens Examined*) are mapped in Cadle (1995).

Recorded dietary items are derived from field observations of feeding, palping freshly collected specimens, or (rarely) dissections. However, I have not routinely surveyed museum specimens for food items, so observations reflect primarily diets within the RNP and other areas of southeastern Madagascar I have investigated.

DESCRIPTIONS OF NEW SPECIES

The first species described has been confused with *Geodipsas infralineata* for at least much of this century, including recent literature (e.g., Glaw and Vences, 1994). During study of specimens of "*infralineata*" from the RNP, it became clear that two species, distinguishable by hemipenial, scale, and pattern characteristics, were present. The new species appears to

be sympatric with *infralineata* over a broad area of eastern Madagascar but, because earlier literature records for "*infralineata*" may refer to the new species, the details of distributions of these two similar species remain to be worked out. This new species is to be known as follows.

Geodipsas laphystia, new species

Figures 1, 3; Table 1

Geodipsas infralineata (not of Günther), part. *Geodipsas laphystia* has been confused with *G. infralineata* previously, including some or all of the following recent literature. Earlier references to *infralineata* will need to be verified with reference to voucher specimens to see whether *laphystia* is represented: Guibé, 1958:235; Brygoo, 1983:42, 55, 1987:23; Nicoll and Langrand, 1989:135; UICN, PNUE, and WWF, 1990:222; Glaw and Vences, 1992:264, 1994:346; Raxworthy and Nussbaum, 1994:68. Published figures of "*G. infralineata*" in Glaw and Vences (1992:figs. 326–327, 1994:figs. 514–515) are actually illustrations of *G. laphystia*, as shown by the diagnostic longitudinal lines (see *Diagnosis*).

Holotype. **Museum of Comparative Zoology, Harvard (MCZ) 181390** (field number JEC 13169), an adult male in good condition (Fig. 1). Specimen obtained 2 January 1996 by John E. Cadle.

Type Locality (Fig. 2). Talatakeley, Ranomafana National Park, 950–1,000 m, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar [21°16'S, 47°25'E].

Paratypes. The following specimens from the same locality as the holotype (elevations vary slightly, 950–1100 m): **MCZ 180339** (JEC 11814), adult female, 6 December 1992; **MCZ 180340–41** (JEC 12341–42), adult females, 1 January 1993; **MCZ 180342** (JEC 12365), adult male, 2 January 1993; **MCZ 181148** (JEC 9640), subadult male, 25 October 1990; **MCZ 181150–51** (JEC 10110–11), adult females, and **MCZ 181152** (JEC 10112), (adult ?) male, 4 December 1990; **MCZ 181164** (JEC 11815), adult female (skin + complete skeleton), 6 December 1992; **MCZ 181165** (JEC 12366), adult female (skin + complete skeleton), 2 January 1993; **MCZ 181391–92** (JEC 13064–65),

adult males, 30–31 December 1995; **MCZ 181393–94** (JEC 13077–78), adult female and male, 30–31 December 1995; **MCZ 181387–89** (JEC 13166–68), adult males, 2 January 1996.

MCZ 180343 (JEC 12279), adult female, 30 December 1992: Vatoharanana, Ranomafana National Park, 1,000 m, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar [21°17'20"S, 47°25'45"E]. **MCZ 181158–59** (JEC 12629–30), adult females, 12 January 1993: Approximately 7 km SW (airline) Midongy du Sud [Midongy Atsimo], near Rianambo ("high waterfall") on Lalampo River,² 670 m, Fivondronana Midongy du Sud, Fianarantsoa Province, Madagascar [23°39'S, 46°57'E]. **MCZ 181395** (JEC 13267), subadult female, 8–11 January 1996: Vevembe Forest,³ 22 km W (by road to Maropaika) Vondrozo, 550 m, Fivondronana Vondrozo, Fianarantsoa Province, Madagascar [22°47'S, 47°12'E].

Distribution (Fig. 2). From at least the vicinity of Midongy Atsimo (= Midongy du Sud; 23°39'S, 46°57'E) in the southeast to central Madagascar in the vicinity of Andasibe (18°56'S, 48°25'E; photos of *laphystia* identified as *infralineata* in Glaw and Vences, 1994:figs. 514–515). The northern distributional limits are unclear because *G. laphystia* has been confused with the widespread species *G. infralineata*, which has been reported from as far north as Montagne d'Ambre (12°30'S, 49°10'E; Glaw and Vences, 1994:344 [map]; Raxworthy and Nussbaum, 1994). The known elevational distribution of *G.*

laphystia is approximately 550–1,100 m, the range encompassed by the type series.

The known geographic ranges of *Geodipsas laphystia* and *G. infralineata* are nearly coextensive, but I have not attempted to extensively document the the northern limits of either species (Figs. 2, 9). The two species are known to be sympatric in the vicinity of Midongy du Sud, in the RNP, and in the Perinet reserve (= Andasibe) (the preceding specimens and those in *Specimens Examined*). In the RNP, the two species may be segregated by habitat (see *Natural History*).

Etymology. *Laphystia* is a Greek adjective meaning "gluttonous." It refers to the seemingly voracious appetite these little snakes have for egg clutches of frogs of the genus *Mantidactylus* (see *Natural History*).

Diagnosis. A species of *Geodipsas* characterized by a relatively high number of ventrals (170–187) and subcaudals (64–81); posterior dorsal scale reduction usually by loss of row 4 or fusion of 4 + 5; compressed body and relatively long tail (21–26% of total length); and, in life, a yellow, gray, or brown ground color, upon which is superimposed a series of fine dark longitudinal lines usually evident on the suture line between dorsal scale rows 4–5 anteriorly (3–4 posteriorly), the suture line between rows 7–8, on the border between the ventrals and dorsal row 1, and on the vertebral row.

Geodipsas laphystia is distinguished from *G. boulengeri* and *G. zeny*, new species, by having more ventrals (170–187) and subcaudals (64–81) (<150 and <50, respectively, in both *boulengeri* and *zeny*) and by different color patterns (see species accounts). *Geodipsas laphystia* also reaches a larger size (>600 mm total length) than either *zeny* (maximum known length <300 mm), or *boulengeri* (maximum known length <400 mm).

Geodipsas laphystia has been confused with *G. infralineata*, but the two species differ most obviously in details of color patterns and more subtly in scale and

² See comment on the type locality for *Geodipsas zeny*, new species, described later, for notes on the name "Lalampo River."

³ "Vevembe" was a word unknown to our guides from the Ranomafana National Park. We learned from questioning locals in the area that a rough translation is "big boundary" or "big fence" (the suffix *be* commonly means "big," "many," or "very" or, in some cases, takes on a meaning akin to "true"). "Vevembe" refers to the location of the forest roughly on the boundary between the Bara tribes to the west and the Taisaka people to the east.

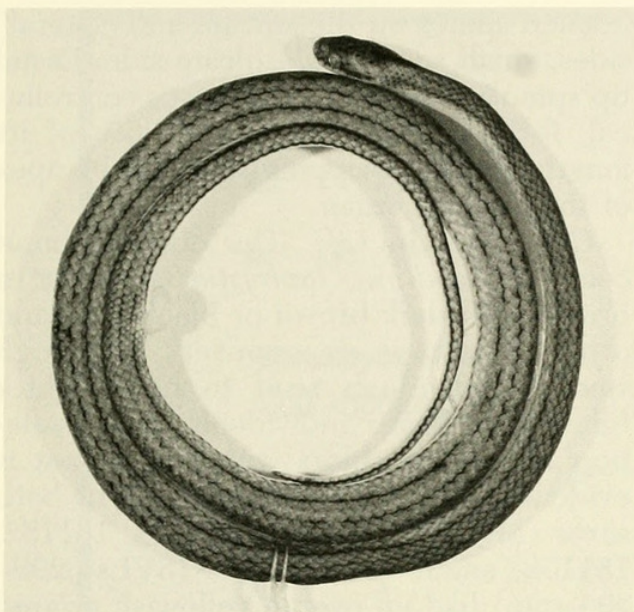


Figure 1. Holotype of *Geodipsas laphystia* (MCZ 181390, male; total length 622 mm). The longitudinal lines distinguish this species from *G. infralineata* (Fig. 10).

hemipenial characters, body proportions, and size. In both species, the dorsal ground color is a shade of yellow to brown (or gray in *infralineata*), upon which is a series of fine dark lines. In *laphystia*, the lines form a series of dark longitudinal lines and flecks distributed as already described (Fig. 1). In *infralineata*, the lines form a lateral series of diagonals or fine chevrons pointed anteriorly (with the vertex on the vertebral scale row); successive lines or chevrons are usually separated by 2 scale rows (Fig. 10). In *laphystia*, the dorsal ground color does not encroach significantly onto the lateral edges of the ventrals, and the ventrals and subcaudals are immaculate except for a series of small midventral spots or a continuous midventral line that may be present on the posterior $\frac{2}{3}$ of the body and on the subcaudals. In *infralineata*, the dorsal ground color may encroach substantially onto the ventrals, which may also be irregularly blotched or flecked with dark pigment in addition to having a midventral line or series of spots (Fig. 11).

Some specimens referred to *Geodipsas infralineata* apparently are nearly unicolor

dorsally and lack distinct darker markings (whether longitudinal lines or diagonals). Although I did not observe this color form at any of the localities I worked, photographs of such specimens have appeared in Glaw and Vences (1994:pl. 336, from Andasibe) and Henkel and Schmidt (1995: 274, locality unknown). See additional comments in the account for *infralineata*.

Other characters distinguishing *Geodipsas laphystia* and *G. infralineata* include (1) differences in the mode of dorsal scale reductions (usually loss of row 4 or fusion of 4 + 5 in *laphystia*, fusion of 3 + 4 in *infralineata*); (2) details of hemipenial morphology (e.g., pair of large basal spines on the asulcate side in *laphystia*, parallel rows of greatly enlarged spines in *infralineata*; see Figs. 14, 17); (3) a somewhat longer tail and more subcaudals, on average, in *laphystia* (see Table 1); and (4) a greater body size in *infralineata* (to >900 mm total length) compared to *laphystia* (maximum known length 622 mm).

Data on the Holotype (MCZ 181390). The holotype is an adult male with fully everted hemipenes. Total length 622 mm; tail length 153 mm (24.5% of total length). Greatest head width (temporal region) 8.15 mm, head length 15.3 mm measured diagonally from tip of snout to end of mandibles. Dorsals in 19–19–17 rows, the reduction occurring by loss of row 4 at the level of ventral 126 (left) and fusion of rows 4 and 5 at the level of ventral 125 (right). One preventral (+ several small intergular scales), 181 ventrals, single anal plate, 81 pairs of subcaudals, 7–7 supralabials (3–4 touching eye), 9–9 infralabials, 1 + 2 temporals on each side.

Description. Measurements, proportions, and scutellation are summarized in Table 1; see also relevant sections later for descriptions of vertebral hypapophyses, skull, and hemipenis. Largest specimen the male holotype (MCZ 181390), 622 mm total length, 153 mm tail length; largest female (MCZ 181151), 608 mm total length, 132 mm tail length. Tail averaging 23% of total length in males, 21% in females.

Body slightly higher than wide and laterally compressed; ventrolateral edge of body angulate. Head distinctly wider than neck. Pupil subcircular (prolate; see *Discussion*).

Dorsal scales smooth, lacking apical pits, in 19–19–17 rows. Posterior scale-row reduction nearly always by loss of row 4 or fusion of 4 + 5 at the level of ventrals 110–131 (N = 31 sides; by fusion of 3 + 4 on 1 side of 1 specimen). Ventrals 180–187 in males, 170–179 in females, usually preceded by 2 preentrals. Anal plate single. Subcaudals 70–81 in males, 64–71 in females.

Loreal rectangular to pentagonal, usually higher than wide, separated from eye by single preocular. Two postoculars; temporals 1 + 2. Supralabials 7–7 with 3–4 touching eye. Infralabials usually 9–9 (N = 13), less frequently 8–8 (4), 8–9 and 9–10 (2 each), and 7–8 (1); the first pair in contact behind the mental, usually 1–4 touching an anterior genial, 4–5 touching a posterior genial. Posterior genials approximately 1.6–1.8× as long as anterior genials. Head plates smooth, apparently without pits or tubercles.

Dentition. Maxillary teeth 18–23 + 2 (N = 15); modal number of prediastemal teeth 19. Diastema broad, about 2–3× the width of the posteriormost solid maxillary tooth. The fangs are deeply grooved, about twice as large as the posteriormost solid teeth, and have a rounded anterior surface, a flattened knifelike posterior surface, and slightly compressed tips. The fangs are offset from the solid tooth row.

Hemipenis (See Fig. 14 and Detailed Description Later). Single (nonbilobed), noncapitate, acalyculate; proximally nude on the sulcate side, proximally spinose on asulcate side. Midsection bearing enlarged

hooked spines on the sulcate and “lateral” sides; small spines on asulcate side. Distal tip spinulate. Sulcus spermaticus centrolin-
eal, forked distally for about 30% of its length, the tips stopping short of the apex of the everted organ.

Coloration in Life. The dorsal ground color of *Geodipsas laphystia* is yellow to brown with dark brown or black lines and other markings superposed. Although smaller individuals *tend* to have lighter tones than larger individuals, no correlation of ground colors with size or sex is evident. Several small individuals of both sexes (MCZ 180341–43, 181148, 181152, 181158; snout–vent lengths [SVLs] 299–494 mm) had an overall yellowish ground color. My notes on other specimens describe the dorsal ground colors as pale yellowish brown (MCZ 180343; SVL 401 mm), medium brown (MCZ 180340; SVL 438 mm), or straw-colored (MCZ 180341; SVL 350 mm). Dorsal rows 1 and 2 are lighter than other dorsal rows.

The dark dorsal markings of *Geodipsas laphystia* (see Figs. 1, 3) consist of a series of longitudinal lines and flecks, but their distinctiveness and consistency vary. On most specimens, a line is present and continuous on the suture between dorsal rows 4–5 anteriorly (3–4 posteriorly). Less consistently, a line may be evident on the suture line between rows 7 and 8 (6 and 7 posteriorly). The border between the ventrals and dorsal row 1 usually has a series of darkened scale borders or a continuous (often wavy) line. Scattered scales in the vertebral row are edged with dark pigment, giving the impression of a linear series of dark flecks middorsally.

The head is usually of the same ground color as, or slightly lighter than, the dor-

Figure 2. Distributions of *Geodipsas laphystia*, new species, and *Geodipsas zeny*, new species. The type locality of *G. laphystia* is within the RNP; that for *G. zeny* is near Midongy du Sud (see text). Open symbol for *G. laphystia* is a literature record (see *Distribution*). The paratype of *G. zeny* from “Imerina” could be from any of the territory between roughly Andasibe and the RNP but more likely closer to the former; technically, the “Imerina country” referred to territory on the high plateau rather than on the eastern escarpment (see text). As explained in the text, *G. laphystia* could well be represented by some literature references to *G. infralineata*. Shaded area is above 1,000 m.

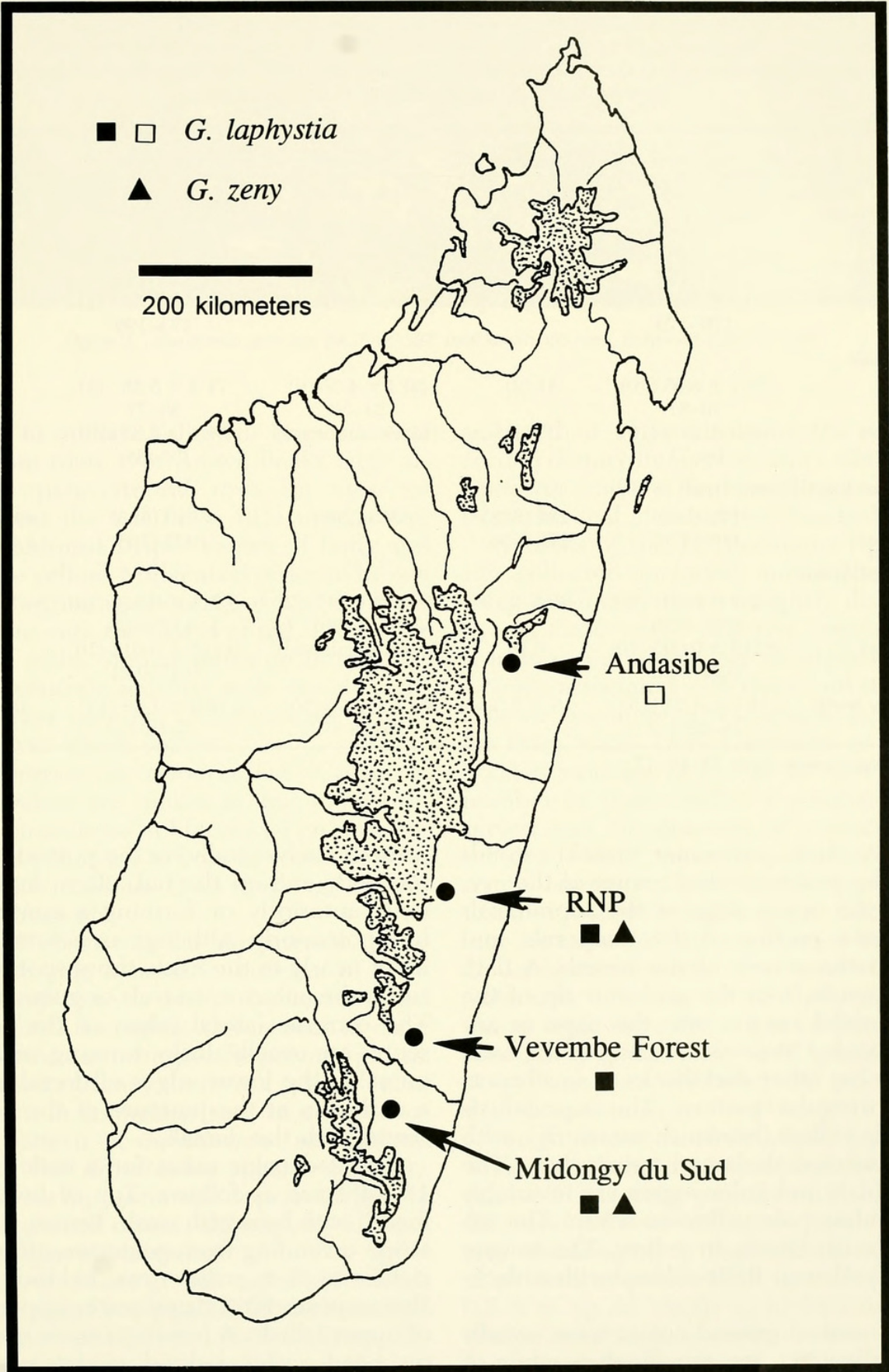


TABLE 1. VARIATION IN MENSURAL AND MERISTIC CHARACTERISTICS OF MALAGASY SPECIES OF GEODIPSAS. MEAN \pm SD ARE GIVEN FOR MEASUREMENTS AND COUNTS FOR *LAPHYSTIA*, *BOULENGERI* AND *INFRALENEATA* (*ZENY* AND *VINCKEI* REPRESENTED BY TOO FEW SPECIMENS). SEXES WERE NOT SEPARATED FOR *GEODIPSAS BOULENGERI* BECAUSE MOST AVAILABLE SPECIMENS OF THAT SPECIES WERE HATCHLINGS, FOR WHICH SEX WAS NOT VERIFIED. SAMPLE SIZES IN PARENTHESES.

	<i>laphystia</i> , new species	<i>zeny</i> , new species	<i>boulengeri</i>	<i>infralineata</i>	<i>vinckei</i> (holotype)
Dorsals	19–19–17	19–19–17	19–19–17 ¹	19–19–17	21–19–17
Ventrals					
Males	182.8 \pm 2.57 (10) 180–187	135–137 (2)	133.8 \pm 1.92 (9) 131–137	186.7 \pm 6.04 (10) 172–193	161
Females	173.8 \pm 2.37 (12) 170–179	132 (1)	(sexes combined)	186.3 \pm 8.38 (11) 173–199	
Subcaudals					
Males	76.7 \pm 3.95 (10) 70–81	41 (2)	30.4 \pm 4.56 (9) 24–36	71.3 \pm 5.28 (8) 53–77	45
Females	66.9 \pm 2.08 (10) 64–71	35 (1)	(sexes combined)	61.4 \pm 4.83 (10) 53–68	
Maximum length (mm) (total [SVL])					
Males	622 (469)	281 (228)	353 (298)	783 (635)	493 (409)
Females	608 (476)	272 (230)	—	933 (765)	
Tail length/total					
Males	0.239 \pm 0.009 (10) 0.23–0.26	0.18–0.19	0.14 \pm 0.017 (9) 0.12–0.16	0.211 \pm 0.020 (9) 0.17–0.23	0.17
Females	0.216 \pm 0.005 (10) 0.21–0.22	0.15	(sexes combined)	0.188 \pm 0.012 (10) 0.17–0.21	
Maxillary teeth	19.7 \pm 1.23 (15) 18–23 + 2	15 + 2 (2)	16.3 \pm 0.95 (10) 15–18 + 2	16.3 \pm 1.18 (15) 15–18 + 2	18 + 2

¹ Two specimens were 18–19–17.

sum. A dark postocular streak extends from the posteroventral corner of the eye, across the upper edge of the supralabials and lower portion of the temporals, and ends at the corner of the mouth. A dark line extends from the posterior tip of the interparietal suture onto the nape or anterior neck. Otherwise, the top of the head usually has other dark flecks or small spots in an irregular pattern. The supralabials are pale yellow (brownish anteriorly), with an occasional darkened suture line. The infralabials and gular region are invariably immaculate pale yellow to white. The iris is yellowish brown to yellow. The tongue is pale yellow or flesh-colored with a blackish tip.

The ventral ground colors were usually pale yellow but occasionally dirty white. A series of dark flecks or spots is usually

present midventrally on the posterior $\frac{2}{3}$ of the body and on the tail, often discontinuous anteriorly or forming a continuous line posteriorly. Although occasionally evident nearly to the neck, these spots never reach the anterior ventrals or gular region. The extreme lateral edges of the ventral scutes are usually dusky, forming, with pigment on the lower edges of dorsal row 1, a dark line at the juncture of the ventral scutes with the dorsals.

Detailed color notes for a male (MCZ 181148) are as follows. Top of head yellowish with brownish wash. Brown median stripe extending from posterior end of parietals to 5–6 scale rows behind head. Brown postorbital stripe across upper edge of upper labials. A few tiny brown speckles on head scales behind prefrontals. Iris light yellowish brown. Dorsum brownish

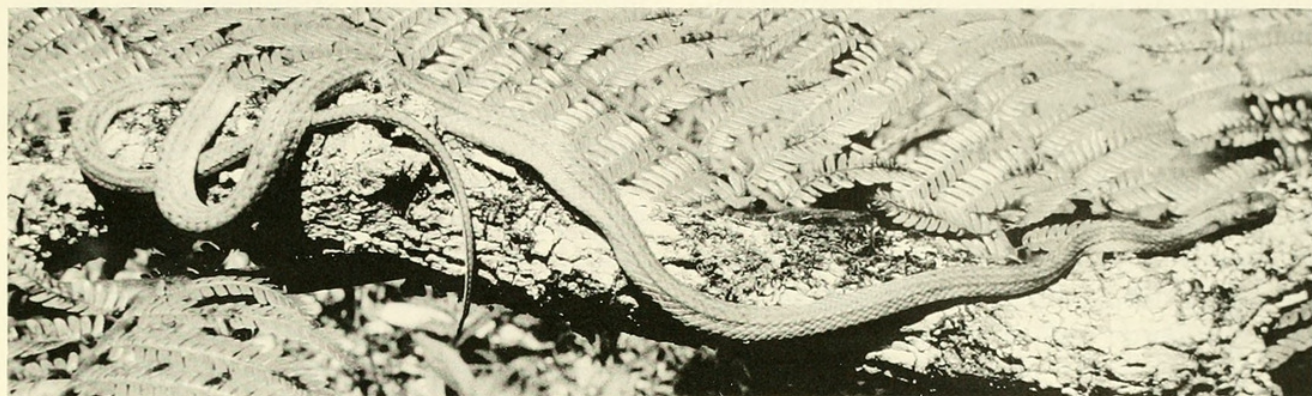


Figure 3. *Geodipsas laphystia* (MCZ 181387; total length 595 mm). Specimen from the RNP.

yellow to yellow. Yellowish brown lateral stripe on rows 4–5. Brown flecks edge alternate paravertebral rows on most of body—on the tail these fuse into a very fine middorsal stripe. Venter of body and tail pale yellow. Midventral series of brown flecks beginning about $\frac{1}{3}$ of way on body continue onto the first $\frac{1}{2}$ of tail, 1 fleck per ventral scale. Similar series on border between ventrals and first scale row, becoming darker on edge of subcaudals. Upper and lower labials yellow.

Coloration in Preservative. Colors in preservative are similar to, but more subdued, than those in life: dorsal ground colors dull yellowish to brown, venter yellowish white to white. Dark markings brownish to blackish.

Until observing the hemipenial differences among sympatric samples of *Geodipsas infralineata* and *G. laphystia*, I had considered the subtle differences in color and pattern as intraspecific polymorphism. As indicated later, there is a great deal of variation in coloration and, to a lesser extent, pattern in *infralineata* (see *Coloration* in the *infralineata* species account). *Geodipsas laphystia* also is polymorphic in dorsal ground colors, although to a lesser extent than *infralineata*.

Natural History. All my observations suggest that *Geodipsas laphystia* is nocturnal and arboreal. Individuals are frequently encountered along small forest streams and rivers, probably in search of frogs

and/or their eggs, which are the only recorded dietary items (see later). *Geodipsas laphystia* emits a foul-smelling secretion from the anal glands when handled.

Habitats of the 22 specimens I personally collected included undisturbed primary rainforest, forests slightly disturbed by old (≥ 50 years) selective logging, and riparian vegetation on floodplains and swamps associated with rivers and streams. I never encountered *Geodipsas laphystia* far from water (forest streams or rivers, flooded swamps, or pools). In view of the number of these snakes I personally observed and the diversity of microhabitats surveyed, their invariant association with water courses seems highly significant. Limited observations suggest that there may be some habitat segregation between *G. laphystia* and the very similar *G. infralineata*. Whereas no *G. laphystia* were found away from the edges of streams or pools, only occasionally were specimens of *G. infralineata* collected in association with water courses.

Most specimens of *Geodipsas laphystia* were found during or immediately after rains (or following periods of heavy rainfall), and all were collected from vegetation overhanging or immediately adjacent to streams or pools. Most specimens were 0.5–4 m up on woody or herbaceous vegetation overhanging water or were crawling among epiphytes on such vegetation. Typically, active *Geodipsas laphystia* were

encountered moving slowly in vegetation or else immobile, either in a loose irregular coil or stretched out; several were observed tongue-flicking the surfaces of leaves while crawling slowly in vegetation.

The body form of *Geodipsas laphystia* shows typical modifications associated with arboreality in colubrids (e.g., Guyer and Donnelly, 1990; Cadle and Greene, 1993). These include compression and attenuation of the body (shift of the center of gravity posteriorly), a long, narrow "neck," an angulate ventrolateral edge to the body, and a rather long, prehensile tail (Table 1).

Food records for *Geodipsas laphystia* obtained by palpating freshly collected specimens were the following (N = 9 stomachs, one item per stomach except as noted): unidentified frog + eggs referred to *Mantidactylus luteus* (Ranidae; MCZ 181151, SVL 476 mm); *Boophis madagascariensis* (Rhacophoridae; MCZ 180340 and 180341, SVLs 438 and 350 mm, respectively), cf. *Boophis* sp. (Rhacophoridae; MCZ 181158, SVL 329 mm), cf. *Mantidactylus* sp. (Ranidae; MCZ 181393, SVL 467 mm), and egg clutches or egg clutches/hatching tadpoles of *Mantidactylus* spp. (Ranidae; MCZ 181387, SVL 458 mm; MCZ 181388, SVL 457 mm; MCZ 181389, SVL 435 mm; MCZ 181390, SVL 469 mm). These are supplemented by three field observations of consumption of frog egg clutches (details given below): *Mantidactylus luteus* (Ranidae; MCZ 180339 or 181164; SVLs 389 and 452 mm, respectively), *M. liber* (Ranidae; MCZ 180342, SVL 431 mm), and *M. cf. blommersae* (MCZ 181393; SVL 467 mm).

These records show that *Geodipsas laphystia* is a consumer of frogs and their eggs (especially *Mantidactylus* spp.). Many species of *Mantidactylus* attach their egg masses to leaves above flowing or standing water, and these may form a significant portion of the diet of *Geodipsas laphystia* during the rainy season when the egg masses are ubiquitous in montane and lowland rainforests where the species occurs. *Geodipsas laphystia* possibly also

consumes eggs of other Malagasy frogs that deposit eggs in sites accessible to an arboreal snake, including many species of cophyline microhylids that lay eggs in tree holes.

Three instances of predation on frog eggs were observed in the field at Talata-kely in the RNP. The following observations pertain to either MCZ 180339 (SVL 389 mm) or 181164 (SVL 452 mm) and were made on 6 December 1992 at the edge of a small temporary pond within rainforest (the two specimens were placed together in a collecting bag and the individual upon which the observations were based is uncertain). Many egg clutches of *Mantidactylus* spp. were attached to leaves around the pond. From 1950 to 2050 hours, the snake was stretched out along top of a large fern frond about 1 m above mud at the edge of the pond. On the frond, several clutches of *Mantidactylus luteus* eggs were suspended. During the hour of observation, the snake moved very slowly (30 cm maximum). I suspected the snake might be eating the frog eggs; one of the egg clutches appeared to have already been predated, as there was very little of it left. Eventually, the snake approached one of the clutches and rapidly moved its head back and forth through the clutch, opening and closing its mouth. Perhaps disturbed by light from my headlamp, the snake started to move away from the clutch, at which time it was collected. The snake was immediately palpated and it regurgitated some of the milky egg clutch.

MCZ 181393 (SVL 467 mm) was observed on 30 December 1995 at the same pond as above, moving slowly and tongue-flicking along a grass stem 50–100 cm above the edge of the pond. Attached to the underside of leaves along this stem were clutches of *Mantidactylus cf. blommersae* eggs. After a few seconds, the snake approached one of the clutches and began consuming the eggs, biting through the clutch several times and then withdrawing.

MCZ 180342 (SVL 431 mm) was ob-

served on 2 January 1993 during a light drizzle on small tree branches about 3 m above a tiny rivulet in the forest. When first seen the snake had nearly finished consuming a clutch of *Mantidactylus liber* eggs attached to the top of a leaf. The snake was moving its head back and forth through the egg mass while at the same time opening and closing its mouth. No eggs appeared to be left in the clutch, although much of the jelly appeared to be intact.

Essentially nothing is known of the reproduction in any species of *Geodipsas*. Rather curiously, no females of any species that I personally collected, nor any museum specimens I examined by palpation, had eggs with enlarged yolks or shells. Two of eight adult females (SVLs 350–486 mm) of *G. laphystia* that I collected had evidence of early vitellogenesis (follicles 2–3 mm diameter; follicles of all other specimens ≤ 1 mm); reproductive condition was not examined for museum specimens. The two vitellogenic females (MCZ 181159 and 181393) were collected on 13 January 1993 and 30–31 December 1995; dates of collection for the nonvitellogenic females were 4 December to 1 January. Given the absence of vitellogenic females earlier in the rainy or dry season, it seems plausible that *G. laphystia* lays eggs well into the rainy season (i.e., February–April) in the southern portion of the eastern rainforest belt. This is somewhat later than several sympatric species of *Liopholidophis* (Cadle, 1996), and may reflect the fact that the period of major annual activity for *Geodipsas laphystia* appears to coincide with the beginning of the rainy season (usually the last half of December), whereas species of *Liopholidophis* are active much earlier (Cadle, 1996). It may require females of *G. laphystia* some time to acquire sufficient fat stores to initiate vitellogenesis after the rainy season begins. Some circumstantial evidence suggests that sexual maturity of males may occur at approximately 300–350 mm SVL (see *Remarks*).

Remarks. Primarily in conjunction with ascertaining the sexual maturity of the male types of *Geodipsas zeny*, new species, to be described next (see *Remarks* for that species), I examined spine mineralization in hemipenes of a size series of *Geodipsas laphystia* by clearing and staining with alizarin (alizarin binds to mineralized tissues, including hemipenial spines, permitting easy visualization of the extent of mineralization). Anecdotal observations, primarily of Charles W. Myers (personal communication), had suggested a general relationship between hemipenial spine mineralization and other gross indications of sexual maturity. These observations included the presence of nonmineralized or weakly mineralized spines in snakes lacking other indications of maturity (e.g., convoluted vasa deferentia, anal ridges) and well-mineralized spines in mature snakes.

I cleared and alizarin-stained one everted hemipenis from each of three specimens of *Geodipsas laphystia*: MCZ 181148 (SVL 299 mm), MCZ 181152 (SVL 360 mm), and MCZ 180342 (SVL 431 mm). In *G. laphystia*, enlarged, curved spines protrude from the midsection of the hemipenis, and these grade distally into long straight spinules; a pair of enlarged spines is present basally on the asulcate side (see detailed hemipenial description, later). Upon inspection under a dissecting microscope, neither the hemipenial spines nor spinules of MCZ 181148 seemed to be mineralized (at most, only very slightly mineralized), whereas those of the other two specimens were well mineralized. The staining revealed that in MCZ 181148 the protruding portions of the enlarged hooked spines on the midsection of the organ and at the base of the asulcate side were mineralized, but none of the elongate spinules on the distal portion, nor the smaller spines of the body, were. All spines and spinules of the other two organs were well mineralized.

A general correspondence of spine mineralization with other signs of reproductive maturity seems to hold. MCZ 181148 has

small, poorly differentiated testes and non-convoluted vasa deferentia, indicating sexual immaturity. Both of the other specimens have large, compact testes obviously packed with coiled tubules, and convoluted vasa deferentia (those of MCZ 181342 more convoluted than in MCZ 181152). Thus, a general relationship between hemipenial spine mineralization and sexual maturation in *Geodipsas laphystia* is corroborated, although much more work needs to be done to quantify that relationship further.

This exercise also permitted some observations on the ontogeny of spine mineralization. In MCZ 181152 and 181342, both of which have fully developed spines, the clearing and staining revealed that each of the enlarged spines has a broadened base just under the surface of the organ and a long spur extending distally from the base through the soft tissue of the organ. The spinules have no such broadened base or spur, their internal portion being the same diameter as the protruding portion. There is a gradual transition in the morphology of the hidden, basal portion of these ornaments from the enlarged spines on the midsection to the elongate distal spinules (a similar gradual transition occurs in the visible external portion). By comparison, in MCZ 181148 only the external, protruding portion of the spines and a small, unexpanded portion of the internal base are mineralized. This suggests that mineralization proceeds from external to internal, at least for the enlarged spines on the midsection.

An unanswered question is whether mineralization of the distal spinules occurs relatively rapidly with the onset of sexual maturity or the transition is more gradual. Whereas there is no apparent difference between MCZ 181152 and 181342 (70 mm difference in body size) in the extent of spine mineralization other than general size increase, the difference between MCZ 181148 and 181152 (60 mm difference in body size) is striking. This suggests that, at least for the distal spinules and the inter-

nal portions of the enlarged midsection spines, onset of extensive mineralization, and perhaps sexual maturity, may occur relatively rapidly at a body size of approximately 300–350 mm.

The suggestion that hemipenial spine mineralization may indicate sexual maturity should be more carefully investigated in snakes, but also in other squamates. For example, some varanid lizards have mineralized “hemibacula” in their hemipenes (Card and Kluge, 1995). Card and Kluge (1995) found no seasonal variation in mineralization of those elements. For *Varanus gouldii*, they also reported that the hemibacula remain unmineralized for at least up to a year posthatching. The implication is that the hemibacula may mineralize coincident with sexual maturity in these lizards, as already suggested for snake hemipenial spines. Thus, extensive mineralization of hemipenial elements may be an indicator of male maturity in those squamates having such elements as adults.

Geodipsas zeny,
new species

Figures 4–6; Table 1

Holotype. Museum of Comparative Zoology, Harvard (MCZ) 181161 (JEC 12580), an adult male in good condition (Figs. 4, 6). Specimen collected 11 January 1993 by John E. Cadle.

Type Locality. Approximately 7 km SW (airline) Midongy du Sud [Midongy Atsimo], near Rianambo (“high waterfall”) on Lalampo River, 670 m elev., Fivondronana Midongy du Sud, Prov. Fianarantsoa, Madagascar [23°39’S, 46°57’E].

Paratypes. MCZ 181162 (JEC 10124), female, apparently adult (see *Remarks*), 6 December 1990: Talatakely (at the village of Ambodiamontana), Ranomafana National Park, 980 m, Fivondronana Ifadiana, Fianarantsoa Province, Madagascar [21°16’S, 47°25’E]. Collected by a villager.

The Natural History Museum, London (BMNH) 95.10.29.62 (Figs. 5, 6), adult male from “Imerina, Madagascar” obtained by the Reverend R[ichard] Bar-

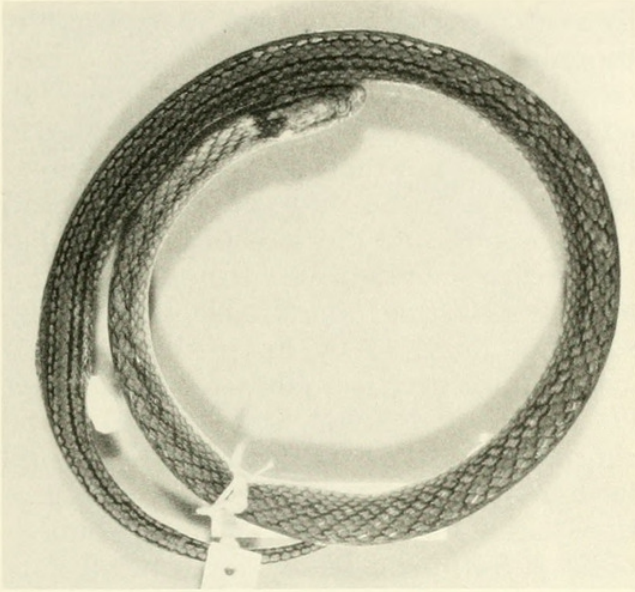


Figure 4. Holotype of *Geodipsas zeny* (MCZ 181161, male; total length 281 mm) from near Midongy du Sud.

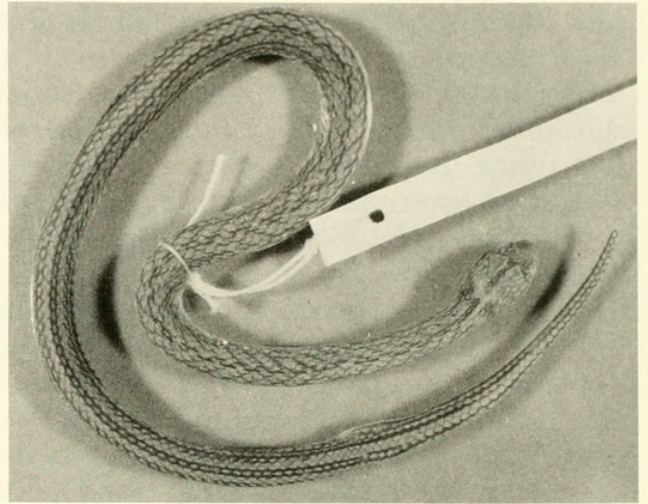


Figure 5. Paratype of *Geodipsas zeny* (BMNH 95. 10. 29. 62, male; total length 266 mm) from "Imerina, Madagascar."

on, probably in the early 1890s. The descriptor "Imerina" refers to the territory occupied by the indigenous people of that name in the central plateau between approximately parallels 18° and 21° (see, e.g., Gallieni, 1908:pl. 6).

Comment on the Type Locality. In field notes and in previously published work (Cadle, 1996:460–461; localities for *Lio-pholidophis infrasignatus*, *L. lateralis*, and *L. sexlineatus*), I originally transcribed the name "Lalampo River" as "Alapo River" based on my interpretation of local informants' pronunciation. Here I correct the name to "Lalampo" following the 1:100,000 "Befotaka" map published by the Institut Géographique National, Paris (1961; available through the Foiben-Taosarintanin'i Madagasikara [FTM], Antananarivo). Neither name appears in recent gazetteers (e.g., Defense Mapping Agency, 1989). Given my original field transcription, it may be referred to locally as any of the variants "Lalampo," "Alampo," or "Alapo." As of 1996, a 1:50,000 topographic map of the area was unavailable to verify the name. The Lalampo is a tributary of the Itomampy River, which is the major

river flowing through the town of Midongy du Sud.

Upstream from the type locality, the river passes over a high precipice and has eroded down to bedrock, forming a waterfall that is a well-known local landmark. *Rianambo* is a compound word from the Malagasy *riana* (= waterfall) + *ambo* (= big or high). From the top of the falls I recorded a compass reading of 63° to the town of Midongy du Sud, visible in the distance, thus making the waterfall and our campsite approximately 243° in a southwesterly direction from the town.

Distribution (Fig. 2). The two known localities are approximately 270 km apart in the southern portion of the eastern rainforest belt of Madagascar. The BMNH specimen with imprecise locality most likely came from the eastern, forested portion of the Imerina territory in central Madagascar. The known elevational range of *Geodipsas zeny* is 670 m at the type locality to 980 m at the other precise locality. The types are the only known specimens.

Etymology. The specific epithet, *zeny* (pronounced approximately as zeh' -nē), used here as a noun in apposition, is a Malagasy word meaning "dwarf" or "dwarfish." It refers to the diminutive size of *G.*

zeny in comparison to other Malagasy *Geodipsas*.

Diagnosis. *Geodipsas zeny* is smaller (maximum known total length 281 mm) than other described species of Malagasy *Geodipsas* (maximum known total lengths ≥ 447 mm) and has the following distinguishing features: low number of ventrals (132–137) and subcaudals (35–41); a bold dark gray midventral line from the neck to the vent (Fig. 6); paired dark nape blotches or a dark collar; and dark borders to the dorsal scales that tend to form a reticulated network or dark diagonals on the flanks anteriorly and dark longitudinal streaks posteriorly.

Geodipsas zeny is essentially indistinguishable from *G. boulengeri* in the usual scutellational features that distinguish snake species (e.g., ventral, subcaudal, dorsal counts). Prior to examining specimens of *G. "heimi"* (= *boulengeri*, as shown later), I had considered specimens of *zeny* possibly as that species solely on this basis (*zeny* will key to "*heimi*" using the key to species in Glaw and Vences [1994]). However, *G. zeny* differs from *boulengeri* in several coloration/pattern differences, including the following (contrasting characters of *boulengeri* in parentheses): (1) a thick, bold midventral dark gray line extending from the neck or anterior body to the vent (venter without continuous, bold midventral line; usually immaculate, but occasionally with a midventral series of scattered small dots); (2) a pair of dark nape blotches that may be connected by dark pigment to form a continuous collar (paired light neck blotches behind the jaw angle); (3) a dark streak from the posterior edge of the frontal scale to the nape along the parietal suture (no dark streak on parietal suture); (4) dark borders of dorsal scales tending to form a fine network or diagonals anteriorly, forming indistinct dark streaks on rows 3–4 and 6–7 posteriorly (dark network present or not, and not forming streaks posteriorly); and (5) light areas on labial scales not forming discrete spots and not bordered

by a discrete dark line (light spots discrete, though often irregularly shaped, and bordered by a discrete narrow dark line). In addition, *zeny* differs from *boulengeri* in hemipenial characters, including fewer spines around the midsection, a more divided sulcus, and absence of a basal lobe.

Geodipsas zeny differs from *G. infralineata* (contrasting conditions in parentheses; see Table 1) by its smaller size (to >900 mm total length), fewer ventrals (172–199) and subcaudals (53–77), and shorter tail (17–23% of total length), and in hemipenial morphology (see descriptions later; Figs. 15, 17). Many specimens of *G. infralineata* have a midventral dark line, but it is usually narrow and anteriorly incomplete, in contrast to the bold thick midventral line that is complete from the neck to the vent in *zeny*. Some specimens of *infralineata* resemble *zeny* in having paired dark nape blotches and a dark streak along the parietal suture (Figs. 10, 12). Virtually the same characters that distinguish *zeny* from *infralineata* also distinguish *zeny* from *laphystia* (see Table 1 and diagnosis of *G. laphystia*).

Geodipsas zeny differs from *G. vinckei* (known only from the holotype; characteristics in parentheses) in having fewer ventrals (161) and in color pattern (light collar on nape; anterior ventrals with dark anterior border, resulting in a ladderlike pattern; posterior ventrals with triangular or halfmoon-shaped dark blotches).

Data on the Holotype (MCZ 181161). The holotype is an adult male with fully everted hemipenes (the left one removed for illustration; Fig. 15). Total length 281 mm; tail length 53 mm (19% of total length). Greatest head width (temporal region) 5.5 mm, head length 11.1 mm measured diagonally from tip of snout to end of mandibles. Dorsals in 19–19–17 rows, the reduction occurring by loss of row 4 at the level of ventrals 95 (left) and 98 (right). Two prefrontals, 135 ventrals, single anal plate, 41 pairs of subcaudals, 7–7 supralabials (3–4 touching eye), 9–9 infralabials, 1 + 2 temporals on each side.

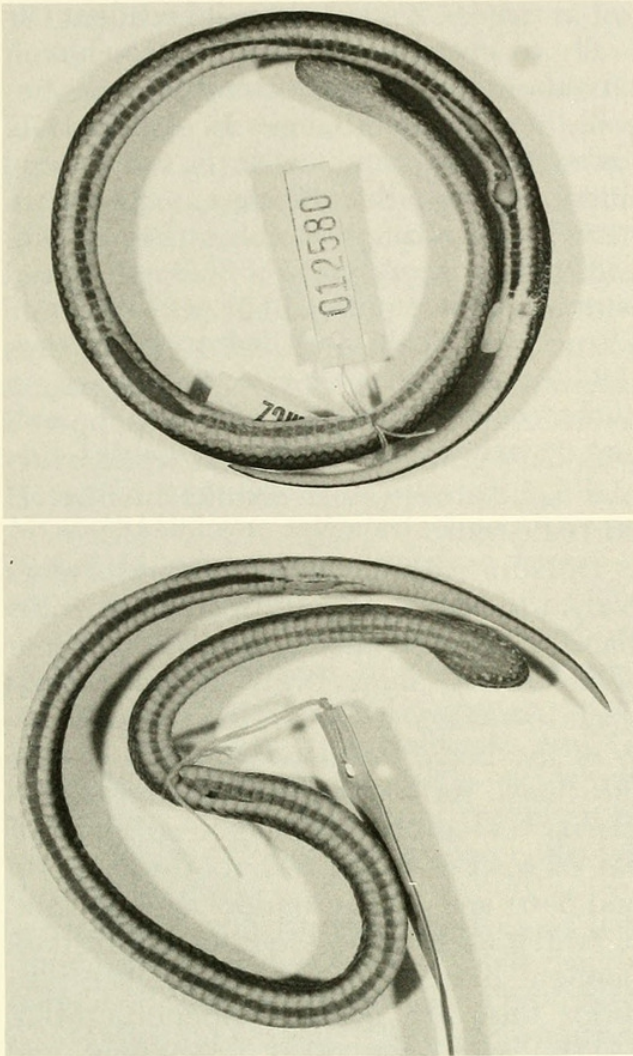


Figure 6. Ventral views of the holotype (top; MCZ 181161) and male paratype (bottom; BMNH 95. 1. 29. 62) of *Geodipsas zeny*. The wide midventral stripe extending the length of the body appears to be diagnostic of this species (cf. *Geodipsas infralineata*, Fig. 11).

Description. Measurements, proportions, and scutellation for the 3 known specimens are summarized in Table 1; the specimens are identified in the following description as "MCZ" and "BMNH" unless individual identity is necessary. Largest male (MCZ 181161), 281 mm total length, 53 mm tail length; female, 272 mm total length, 42 mm tail length. Tail length 18–19% of total length in males, 15% in female. Body slightly higher than wide; ventrolateral edge of body angulate. Head slightly wider than neck. Pupil subcircular (prolate; see *Discussion*).

Dorsal scales smooth, lacking apical pits, in 19–19–17 rows. Posterior dorsal scale reduction by loss of row 4 at the level of ventrals 91–105 ($N = 5$ sides). Ventrals 135–137 in males, 132 in female; preceded by 1 or 2 preventrals. Anal plate single. Subcaudals 41 in males, 35 in female.

Loreal rectangular to pentagonal, usually higher than wide, separated from eye by single preocular. Two postoculars; temporals 1 + 2. Supralabials 7–7 with 3–4 touching eye. Infralabials 7–9, the first pair in contact behind the mental, 1–4 (MCZ specimens) or 1–3 (BMNH) touching an anterior genial, 4–5 (MCZ) or 3–4 (BMNH) touching a posterior genial. Anterior genials shorter than (MCZ 181161, BMNH) or approximately equal to (MCZ 181162) posterior genials. Head plates smooth, apparently without pits or tubercles.

Dentition. Maxillary teeth 15 + 2 ($N = 2$). Diastema about 1.5–2 \times the width of the posteriormost solid maxillary tooth. The fangs are deeply grooved, about twice as large as the posteriormost solid teeth, and have a rounded anterior surface, a flattened knifelike posterior surface, and slightly compressed tips. The fangs are offset from the solid tooth row.

Hemipenis (See Fig. 15). Single (nonbilobed), noncapitate, acalyculate; proximally nude, with a spinose midsection, and distally spinulate. Distal ornamentation sharply set off from that of the midsection, resulting in a rather distinct head region. Sulcus spermaticus centrolineal and forked distally for approximately 15% of its length.

Coloration in Life (MCZ 181162). Dorsum dark brown, somewhat iridescent, with tiny scattered dark punctations forming a fine reticulated network over most of body, indistinct lines posteriorly. Top of head dark brown, with dark brown longitudinal line from posterior edge of frontal to nape. An indistinct dark brown postocular bar is present. Upper and lower labials dusky grayish brown. Throat grayish brown with some whitish punctations.

Outer edges of ventrals dusky grayish brown; center part of each ventral with a squarish dark brown blotch, giving impression of broad midventral dark brown stripe (approximately $\frac{1}{4}$ the width of the ventral scutes). Portion of ventrals between center blotches and lateral edges is whitish with grayish brown irregular markings. Subcaudals whitish, with midventral dark line. A very indistinct lighter stripe (brown with very thin darker border) is present on extreme posterior body, continuing onto tail (evident only on close inspection).

Coloration in Preservative. MCZ 181161–62 are dark brown dorsally with a fine network of very dark brown/blackish markings over the entire body, tending to form narrow diagonals anteriorly and longitudinal lines posteriorly (Fig. 4). BMNH 95.10.29.62 has a lighter grayish brown ground color with similar dark markings (Fig. 5). Top of head medium brown with dark brown markings. The venter is dirty white and the midventral stripe is dark gray to medium brown. The dorsal pigment encroaches as fine stippling laterally onto the ventral plates, where it forms a narrow border (MCZ 181161, BMNH 95.10.29.62) or more extensive coverage toward the midline (MCZ 181162).

The head bears a dark brown line from (and including) the posterior edge of the frontal, narrowly bordering the interparietal suture, and connecting to the neck collar (MCZ specimens) or ending on the neck just posterior to a pair of nape blotches (BMNH). Top of head otherwise with a complex marbled pattern composed of various shades of brown, black, and gray. An indistinct dark brown postocular stripe occupies the ventral edges of the temporals (most discrete in the holotype, less so in MCZ 181162, and not evident in the BMNH specimen). Upper labials whitish, heavily speckled with dark gray or brown, with unpigmented areas forming discrete spots in the holotype and BMNH specimen, but not in MCZ 181162. A dark brown nape collar 2–3 scales wide is pres-

ent in the MCZ specimens; it broadens laterally to give the appearance of a blotch on either side of the neck and extends ventrally to the mouth line. In the BMNH specimen the nape collar is interrupted middorsally so this specimen appears to have a pair of nape blotches (Fig. 5). Infralabials and gular region finely peppered with dark gray infralabials with discrete white spots in BMNH 95.10.29.62, less discrete in MCZ 181161, and not apparent in MCZ 181162. Gular region peppered with dark gray, but having indiscrete irregular light areas (most distinct in BMNH 95.10.29.62).

Dorsum with complex network of dark brown/black, forming posteroventrally slanting diagonal lines anteriorly that occur along suture lines every second dorsal scale row (Figs. 4–5). On the posterior $\frac{1}{2}$ – $\frac{2}{3}$ of the body, the network tends to fuse into lines. At about midbody, these lines are on the suture line and/or adjacent areas of rows 4–5 and 6–7 (posteriorly 3–4 and 5–6) and on the middorsal scale row, in which each scale is outlined with dark pigment but has a light center. The posterior lines are not so evident in MCZ 181162 as in the other specimens, and they are evident much farther anteriorly in BMNH 95.10.29.62 than in MCZ 181161. The lines continue to the tail tip, tending to fuse with one another on the tail.

The midventral dark stripe is composed of a series of bold, squarish blotches with more or less regular edges, one in the center of each ventral plate (Fig. 6). These align to form a broad midventral stripe extending from just behind the head to (and including) the anal plate (Fig. 6). Under magnification the midventral stripe is seen to be composed of a very dense fine stippling. Anteriorly the stippling is less dense and the overall appearance of the stripe lighter than posteriorly. BMNH 95.10.29.62 has a short, thin, dark line on the ventral surface of the proximal portion of the tail; MCZ 181162 has a similar line extending about $\frac{3}{5}$ the tail length; and in MCZ

181161 the ventral surface of the tail is immaculate.

Natural History. The holotype was collected while active at night 2 m above-ground in a shrub at the edge of a flooded, meadowlike, vegetation-choked bog (with grasses and ferns up to about 1.2 m high) in riparian forest. Many frogs were calling at the site, including *Scaphiophryne marmorata* (Microhylidae), *Mantidactylus liber* and *Ptychadena mascareniensis* (Ranidae), *Heterixalus betsileo* (Hyperoliidae), and *Aglyptodactylus madagascariensis* and *Boophis granulosus* (Rhacophoridae). MCZ 181162 was collected while active on a trail in moderately disturbed forest at about 0730 hours. These two observations do not permit any general statement about daily activity patterns of *Geodipsas zeny* (of the other species of *Geodipsas* occurring in the RNP, *G. infralineata* and *G. laphystia* apparently are nearly exclusively nocturnal, whereas the only specimen of *G. boulengeri* from the park was collected during the day).

Similarly, with so few observations it is difficult to speculate on the usual macrohabitat (arboreal, terrestrial, cryptozoic; see Cadle and Greene, 1993) of *Geodipsas zeny*. Although the type was collected from a small tree, the body form of *G. zeny* shows few clear modifications associated with arboreality. Nevertheless, the ventrolateral edge of the body is angulate, a character often, but not invariably, associated with arboreality in snakes. However, the short body and tail and the lack of body compression and attenuation suggest a terrestrial snake.

Geodipsas zeny is broadly sympatric with *G. infralineata*, *G. laphystia*, and *G. boulengeri* in the RNP and with at least *infralineata* and *laphystia* at the type locality. Both *G. zeny* and *G. boulengeri* were the least commonly encountered colubrids in the RNP survey (one specimen each over several long field expeditions).

Remarks. All three specimens of the type series are small snakes and it might be questioned whether they are adults.

Sexual maturity is indicated in the two males by well-mineralized hemipenial spines and spinules, by convoluted vasa deferentia, and by the convoluted surface of the kidneys, which indicates secretory activity of the sexual segments of the renal tubules (e.g., Fox, 1952; Myers, 1965). To a first approximation, a general correlation between the extent of hemipenial spine mineralization and sexual maturity seems to hold for *Geodipsas laphystia* (see *Remarks* for that species). Assuming that the same general pattern holds for *G. zeny*, sexual maturity of the males of *zeny* is indicated by the mineralization of *both* the enlarged spines and (especially) the spinules on the distal end of the organ.

Sexual maturity of the female paratype of *Geodipsas zeny* is suggested by enlarged and slightly convoluted oviducts, which are about as convoluted as those of some apparently mature *G. infralineata* and *G. laphystia*.

The female of *Geodipsas zeny* is approximately the same size as the two known males, which suggests little sexual size dimorphism in this species. Nevertheless, given the small sample size it would be premature to make firm conclusions. Of the other species of *Geodipsas* for which I have examined adequate samples ($N > 20$ individuals), *G. laphystia* shows no evidence of strong sexual dimorphism (largest specimen a male; Table 1), whereas *G. infralineata* shows the usual colubrid pattern wherein females reach larger body sizes than males (Table 1).

SYNONYMY OF *TACHYMENIS BOULENGERI* PERACCA AND *GEODIPSAS HEIMI* ANGEL

Peracca (1892) described *Tachymenis* (now *Geodipsas*) *boulengeri* on the basis of a single adult male (Museo Regionale di Scienze Naturali, Torino [MZUT] 1874; see Figs. 7–8) from near Andrangoloaka (19°02'S, 47°55'E; Fig. 9; see Cadle [1996: 401] for discussion of this locality). Mocquard (1894) described *Compsophis albi-*

ventris, new genus and species, on the basis of a single juvenile (Muséum National d'Histoire Naturelle, Paris [MNHN] 1893.212) from Montagne d'Ambre (= Ambohitra, Antsiranana Province; 12°30'S, 49°10'E; Fig. 9 [star]). Angel (1936) described *Geodipsas heimi* on the basis of an adult male (MNHN 1936.19) from near Tsianovoha (= Tsianovoho, Fianarantsoa Province; 21°57'S, 47°21'E; Fig. 9). *Geodipsas boulengeri* and *Compsophis albiventris* have been recognized only from the type specimens until the additional specimens of *boulengeri* reported herein. *Geodipsas heimi* has been reported from the type locality and from the vicinity of Montagne d'Ambre at the northern tip of Madagascar (Raxworthy and Nussbaum, 1994; Glaw and Vences, 1994; *Specimens Examined*). Several authors (e.g., Brygoo, 1983; UICN, PNUE, and WWF, 1990; Glaw and Vences, 1994) have expressed uncertainty as to whether or not *boulengeri*, *albiventris*, and *heimi* represent distinct taxa, but the problem has not received detailed attention. I have had the opportunity to simultaneously compare the holotypes of all three nominal taxa.

The relationship of *Compsophis albiventris* to the other two taxa is complicated by the interpretation of dentitional variation that is currently under study; it will be considered in a separate report. Nonetheless, that complication does not preclude, for the present, an assessment of whether *boulengeri* and *heimi* represent the same taxon. Because my immediate goal is to assign a name to the Ranomafana population, and because *boulengeri* is the earliest available name involved, the eventual fate of *C. albiventris* relative to the other two taxa has no bearing on the species designation applied to the RNP population. Thus, I set aside for later consideration the relationship of *Compsophis albiventris* to the other nominal taxa here under discussion.

The taxonomic status of *heimi* vis-à-vis *boulengeri* is relatively straightforward. Angel (1936) considered *G. heimi* "very

close" to *G. boulengeri*. The type localities of *Tachymenis boulengeri* and *Geodipsas heimi* are approximately 335 km apart on the eastern escarpment. A single specimen referred to *boulengeri* (*Specimens Examined*) is known from the RNP, a locality between the two type localities (Fig. 9). Basic meristic and mensural data on the types of these taxa are given in Table 2; original descriptions of the type specimens are good (*heimi*) to excellent (*boulengeri*). As shown in Table 2, the types of *boulengeri* and *heimi* are very similar. The major difference is the point of posterior dorsal scale-row reduction, but the difference between the two types is the sort of range observed intraspecifically in many colubrids. Angel (1936) noted as additional differences between *heimi* and *boulengeri* "head plates of different dimensions," a longer tail in *heimi*, a single (*heimi*) versus double (*boulengeri*) loreal, and "coloration." Angel apparently was referring to the frontal plate dimensions for the first character ("twice as long as wide" in *boulengeri* [Peracca, 1892:3], and "1½ as long as wide" in *heimi* [Angel, 1936:127]); these are minor differences, especially considering that no estimations of variance in this character are available. Likewise, relative tail proportions are very similar in the two types (Table 2). The loreal and coloration characters require more extended discussion.

In the holotype of *boulengeri*, each loreal is divided into a small superior portion, ¼ to ⅓ the size of a larger inferior portion. The supernumerary scales are well formed in each case and appear as the sort of normal variation seen in, for example, divisions of circumorbital head plates in many colubrids (e.g., the divided postocular on one side of the type of *boulengeri*; cf. Table 2). The holotype of *boulengeri* is the only specimen examined that had a divided loreal, and this variant seems to be less common in colubrids than divisions of other lateral head plates. Nonetheless, it seems a rather minor difference upon which to base a species distinction, given

TABLE 2. MERISTIC AND MENSURAL CHARACTERISTICS OF THE HOLOTYPE OF *TACHYMENIS BOULENGERI* PERACCA AND *GEODIPSAS HEIMI* ANGEL.

	<i>Tachymenis boulengeri</i> Peracca, 1892 MZUT 1874	<i>Geodipsas heimi</i> Angel, 1936 MNHN 1936.19
Sex	male (adult)	male (adult)
Length		
Total	329 mm	352 mm
Tail	48 mm	55 mm
Tail/total	0.14	0.16
Dorsal scales	19–19–17	18–19–17
Ventral scales	135 (+2 preventrals)	132 (+3 preventrals)
Posterior scale		
Reduction (L/R) (ventral scale position)	–4 (104)/3 + 4 (108)	–4 (87)/–4 (91)
Subcaudal scales	31	34
Preocular scales	1–1	1–1
Postocular scales	3–2	2–2
Temporal scales	1–1, 2–2	1–1, 2–2
Labial scales		
Upper (bordering eye)	7–7 (3–4)	7–7 (3–4)
Lower	8–9	9–8
Maxillary teeth	15 + 2	17 + 2

other strong and unusual similarities (Table 2).

As for coloration, the types of both *boulengeri* and *heimi* were reported as having a generally brown dorsum and a “brilliant yellow” (*heimi*; Angel, 1936) or “orangish yellow” (*boulengeri*; Peracca, 1892) venter, an unusual pattern of yellow to orange blotches on the side of the neck, and yellowish spots on the supra- and infralabials and gular scales (Fig. 8). Both Angel and Peracca were undoubtedly describing the coloration of preserved specimens, so any differences in coloration could easily reflect preservation methods and the amount of time in preservative. The type of *heimi* has a median ventral series of small irregular dark punctations from the neck to the vent that is absent in the type of *boulengeri*.

Comparison of coloration of the types of *boulengeri* and *heimi* now is difficult because of considerable darkening of the type of *heimi*; it is presently rather dessicated and very dark brown dorsally and dirty gray ventrally. The labial spots and nape blotches are still evident but are dirty gray. Except for fading of the ventral color,

the type of *boulengeri* is much as Peracca described it and is more or less the same color as a recently collected specimen referred to *boulengeri* from the RNP (MCZ 181163, preserved in 1990).

Despite preservational differences, several aspects of the dorsal and head patterns shared by the types of *Geodipsas boulengeri* and *G. heimi* are so unusual as to make it virtually certain that these are the same taxon. All of these features are also observed in the RNP specimen assigned to *boulengeri* (*Specimens Examined*). They are (see Figs. 7–8) (1) rounded, light spots on the supra- and infralabial scales, each with a dark border; (2) a pair of large, light, curved spots on the neck behind the angle of the mouth; (3) a dusky gular region with irregular light spots; and (4) light dark-bordered flecks on many dorsal scales (these are obscured by general darkening of the type of *heimi* but are still visible under close scrutiny).

The left hemipenis of the holotype of *Geodipsas heimi* was studied superficially *in situ*, and then everted by the method of Pesantes (1994) and compared with the everted organ of the specimen of *G. bou-*

lengeri from Ranomafana (MCZ 181163; described later; see Fig. 16). The organs are essentially identical insofar as general structure and details of ornamentation.

Given that the holotypes of *Tachymenis boulengeri* Peracca and *Geodipsas heimi* Angel are exceedingly similar in scutellation, body proportions, maxillary dentition (Table 2), and hemipenial morphology, and share highly unusual features of coloration, I interpret the double loreals of the type of *boulengeri* as an unusual scutellational variant, but not a substantive indication of distinct taxa. Hence, *Geodipsas heimi* Angel (1936) is synonymized with *Tachymenis boulengeri* Peracca (1892).

KEY TO SPECIES OF *GEODIPSAS* IN MADAGASCAR

I recognize six species of *Geodipsas* in Madagascar: *boulengeri* Peracca, *infralineata* Günther, *laphystia* Cadle, *vinckei* Domergue, *zeny* Cadle, and a species referred to herein as *Geodipsas* species inquirenda. This last species, of which all known specimens are from the vicinity of Montagne d'Ambre in northern Madagascar (*Specimens Examined*), is discussed in the species account for *Geodipsas boulengeri*. Final determination of its status will be considered in a separate report dealing with the status of *Compsophis albiventris* Mocquard, which is known only from the same locality. The following key should allow identification of all species of *Geodipsas* in Madagascar. Because of small sample sizes, the ventral scale character used in couplet 3 may, in fact, overlap between the two species when more specimens are examined.

1. Fewer than 155 ventrals and fewer than 45 subcaudals. Body rounded 2
- More than 155 ventrals and 45 or more subcaudals. Body strongly compressed⁴ 4
2. Bold dark gray or brown midventral line from the neck to the vent; large dark brown spot on each side of the nape or a dark collar. If light areas are present on labial scales, they

do not form discrete spots
..... *Geodipsas zeny* Cadle

Midventral line, if present, not bold: at most, an interrupted series of small dots, present mainly on posterior body. A large, single light spot on neck behind the jaw angle; light areas on labials form discrete (though often irregular) spots surrounded by a dark line 3

3. Fewer than 140 ventrals (131–137 in 9 specimens). Gular region dusky with light spots. Light spots on supralabials small (covering much less than $\frac{1}{4}$ of each scale), rounded, not reaching the labial border. Spots on neck behind the jaw angle at least 2 scales wide at broadest point. Gular regions dusky with irregular light areas. Discrete light flecks on many dorsal scales
..... *Geodipsas boulengeri* (Peracca)

More than 140 ventrals (143–150 in 5 specimens). Gular region immaculate (light). Light supralabial spots larger (some covering $\frac{1}{4}$ or more of each scale), elongate or irregular, and at least some reaching the labial border. Spots on neck behind the jaw angle 1 scale or less in width at the widest point. Gular region immaculate. Discrete light flecks on dorsals usually absent (when present, on few dorsals only)
..... *Geodipsas* species inquirenda (Montagne d'Ambre region only)

4. No light collar on posterior part of head and on nape. Venter more or less immaculate or with a midventral line (especially posteriorly), interrupted or not; lateral encroachment of dorsal pigment onto ventrals, and other irregular ventral spotting may be present. Subcaudals >50. Two postoculars 5

Light collar across temporal region and nape. Each ventral scute with a transverse dark marking along its anterior edge, forming a ladder-like pattern. Subcaudals 45 and 3 postoculars in only known specimen
..... *Geodipsas vinckei* Domergue

5. Dorsal pattern including a series of fine, dark chevrons or diagonals (rarely unicolor) on a highly variable ground color (dark gray, brown, grayish brown, or yellowish). Posterior scale reduction usually by fusion of rows 3 + 4 *Geodipsas infralineata* (Günther)

Dorsal pattern including a series of fine, dark longitudinal lines (on anterior body on suture lines and adjacent scales between rows 4 and 5, 7 and 8, and/or the border between the ventrals row 1; sometimes on vertebral row). Ground color variable (grayish, brownish, or yellowish). Posterior scale reduction usually by fusion of rows 4 + 5
..... *Geodipsas laphystia* Cadle

⁴ Equivocal in *Geodipsas vinckei*, as noted in the diagnosis of *G. infralineata*.

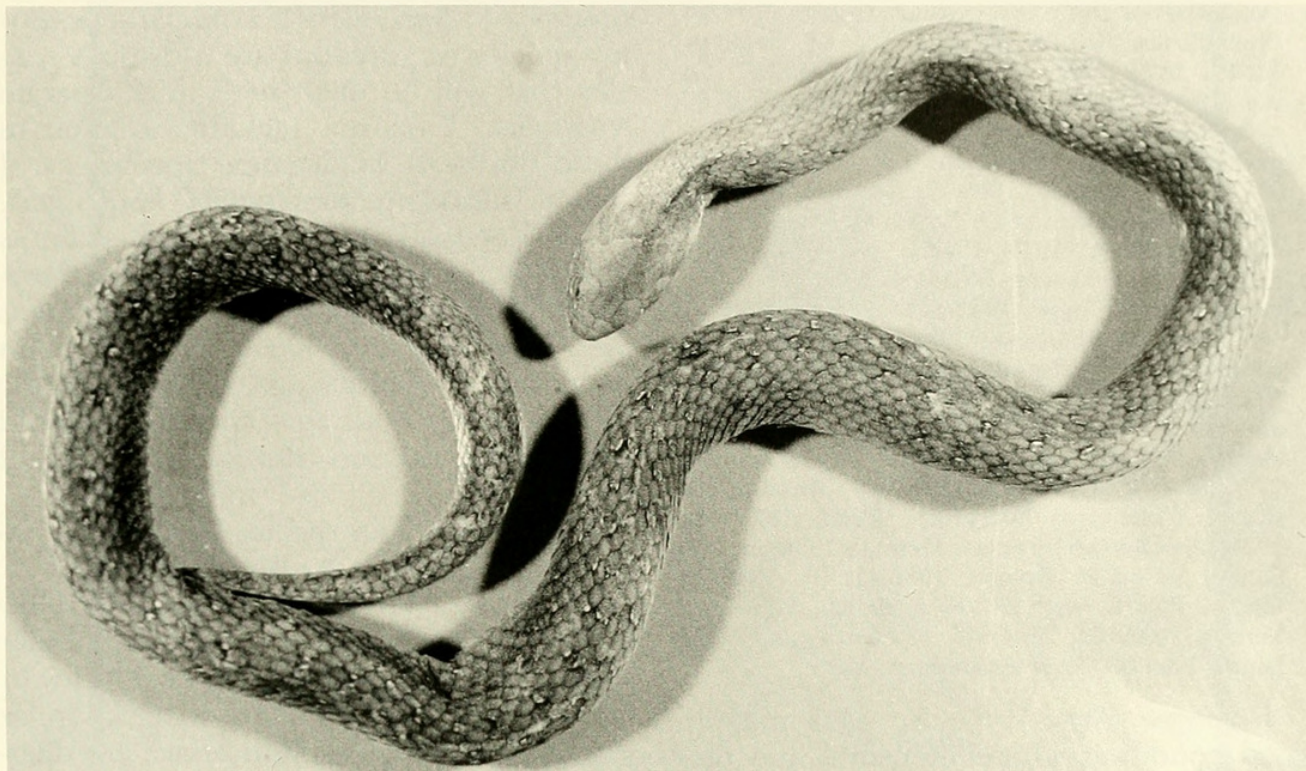


Figure 7. Holotype of *Tachymenis boulengeri* Peracca (MZUT 1874; total length 329 mm).

SUMMARY OF TAXONOMIC AND NATURAL HISTORY DATA FOR *G. BOULENGERI* AND *G. INFRALINEATA*

In addition to *Geodipsas laphystia* and *G. zeny*, *G. boulengeri* and *G. infralineata* are known from the RNP. Here I summarize variation in taxonomic characters for these two species and aspects of their natural history and behavior. The other two species, *G. vinckei* Domergue and *Geodipsas* species inquirenda, are not known from the RNP. *Geodipsas vinckei* is known only from the type specimen from Andasibe (Domergue, 1988). *Geodipsas* species inquirenda is known from specimens referred to *G. heimi* (= *boulengeri*) from the vicinity of Montagne d'Ambre. As discussed later (species account for *G. boulengeri*), these specimens are not conspecific with *boulengeri*. The distributions of all of these species are shown in Figure 9.

Geodipsas boulengeri (Peracca)

Figures 7, 8; Tables 1, 2

Tachymenis boulengerii Peracca, 1892:3–4, Figs. 2a–d (type locality, “Valle dell’Umbi (Andrangoloka)”)

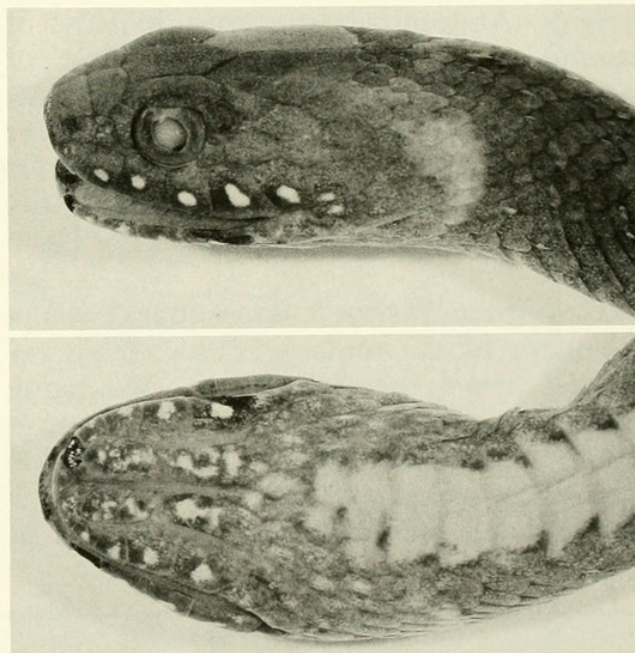


Figure 8. Head of the holotype of *Tachymenis boulengeri* Peracca (MZUT 1874) in dorsolateral and ventral views. Diagnostic features visible include the light postmandibular spot, light spotting on upper and lower labials, and dusky gular region with irregular light spotting.

[Valley of the Umbi River (Andrangoloka)] [= Andrangoloka; 19°02'S, 47°55'E; Fig. 9]. Holotype, MZUT 1874 (Figs. 7–8). Mocquard, 1909:47. Cadle (1996:401) discussed the type locality and the collection from which the type came.

Geodipsas boulengeri (Peracca): Boulenger, 1896:32, 1915:378; Mocquard, 1909:47; Boettger, 1913:373; Werner, 1925:112; Guibé, 1958:236; Brygoo, 1983:42, 55, 1987:23; UICN, PNUE, and WWF, 1990:224; Glaw and Vences, 1992:264, 1994:347.

Geodipsas heimi Angel, 1936:127–128 (type locality, “au long de la rivière Sahandrato, en amont de Tsianovoha” [along the Sahandrato River, upstream from Tsianovoha]). Angel (1936:125) described Tsianovoha as being “SSW of Fort Carnot and of the Ikongo Massif (alt. 600 m)” (= Tsianivoho; 21°57'S, 47°21'E; Fig. 9). Holotype, Muséum National d'Histoire Naturelle, Paris (MNHN) 1936.19, collected by Roger Heim in 1934 or 1935. Guibé, 1958:236; Brygoo, 1983:42, 55, 1987:23; UICN, PNUE, and WWF, 1990:222; Glaw and Vences, 1992:264, 1994:347; Raxworthy and Nussbaum, 1994:68. **New synonymy.**

Holotype (Figs. 7, 8). An adult male in good condition whose mensural and meristic characters are reported in Table 2.

Distribution (Fig. 9). Known from few specimens from the following localities on the eastern escarpment (*Specimens Examined*): the vicinity of the RNP and the nearby locality, Tsianovoho (type locality of *heimi*), Andrangoloka (type locality of *boulengeri*), “Pays Zafimaniry” (east of Ambositra), and from Perinet (= Andasibe; 18°56'S, 48°25'E; C. A. Domergue, *in litt.*). The recorded elevational range is 600 m (Tsianovoho) to approximately 1,400 m (Andrangoloka; see Cadle, 1996: fn. 6).

Geodipsas “*heimi*,” here considered a synonym of *G. boulengeri*, has been reported from the vicinity of Montagne d'Ambre (Raxworthy and Nussbaum, 1994; Glaw and Vences, 1994), but all specimens referred to *Geodipsas* “*heimi*” that I have seen from that area (*Key to*

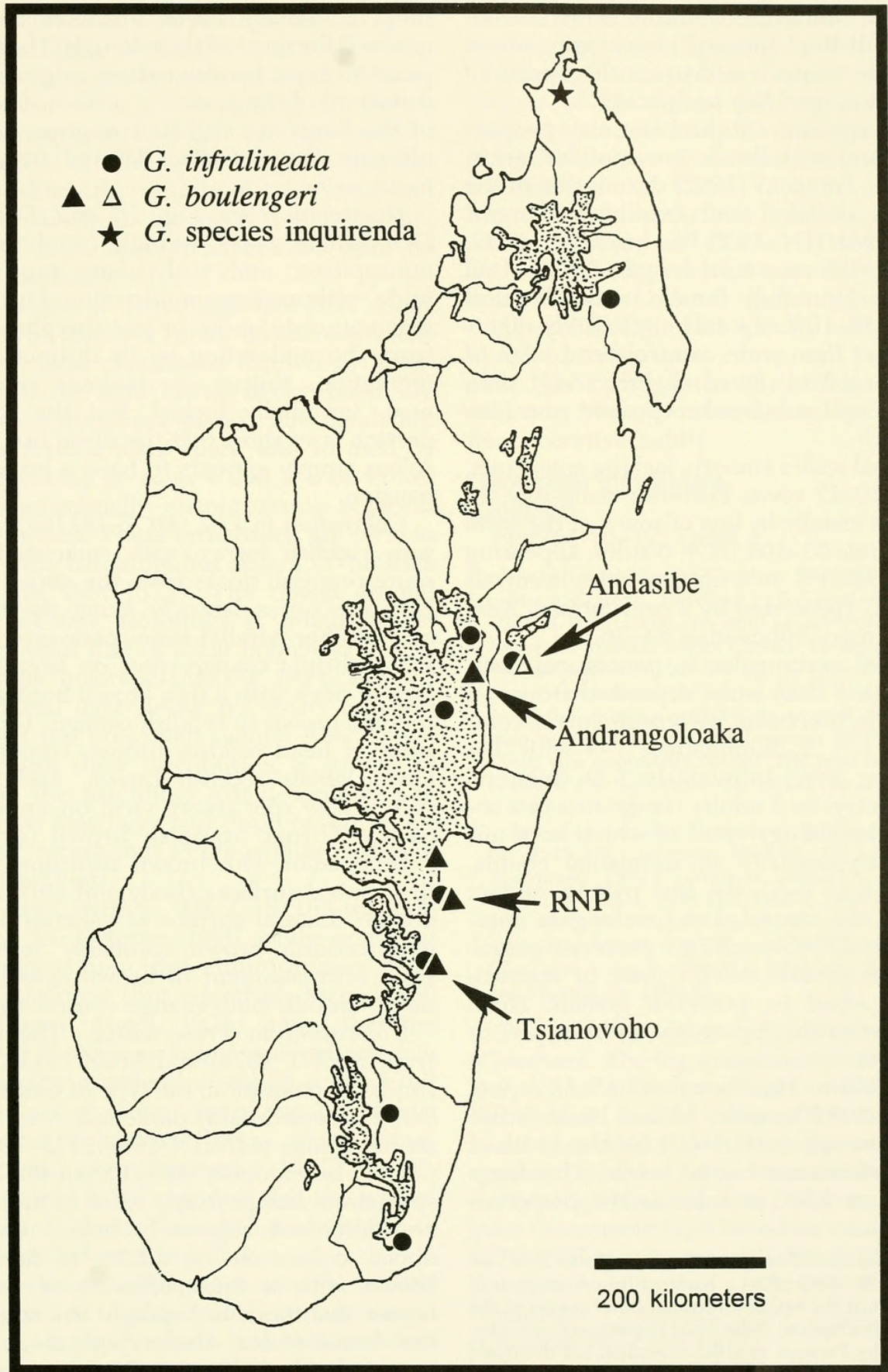
species and *Specimens Examined*: *Geodipsas* species inquirenda) are a distinct species that will be dealt with in a separate treatment. I do not include variation in these northern Madagascar specimens of “*heimi*” in my treatment of *boulengeri*, which I consider to be restricted, as far as presently known, to the eastern escarpment. However, given the few specimens that have appeared since its description more than a century ago, it would hardly be surprising that new specimens could significantly increase the known range of *boulengeri*.

Etymology. The species epithet is a patronym for George A. Boulenger.

Diagnosis. The light (orangish to yellowish in life), curved, postmandibular spots, light spots on the upper and lower labials and gular region, and dusky gular region with irregular light areas, are diagnostic features of *Geodipsas boulengeri* (Fig. 8); the RNP specimen had a brilliant orange venter in life but whether or not this is typical is unknown. The species is essentially indistinguishable from *G. zeny* in scutellational features, but aspects of coloration distinguish the two (see *Diagnosis* in the previous description of *zeny*). *Geodipsas boulengeri* has, in comparison with *G. infralineata* and *G. laphystia* (combined ranges for characters given), fewer ventrals (131–137 vs. >170) and subcaudals (24–36 vs. >50), a shorter tail that is not prehensile (12–16% of total length vs. 17–26% and prehensile), and a different coloration (see species accounts). In comparison to *G. vinckei*, *boulengeri* has fewer ventrals (131–137 vs. 161) and a different color pattern. *Geodipsas boulengeri* differs from specimens referred to *Geodipsas* species inquirenda from the vi-

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Figure 9. Distributions of species of *Geodipsas* (*boulengeri*, *infralineata*, and *Geodipsas* species inquirenda) discussed in the text. Type localities are as follows: Andasibe (= Perinet), *Geodipsas vinckei* Domergue (known only from the holotype); Andrangoloka, *Geodipsas boulengeri* (Peracca); Tsianovoho, *Geodipsas heimi* Angel. All plotted localities based on specimens examined, except for the open triangle for *boulengeri* (see *Distribution*). *Geodipsas infralineata* is reported from many additional localities in the literature (e. g., Glaw and Vences, 1994), but because of its previous confusion with *G. laphystia* these localities are not plotted; it has been reported as far north as the vicinity of Montagne d'Ambre (star). Shaded area is above 1,000 m.



cinity of Montagne d'Ambre (here considered a distinct species) in averaging about 13 fewer ventrals and in subtle aspects of coloration (see *Key to Species*).

Description. Measurements, proportions, and scutellation are summarized in Table 1. Peracca's (1892) description of the type is detailed and excellent.⁵ Largest male (MNHN 1936.19, holotype of *G. heimi*), 353 mm total length, 55 mm tail length. No adult female available. Tail length 12–16% of total length. Body slightly higher than wide; ventrolateral edge of body angulate. Head slightly wider than neck. Pupil subcircular (prolate; see *Discussion*).

Dorsal scales smooth, lacking apical pits, in 19–19–17 rows. Posterior scale-row reduction usually by loss of row 4 at the level of ventrals 83–108 ($N = 6$ sides; appearing as fusion of 3 + 4 on one side). Ventrals 131–137 (preceded by 2 preentrals). Anal plate single. Subcaudals 24–36.

Loreal rectangular to pentagonal, usually higher than wide, separated from eye by single preocular. Two postoculars; temporals 1 + 2. Supralabials 7–7 with 3–4 touching eye. Infralabials 8–9 (bilateral asymmetry) in 3 adults (range 6–9 in a series of hatchlings, most of which have unusual asymmetries in infralabial counts, e.g., 7–6 to 9–9); the first pair in contact behind the mental, 1–4 touching an anterior genial, 4–5 touching a posterior genial. Anterior genials shorter than, or approximately equal to, posterior genials. Head plates smooth, apparently without pits or tubercles.

Dentition. Maxillary teeth 15–18 + 2 ($\bar{x} = 16.3 \pm 0.95$; modes 17 and 16; $N = 10$). Diastema approximately $1.5\times$ the width of the posteriormost solid teeth. The fangs are about $1.5\times$ as large as the posterior-

most maxillary teeth and are deeply grooved for most of their length. There appears to be a narrow cutting edge on the distal end of the posterior surface. The tips of the fangs are slightly compressed. The ultimate fang is offset laterad from the tooth row.

Hemipenis (See Fig. 16 and *Detailed Description, Later*). Single (nonbilobed), noncapitate, and acalyculate; proximally nude, with a spinose midsection. Distal region spinulate, more or less sharply set off from the midsection by its distinct ornamentation. Sulcus spermaticus centrolinial, terminally forked, but the forked portion is so short that the distal tip of the sulcus simply appears to have a broad expansion.

Coloration in Life (MCZ 181163). Dorsum reddish brown with somewhat obscure orangish flecks from the nape to the tail, one series laterally along the flanks and another parallel series paravertebrally. Paired bright orange spots on lateral surface of neck with a thin brown border. Iris reddish brown to reddish orange. Top and sides of head reddish brown. Upper and lower labials reddish brown, each with pale yellow spot (more vivid on upper labials). Throat orangish brown (orange ground color with brown suffusion). Entire ventral surfaces (body and tail) bright orange. Lateral surface of ventrals edged with reddish brown (probably resulting from encroachment of brown dorsal pigment laterally onto orange ventral scutes).

Coloration in Preservative. The holotype (MZUT 1874) and MCZ 181163 are similar in coloration; the type of *Geodipsas heimi* is considerably darkened. A series of six hatchlings (MNHN 1986.1373–78) appear to be naturally darker than the adult specimens and probably were in life; they are described separately below. Overall dorsal coloration of adults is medium brown with a fine suffusion of darker brown that tends to highlight the edges of the dorsal scales. Under high magnification, individual dorsal scales are marbled with brown and tan flecks and reticula-

⁵ The subcaudal count of the type (Table 2) is correct and is identical to a hand-written correction of the count in the MCZ library and other copies of the original description; these hand corrections, very likely made by Peracca or at his direction, are discussed by Cadle (1996:Remarks under *Liopholidophis doliocercus*).

tions. The labial and postmandibular spots and the light dorsal flecks are off-white. Gular region dusky with light spots. Venter off-white, with encroachment of brown dorsal pigment laterally. MNHN 1936.19 has a line of dark speckling (not discrete spots) down the middle of the venter and subcaudals from the neck to the tail tip; MZUT 1874 and MCZ 181163 have no such markings.

A series of hatchlings (MNHN 1986.1373–78) shows a series of narrow, interrupted, light crossbands formed by alignment of the light dorsal flecks; these are offset on the lower flanks. The bands are about 2 scale rows apart, and formed by light flecking on rows 4 and 7–8 on either side, occasionally encompassing adjacent rows as well. These crossbands are vivid in five of the hatchlings but absent in the sixth (MNHN 1986.1374). The dorsal ground color of the hatchlings is much darker brown than that of adult *boulengeri*.

In the holotype (MZUT 1874; Fig. 7), the dorsal light flecks are more apparent than in the preserved (adult) RNP specimen, and their distribution is similar to that in the hatchlings just described. The holotype may have had discrete, but interrupted, crossbands in life similar to that of the hatchlings.

Natural History. MCZ 181163 was collected 24 October 1990 while active at 1435 hours on a trail within primary montane rainforest (but selectively logged >50 years ago). Angel (1936) stated that the type of *Geodipsas heimi* was collected in “a marshy grassland along [a river],” but he did not give the time of day. No special defensive behaviors (biting, gland secretions, etc.) were observed in MCZ 181163, and Angel (1936) reported that the type of *G. heimi* “never [sought] to react or to bite” while being handled.

Geodipsas boulengeri is an infrequently encountered snake in its known range. Only a single specimen was obtained during the 1990–95 Ranomafana survey, and other localities, except for the series of

hatchlings from one locality, also are represented by single specimens.

Although there are few reported observations of *Geodipsas boulengeri*, several characteristics of body form suggest cryptozoic habits (see Cadle and Greene, 1993, for discussion). These include a short, blunt head little distinct from the neck, a relatively short tail (Table 1), and round body. Certainly, no characteristics of the body form of *G. boulengeri* suggest arboreal proclivities in this species as has been observed in *laphystia*, *zeny*, and *infralineata*. The rarity with which this species seems to be encountered may, in part, reflect secretive habits.

Geodipsas infralineata (Günther)

Figures 10–12; Table 1

Tachymenis infralineatus Günther, 1882:265 (type locality, “Eastern Betsileo”). *Inferred* holotype, BMNH 95.10.29.61, an adult female collected by Reverend William Deans Cowan. This specimen is *not* the specimen labeled as the type during the period immediately following World War II, and it bears this number probably as a result of a specimen mixup that occurred between 1896 and the 1940s (see comments below). The type is unquestionably the specimen illustrated by Boulenger (1896:pl. III, fig. 1).

Geodipsas infralineata (Günther): Boulenger, 1896:32, 1915:378; Boettger, 1898:89; 1913:271, 373; Mocquard, 1909:47; Werner, 1925:112; Mertens, 1933:273; Angel, 1936:127; Guibé, 1958:235; Brygoo, 1983:42, 55, 1987:23; Nicoll and Langrand, 1989:135; UICN, PNUE, and WWF, 1990:222; Glaw and Vences, 1992:264, 1994:346; Raxworthy and Nussbaum, 1994:68.

The Holotype of *Geodipsas infralineata* (Günther). During examination of the holotype and other specimens of *Geodipsas infralineata* in The Natural History Museum (London) (BMNH), I discovered an apparent mislabeling and misnumbering of the type specimen. I was, however, able to infer the correct type based on comparison of BMNH specimens with details given for the type by Günther (1882:265–266) and Boulenger (1896:32). Here I clarify this confusion over the type.

The specimen presently (but, I believe, erroneously) labeled “holotype” of *Geodip-*

sas infralineata is an adult female, BMNH 1946.1.7.20 (old number 82.5.8.1).⁶ My measurements and ventral/ subcaudal counts for this specimen are as follows: total length 679 mm, tail length 122 mm, ventrals 173, subcaudals 53. Günther's (1882) description gave the following for the holotype (and then the only specimen available): total length 31 in. (= 787 mm), tail length 6 in. (= 152 mm), ventrals 186, subcaudals 62. Boulenger (1896) reported ventral and subcaudal counts for the type as 187 and 62, respectively. Clearly, BMNH 1946.1.7.20 conforms poorly with these details.

However, my scale counts and measurements for another adult female, BMNH 95.10.29.61, conform well with the details reported by Günther and Boulenger for the type of *Geodipsas infralineata*: total length 761 mm, tail length 151 mm, ventrals 183.5 + 2 preentrals (= 185.5), subcaudals 61. I conclude that an apparent switch of specimens occurred sometime between 1896, when Boulenger's catalog was published, and the early 1940s, when types were evacuated to caves for safe-keeping. Because the specimens would have been untagged during the intervening period, the possibility of a mixup was greatly increased. When types were recataloged in 1946, the incorrect specimen was reinstalled in the type collection and subsequently tagged with the incorrect catalog number.

Additional circumstantial evidence that BMNH 95.10.29.61 is the type of *infralineata* is that, of the two specimens in question, this is clearly the one illustrated by Boulenger (1896:pl. III, fig. 1), as indicated by two unusual features: (1) a peculiar circular marking on the nape that has a pair of asymmetrical posterior "spurs" and (2) a distinct postocular stripe on the left

side (the one illustrated by Boulenger) that is connected to the dark markings on the dorsum of the neck. Neither of these features is evident in BMNH 1946.1.7.20, which has different dark neck and head markings. Boulenger seems to have used type material for illustrations in his catalogs when such specimens were available. Thus, the conjunction of the measurements, scale counts, and illustration virtually prove that BMNH 95.10.29.61 is the type of *Geodipsas infralineata* (Günther).

The scale counts for the other specimen, BMNH 1946.1.7.20, correspond to those Boulenger (1896:32) gave for the only other specimen of *Geodipsas infralineata* in the British Museum collection at that time: 172 ventrals and 55 subcaudals. Other details given by Günther and Boulenger on the holotype do not permit unambiguous association with either BMNH 1946.1.7.20 or 95.10.29.61. Hence, I infer that the correct original identity of BMNH 1946.1.7.20 is the specimen with similar ventral and subcaudal counts reported by Boulenger (1896), and its correct catalog number should be 95.10.29.61. The specimen now residing under number 95.10.29.61 is the holotype of *Geodipsas infralineata* (Günther) and would have originally borne the old number 82.5.8.1.

BMNH 95.10.26.61 is an adult female (measurements and basic scale counts already given), rather soft, and in fair condition. It is now faded to a dirty yellowish white, although narrow diagonal dark dorsal lines, a posterior middorsal dark longitudinal stripe, and a dark midventral stripe are still evident. Narrow, dark dorsal diagonals are evidenced by dark brown edges to the dorsal scales, which are otherwise beige; successive diagonals are separated generally by two scale rows (typical for other specimens I have examined) and are evident from the head to the vent (more distinct posteriorly). The skin has been peeled back from the cranium and mandible, and the posterior abdominal region and proximoventral tail regions have

⁶ Through consultation with Drs. E. N. Arnold and C. J. McCarthy, this specimen will be retained in the type collection with its current labeling as the holotype, but the inferred correct holotype (see later) will also be placed in the type collection.

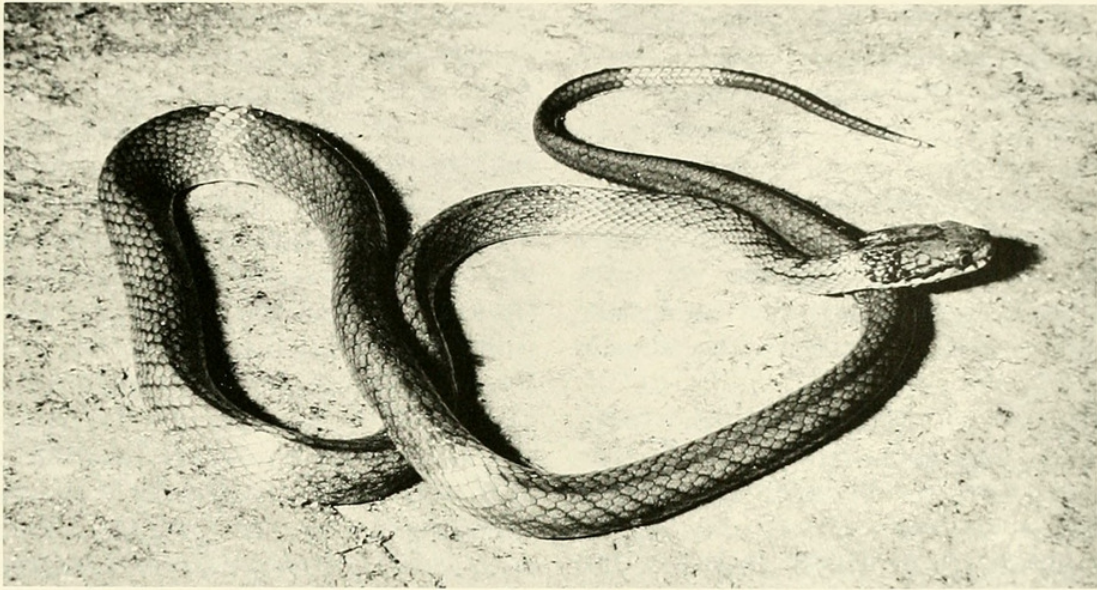


Figure 10. *Geodipsas infralineata* (MCZ 181153; total length 597 mm). Specimen from the RNP. The fine dark diagonals on the flanks are characteristic of most specimens of this species. The dark vertebral line and dark nape blotches are present in many specimens, but not universally.

been slit. The details of scutellation and pattern reported by Günther (1882) are essentially correct (differences as already noted above), although the pattern is now greatly faded and Günther did not mention the fine diagonal dark dorsal lines visible in the specimen; the last feature is here considered a diagnostic difference between *infralineata* and *laphystia* (see *Diagnosis* in the description of *laphystia*).

Distribution (Fig. 9; *Specimens Examined*). *Geodipsas infralineata* is widely distributed in the eastern rainforests and adjacent plateau, but its precise range will not be known until older records are re-examined to verify whether *infralineata* or *laphystia* was their basis. I have seen specimens unquestionably referable to *infralineata* from "mountains north of Fort Dauphin" (= Tolagnaro; 25°02'S, 47°00'E; MNHN 1986.1390) in the south to approximately latitude 18°S in the north (e.g., MNHN 1986.1392, 1978.91–92, 1978.94); all of these compare well with the type and to the diagnosis given later. One specimen from Marojezy (14°26'S) has an unusual pattern but is referred to *G. infralineata* for lack of a reasonable alternative (see *Coloration in Preservative*).

At least one specimen I examined confirms a locality on the high plateau (Manjakatempo, 19°20'S 47°26'E; MNHN 1957.731; another specimen is questionably from the plateau: MNHN 1986.1392; see *Specimens Examined*). Most specimens seem to be from upland rainforests, although the recorded elevational range is broad (300–2,000 m).

Glaw and Vences (1994) reported several localities from northern Madagascar from the vicinity of Maroantsetra to Montagne d'Ambre (15°30' to 12°30'S), and Raxworthy and Nussbaum (1994) listed *G. infralineata* for Montagne d'Ambre. Glaw and Vences, at least, included *G. laphystia* within their concept of *infralineata* (e.g., their figs. 514–515), so these records should be reexamined to confirm their identity.

Etymology. The species epithet refers to a narrow dark midventral line that is present in many specimens, including the holotype (Boulenger, 1896:pl. III, fig. 1b; Fig. 12).

Diagnosis. *Geodipsas infralineata* is larger than other species of *Geodipsas* (to >750 mm total length in males, >900 mm in females). It has a relatively high number

of ventrals (172–199) and subcaudals (53–77), a distinctly compressed body, and a prehensile tail. The typical pattern for most specimens (Fig. 10; see sections on coloration, later) is a series of fine dark diagonal lines on the flanks superimposed on a yellowish, grayish, or brownish ground color; the diagonals are formed by darkened edges to scale rows, and successive diagonals are usually separated by 2 scale rows.

Geodipsas infralineata differs from *vinckei* in averaging more subcaudals ($\bar{x} > 60$ in both sexes, vs. 45) and in lacking a light collar on the nape (present in *vinckei*). Domergue (1988) reported the body of *G. vinckei* as “cylindrical,” but the type (only known specimen) is rather desiccated and has the appearance of having a somewhat compressed body and, thus, may be similar to *infralineata* in this respect. *Geodipsas infralineata* is easily separated from *G. zeny* and *G. boulengeri* on the basis of both color pattern and scale counts (see Table 1 and species accounts for the latter species for details). *Geodipsas infralineata* is most easily confused with *G. laphystia*, which differs from *infralineata* primarily in having a series of longitudinal lines (rather than diagonals) on the flanks and in other scutellational and hemipenial characters; see the description and diagnosis of *laphystia* for details.

Description. Measurements, proportions, and scutellation are summarized in Table 1. Largest specimen a female (MCZ 181142), 933 mm total length, 168 mm tail length; largest male (MNHN 1978.90) 783 mm total length, 148 mm tail length. Tail length 17–23% of total length in males, 17–21% in females. Body strongly compressed, higher than wide, and with a strongly angulate ventrolateral edge; neck and anterior body somewhat attenuate. Head wider than neck. Pupil subcircular (prolate; see *Discussion*).

Dorsal scales smooth, lacking apical pits, in 19–19–17 rows. Posterior scale-row reduction usually by fusion of rows 3 + 4 at

the level of ventrals 114–129 ($N = 16$ sides); rarely fusion of rows 4 + 5 (both sides of 1 specimen). Ventrals 172–193 in males, 173–199 in females, usually preceded by 2 preentrals. Anal plate single. Subcaudals 53–77 in males, 53–68 in females.

Loreal rectangular to pentagonal, usually higher than wide, separated from eye by single preocular. Two postoculars; temporals 1 + 2. Supralabials 7–7 with 3–4 touching eye. Infralabials 9–9 ($N = 13$), 9–10 (4); or 8–9, 8–10, or 10–10 (1 each); the first pair in contact behind the mental, 1–4 touching an anterior genial, 4–5 touching a posterior genial. Anterior genials shorter than posterior genials. Head plates smooth, apparently without pits or tubercles.

Dentition. Maxillary teeth 15–18 + 2 ($N = 15$). Modal number of prediastemal teeth 16 ($N = 6$), followed by 15 and 18 (4 each) and 17 (1). Diastema very short, equal to or less than the width of posterior solid maxillary teeth. The fangs are deeply grooved, about twice as large as the posteriormost solid teeth, have a narrow knifelike posterior edge distally, and are slightly compressed at the tips. The ultimate fang is offset laterad from the tooth row.

Hemipenis (See Fig. 17). Single (non-bilobed), noncapitate, and acalyculate; proximally more or less nude, having a spinose midsection, and distal spinulate region that forms a more or less distinct head. Sulcus spermaticus centrolinal, forked distally for approximately 20% of its length, and not reaching the apex of the everted organ. The asulcate side bears 2 rows of large, hooked spines, the rows slightly diverging distally and each having 4 spines.

Coloration in Life (See Glaw and Vences, 1994:pl. 336). *Geodipsas infralineata* is highly polymorphic in coloration, even within the limits of the RNP. The color tones do not appear to be correlated with size or sex, although smaller individuals tend to be of lighter shades than larger ones having similar tones. Although I

have seen live specimens only from the RNP and from the vicinity of Midongy du Sud (MCZ specimens listed in *Specimens Examined*), coloration of specimens from the latter locality ($N = 2$) was within the range of colors seen in the RNP ($N = 7$). My description of colors in life are based on these specimens.

The general dorsal ground color is pale yellow or deep yellow, medium brown, grayish brown, or dark grayish brown. Most specimens have some indication of narrow dark brown or blackish diagonal lines on the flanks from the neck to the tail base. These diagonals extend from the vertebral scale row posteriorly, following a suture line between 2 dorsal rows, down to row 3 or 4 from the ventral plates. The bilateral arrangement of the diagonals is symmetrical, so that when viewed middorsally pairs of diagonals on either side form narrow chevrons. Successive diagonals are separated by 2 dorsal rows, although occasionally another diagonal may be intercalated or an extra scale row may be "skipped."

Many specimens have a middorsal series of dark dashes or dots that may fuse posteriorly to form a dark vertebral line. Most specimens have some indication of a dark postocular bar or streak extending from the posteroventral edge of the eye, across the upper edge of the posterior supralabials, and ending at the jaw angle. A pair of dark nape spots, as well as a dark streak along the interparietal suture, may be prominent or indistinct (Fig. 10). Iris grayish brown to yellowish brown.

Ventral ground color whitish to yellow, occasionally with an orange suffusion, and with varying amounts of dark (brownish to grayish) flecking, spotting, or suffusion. The dark ventral spots or flecks often concentrate toward the midventral line posteriorly, forming a line of spots or an unbroken midventral line (Fig. 11). After a brief interruption at the vent, the line continues to the tail tip; although often discontinuous anterior to the vent, the midventral line is usually more or less contin-

uous on the tail, although of variable width. In individuals with a brownish to grayish dorsal ground color, the dorsal color encroaches laterally onto the ventral scales.

The lack of correlation between dorsal coloration and either size or sex is emphasized by comparison of several specimens with contrasting colors: Of the 2 largest specimens, both females, one (MCZ 181147; SVL 765 mm) has a dark grayish brown ground color, whereas the other (MCZ 181160; SVL 713 mm) is bright yellow, somewhat darkened by brownish suffusion. A much smaller male (MCZ 181153; SVL 460 mm) is similar in coloration to MCZ 181147, whereas another male of similar size (MCZ 181157; SVL 491 mm) had an overall yellowish ground color.

The following color notes for particular specimens give additional details and characterize the color variation further.

MCZ 181147 (female, SVL 765 mm): Dorsum gray-brown with heavy black speckling, tending to form ill-defined vertebral stripe along most of body. From the vertebral line, narrow blackish diagonals extend posteriorly along dorsal scale sutures, reaching approximately the third dorsal row; successive diagonals separated by 2 scale rows. Ground color of top of head similar to dorsum, with paired black nape patches (not very distinct). Black postorbital stripe to corner of mouth. Venter dull white with black squarish spots concentrated midventrally and forming a line. Chin, throat, and anterior venter whitish without markings (Fig. 11).

MCZ 181149 (female, SVL 661 mm): Dorsum brown, but under magnification each scale is minutely mottled with brown/grayish brown. Interrupted vertebral black stripe beginning about midbody and continuing to tail tip; narrow dorsal diagonals as in MCZ 181147. Scattered black flecks on anterior $\frac{1}{2}$ of dorsum. Iris reddish brown. Top of head brown flecked with black. A pair of brown nape blotches slightly darker than ground color. Upper

labials brownish cream flecked with black. Indistinct black postorbital bar to corner of mouth. Lower labials and throat creamy white flecked with dark brown. Venter anteriorly dull cream, with yellowish wash posteriorly (last $\frac{2}{3}$ of body), heavily speckled with dark brown. Lateral edges of ventrals brown. Posteriorly on body and tail, dark pigment of ventrals concentrated medially, giving impression of irregular mid-ventral stripe. Vague black ventrolateral stripe on tail. Subcaudals creamy with dark brown/blackish midventral stripe.

My other notes on individual specimens describe the dorsal ground colors as rich yellowish to orangish brown (MCZ 181155), tan with yellowish wash (MCZ 181156), or dark grayish brown (MCZ 181153). The ventral ground colors were usually pale yellow, but occasionally dirty white heavily speckled with dark brown/gray (MCZ 181153), or had an orange wash that intensified posteriorly (MCZ 181155).

Coloration in Preservative. Dorsal ground color yellowish, gray, brown, or grayish brown. Many scale borders outlined in black, often forming narrow chevrons, a dark network, a pair of lines on the flanks, or a middorsal line (sometimes a combination of these). A narrow dark postocular stripe extending across top of posterior supralabials and ending at the jaw angle. Ventrals and subcaudals pale yellow or whitish with a median series of punctations or a median line; outer edges of ventrals often with dark markings forming a more or less continuous line at border between ventrals and dorsals.

In addition to considerable variation in coloration in life, *Geodipsas infralineata* also shows much variation in overall dorsal pattern, but I have detected no geographic trends. Some specimens are virtually unicolor dorsally (e.g., Glaw and Vences [1994:pl. 336], MNHN 1986.1391, BMNH 1946.1.7.20) and show no indications of darker markings. In other specimens, the dorsum is virtually unicolor except for a dark brown vertebral stripe from the head to the tail tip (e.g., Henkel and

Schmidt [1995:274] and MNHN 1947.7; this last specimen appears to have been sun-bleached and may have lost pattern elements, but the photograph in Henkel and Schmidt is of a live animal). In yet another specimen (MNHN 1978.93), the dark diagonals were manifested only by series of dark flecks, so that the snake appeared spotted and only by close inspection could the details of the diagonals be made out. Although I have referred these unusually patterned snakes to *Geodipsas infralineata*, additional study could demonstrate that other taxa are involved—a possibility that should especially be kept in mind given the previous confusion of *laphystia* with *infralineata*.

Natural History. Because of the confusion of *Geodipsas infralineata* with *G. laphystia*, it is impossible to discern with certainty to which species statements about natural history in previous literature apply. For example, Glaw and Vences' (1994) observation of active specimens of "*infralineata*" at night at the edge of a pool (Andasibe) and during rains (Manjakatompo) appear more typical of *G. laphystia* than of *infralineata*, based on comparison with my observations of habitat and behavioral differences between the two species (see species account for *laphystia*). Glaw and Vences also reported finding two specimens of *infralineata* in a Travellers' Palm (*Ravenala*) and in the trunk of a tree fern (both presumably inactive during the day, although not stated). Angel (1936) reported a specimen of *Geodipsas infralineata* found in a "grassy clearing in islands of degraded forest" at 1,220 m elevation.

All specimens I collected were from primary montane rainforest except MCZ 181157, which came from a relatively high-elevation (1,130 m) forest with a low canopy (6–8 m) and interspersed with grassy meadows; this habitat seems qualitatively similar to the high-elevation habitat reported by Angel (1936) and may be characteristic of some of the "plateau" localities known for *G. infralineata* (see *Distribution*). The following paragraphs ex-

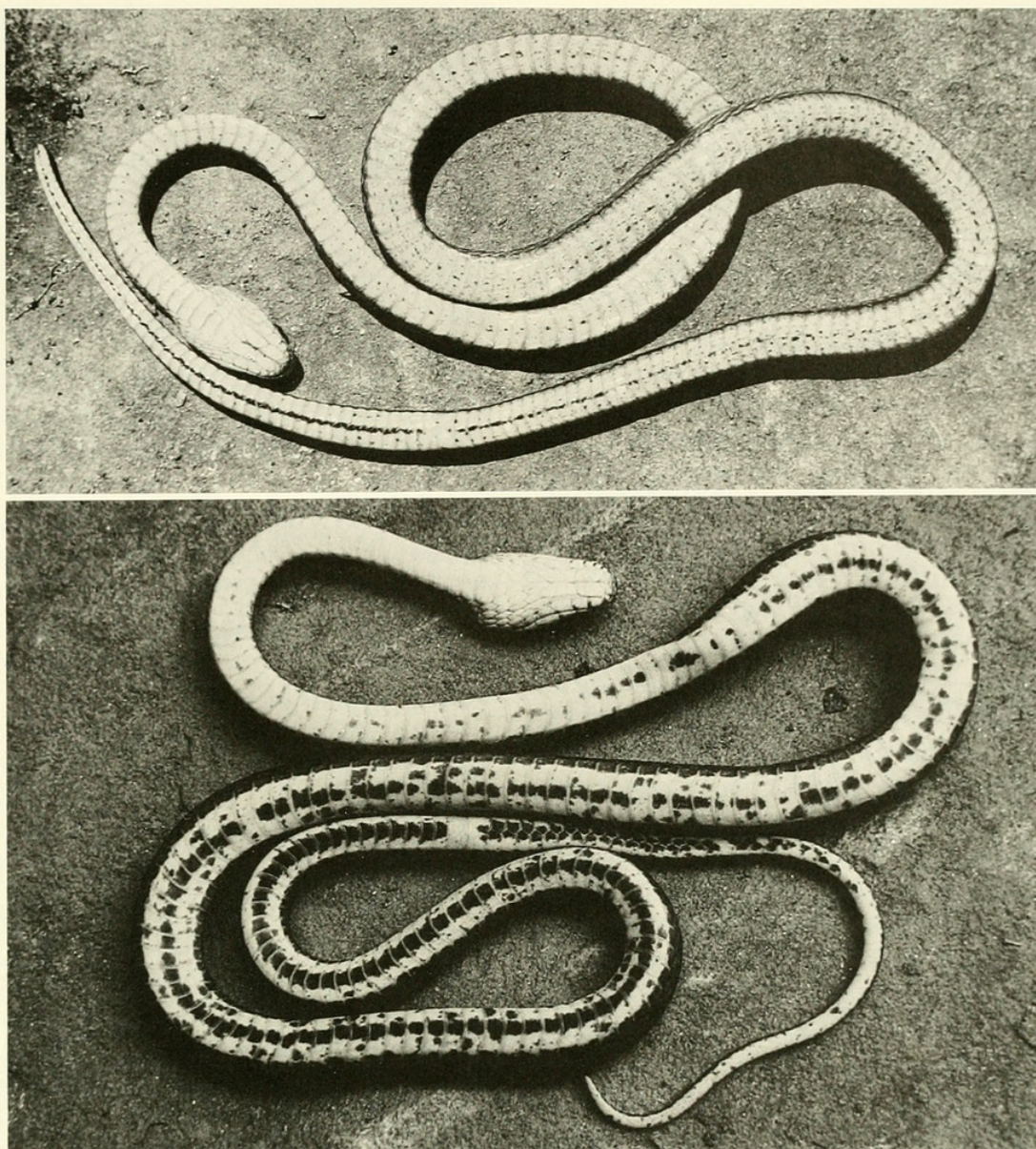


Figure 11. Variation in ventral pattern of *Geodipsas infralineata*. Top, MCZ 181154. Bottom, MCZ 181147. Both specimens from the RNP. Most specimens have some indication of a midventral line at least posteriorly (sometimes much more extensive). Some individuals have much more extensive ventral pigmentation than MCZ 181147.

tracted from my field notes discuss specific circumstances in which this species was encountered; with the exception of the first instance described, all observations were nocturnal.

The only specimen of *Geodipsas infralineata* found during the day (MCZ 181147) was collected by ornithologist Steve Zack. The snake was encountered during morning (daylight) hours within 1 m of a nest of *Tylas edwardii* (Aves: Vangidae) placed about 4 m up in a small tree; the nest con-

tained young. The snake, a large female (total length 933 mm), was being mobbed by the adult birds using calls and spread wing postures. A color slide taken by Zack of the head and anterior portion of the snake in ventral perspective shows the anterior 15 cm of the body dorsoventrally flattened (Zack, *in litt.*, reported that the anterior 20 cm of the body was flattened, not all of which was captured in the photograph). The snake was immobile during the period of observation. Such a display was not seen

in other individuals of *G. infralineata* that I observed.

Dorsoventral flattening of the neck is a very unusual defensive display for arboreal snakes. For example, Greene (1979) surveyed 77 genera (129 species) of snakes for three defensive displays (tail displays, lateral neck compression, dorsoventral neck flattening) and found no arboreal snakes using neck flattening (neck compression is a common display in arboreal snakes). He later (Greene, 1988) reported three species of arboreal elapids (*Dendroaspis* and *Pseudohaje*) that use neck flattening. Nevertheless, neck flattening as seen in *Geodipsas infralineata* seems to be a very uncommon display in arboreal snakes. (Greene [1988] also listed this behavior for the arboreal African colubrid, *Dispholidus*, but that seems to be based on a qualitatively different behavioral repertoire in which the neck is actually inflated in a horizontal plane.)

Other circumstances of capture of *Geodipsas infralineata* were as follows (all nocturnal observations). MCZ 181157 was loosely coiled about 2 m up in a small tree in high-elevation forest interspersed with meadows. MCZ 181149 was collected 6–7 m above ground in montane rainforest away from streams, and MCZ 181153 was in montane rainforest 4 m aboveground on a vertical climbing bamboo stem that was suspended from high in the overlying canopy. The only *infralineata* on the “ground” was MCZ 181160, a large female, which was crawling (not swimming) slowly across a small, flowing forest stream with its body submerged onto the stream bottom (20 cm deep) and its head projecting above the surface.

MCZ 181149 was observed on two occasions 30–45 min apart in more or less the same position, 6–7 m aboveground in a tree; although moving slowly in each case, the snake clearly had no strong directional orientation. Several other snakes on low vegetation exhibited the same sort of nondirectional movements, and for many specimens it seemed likely that they

could have been found in more or less the same positions over extended periods in a single night.

All observations suggest that *Geodipsas infralineata* is a primarily arboreal snake. Even in the absence of direct observations, however, this could be inferred from aspects of body form (see Cadle and Greene, 1993:table 25.1; Guyer and Donnelly, 1990). The body is relatively attenuate and compressed, with a narrow “neck” region and relatively broad head. The ventrolateral edge of the body is angulate and the tail is relatively long and strongly prehensile. All of these are characteristic of arboreal colubrids and suggest strong arboreal proclivities for *Geodipsas infralineata*. *Geodipsas infralineata* also has a bright yellow eyeshine, which is characteristic of some nocturnal snakes.

Only two food records were obtained for *Geodipsas infralineata*, both from the same specimen. MCZ 181149 (SVL 661 mm) contained an unidentified frog in its stomach and four tiny mammal claws and a few mammal hairs in its intestine (along with fragments of arthropod chitin, which may have been secondarily ingested). This specimen is one of the larger *infralineata* collected. I suspect that frogs (and possibly their eggs, as in *G. laphystia*) are the dietary staple of smaller individuals of *G. infralineata*, whereas larger adults probably consume frogs as well as mammals. Such ontogenetic broadening of the diet is known for many species of colubrids that consume ectothermic vertebrates at small body sizes (e.g., Greene, 1989). The identity of the mammal in MCZ 181149 can only be guessed but was likely one of the arboreal rodents known from Talatakely in the Ranomafana National Park (*Eliurus tanala* and *Brachytarsomys albicauda* [Muridae: Nesomyinae]). Based on size alone the claws were probably of a juvenile or nestling. Henkel and Schmidt (1995: 274) stated that *Geodipsas infralineata* (probably including *laphystia*) ate frogs but that “lizards and small rodents were

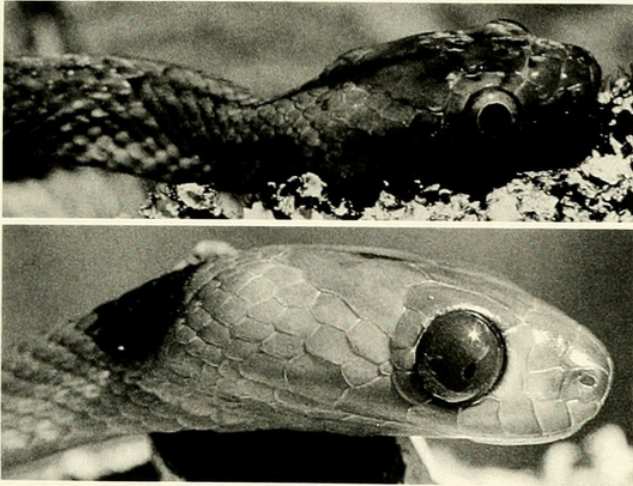


Figure 12. Prolate pupils in *Geodipsas laphystia* (top, MCZ 181387) and *Lycodryas* [*Stenophis*] *arctifasciatus* (bottom, MCZ 181431). In *Geodipsas* the pupil is a large, broad oval, whereas in *Lycodryas arctifasciatus* (but not *L. betsileanus*; see text) the pupil contracts to a small ellipse. These are qualitatively different from narrowly elliptical (slitlike) pupils (see Fig. 13).

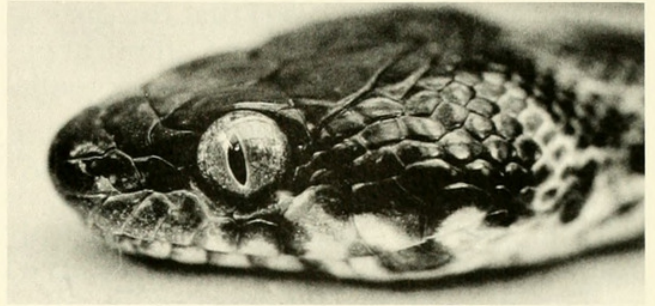


Figure 13. Elliptical pupil of *Madagascarophis* sp. (MCZ 181433). Note the strongly angulate dorsal and ventral borders in this slitlike pupil.

not scorned"; these observations were probably based on captive feeding records.

Geodipsas infralineata is presumably oviparous, as apparently are two of the African species of *Geodipsas* (Rasmussen et al., 1995) and most other Malagasy snakes for which that information is available (Glaw and Vences, 1994; Cadle, 1996). Henkel and Schmidt (1995) stated, without documentation, that *G. infralineata* lays eggs. Three adult females of *infralineata* (SVLs 661–765 mm; MCZ 181147, 181149, 181160) were collected, but only MCZ 181160, collected 13 January 1993, showed evidence of vitellogenesis (follicles <5 mm diameter). The other two females were collected from 25 October to 4 November 1990 and had nonyolk follicles.

No *Geodipsas infralineata* attempted to bite, although individuals struggled to escape upon capture. Most specimens emitted a foul-smelling secretion from the scent glands in the base of the tail.

Remarks. Two Malagasy names are used for *Geodipsas infralineata* in the Ranomafana region. *Mandochala* (män-dū'-chälä) was used near the village of Sahavan-drona (western edge of the RNP) and does not seem widespread. More commonly en-

countered was the name *lapata* (lä-pät'-ä). This name is also used for the other nocturnal arboreal colubrids known from the area, *G. laphystia* and *Lycodryas betsileanus*, and seems to be a general term for nocturnal arboreal colubrids (*G. infralineata* and *G. laphystia* are not distinguished by locals).

DISCUSSION

Pupil Shape in *Geodipsas*

My observations of pupil shape in Malagasy *Geodipsas* differ from those given in the literature and here I clarify these discrepancies. Boulenger (1896), Guibé (1958), and Glaw and Vences (1994) have described pupil shape of Malagasy *Geodipsas* as "round" or "circular" (in fact, this character is part of the definition of the genus given by Boulenger). However, most Malagasy specimens I examined are better characterized as "subcircular" in the sense of Myers (1984). In preserved specimens, the pupil shape varies from more or less round to prolate (narrowed laterally); the latter seems to be the usual condition. In daylight, the pupil contracts to a broad ellipse (Fig. 12; see also Glaw and Vences, 1994:pl. 336, fig. 515), but not to the extent usually connoted by the descriptor "elliptical," which refers to a qualitatively different pupil form in its fully contracted state. Rather than a broad prolate ellipse, truly elliptical pupils (e.g., in *Madagascarophis*, Fig. 13; see also Glaw and Vences, 1994:fig. 497) form a narrow vertical slit. I

concur with Myers (1984) that the distinction between subcircular and elliptical pupils is a useful one because of its potential systematic or functional significance.

The prolate pupil of Malagasy species of *Geodipsas* contrasts with that of the three African species, which seems to be truly round based on examination of preserved specimens of all three species in the MCZ (one of 16 *G. vauerocegae* examined appeared to have a prolate pupil). This is one character in which the African species differ from the Malagasy species.

Similar confusion in the literature concerning pupil shape exists for other Malagasy colubrid genera. For example, Guibé (1958:243) described the pupil of *Alluaudina*, which is possibly closely related to Malagasy *Geodipsas* (see later), as "vertically elliptical," although none of his figures, nor those of Domergue (1984) for *A. bellyi* or *A. mocquardi*, show such a shape. Domergue (1984) expressed similar confusion. Glaw and Vences (1994:330) commented "Pupil is circular [in *Alluaudina*], but has also been described as vertical elliptic." The confusion seems to stem from failure to distinguish subcircular and more strongly elliptical forms. Mocquard's (1894:9) original description was probably correct when he stated that *Alluaudina* has a "pupil a little elongate vertically," that is, subcircular in the sense of Myers (1984) (see also Domergue, 1984:539). A subcircular pupil shape is one of several characters shared by *Geodipsas* and *Alluaudina* that might suggest a relationship between these two genera (see later). Domergue (1984:539) remarked that one specimen of *Alluaudina bellyi* had a small pupil, weakly elongated vertically, and "could be compared to that of certain *Lycodryas*" (*Stenophis sensu* Domergue [1994] and Glaw and Vences [1994]). My study of *Lycodryas sensu lato* in the MCZ (including *betsileanus*, *arctifasciatus*, and *granuliceps*) suggests that these species also have prolate pupils. The pupil of *L. betsileanus* appears similar to that of *Geodipsas* (i.e., a broad prolate ellipse when contracted),

whereas the pupil of the other two *Lycodryas* contracts to a much smaller prolate opening (Fig. 12).

Osteology of *Geodipsas laphystia* (Hypapophyses and Skull)

Because of the scarcity of osteological material of species of *Geodipsas* in collections, I do not attempt comprehensive comparisons here. I record salient features of the skull and hypapophyses of *Geodipsas laphystia*, the only species whose osteology I have studied. I examined two skeletons of *Geodipsas laphystia* (MCZ 181164–65; both adult females ≥ 578 mm total length; the skull of MCZ 181164 is largely disarticulated). In the following account, when specific observations are reported for each specimen separately, the observations are given first for MCZ 181164, then 181165.

Vertebral Hypapophyses. Well-developed hypapophyses are present on all trunk vertebrae of *Geodipsas*.⁷ In *G. laphystia*, there are few substantive qualitative differences between the anterior and posterior hypapophyses aside from somewhat greater robustness of the posterior ones. Thus, this account refers specifically to the posterior hypapophyses. The overall form of the hypapophyses is sigmoidal: after a short projection posterovertrally from the centrum, the hypapophysis turns posteriorly so that the distal tip is directed posteriad. The distal tip is slightly bifid (not observed on anterior hypapophyses) and extends well beyond the condyle edge. A prominent anterior keel extends forward from the base of the hypapophysis to the rim of the cotyle. The ventral edges of the hypapophyses are a slightly flattened blade.

General Features of the Skull of *Geodipsas laphystia*. The skull of *Geodipsas laphystia* is lightly built and of ordinary

⁷ Other than superficial examination of *G. zeny*, *G. boulengeri*, and *G. infralineata* to verify the presence of posterior hypapophyses, I did not examine the morphology of these species in detail.

colubrid proportions (e.g., not showing unusual proportions of features such as the orbits or snout that are sometimes observed in burrowing or arboreal snakes).

Tooth Counts, Fangs, and Tooth-Bearing Bones. Maxillary teeth (left and right counts separated by a solidus for each specimen): 19/19, 20/19 prediastemal teeth, followed in each case by two enlarged grooved fangs. The fangs are approximately $1.5\times$ the size of the posterior solid tooth; they bear a prominent groove on the anterior face and narrow cutting edges on the distal $\frac{1}{3}$ of both anterior and posterior faces. Palatine teeth 12/11, 13/12. Pterygoid teeth 21/21, 24/25. Dentary teeth 27/28, 29/28. The maxillary diastema is approximately $1.5\times$ the width of the posteriormost prediastemal tooth in MCZ 181164 and approximately twice the width in 181165. The teeth on all bones are rather long, narrow, and strongly curved. The pterygoids are toothed nearly to the point of lateral flaring.

Skull Roof. The dorsal laminae of the nasals are greatly emarginated anterolaterally and posterolaterally (nasals abut the frontals only narrowly at the midline). The maxillary processes of the premaxilla are long and overlap the anterior ends of the maxillae to approximately the second maxillary tooth. The nasal process of the premaxilla is rectangular and somewhat concave and meets the nasals in a short transverse joint. The two posteromedial processes of the premaxilla are separated by a deep indentation. The postorbital narrowly, but clearly, is separated from the frontal by a short parietal flange. The parietal table is flat, bordered posterolaterally with prominent ridges for muscle attachment that converge posteriorly; posterior angle of the parietal broad, obtuse.

Orbital Region. The frontals extend ventrally to slightly overlap the dorsal margin of the trabecular grooves, but at no point are the grooves completely obscured from lateral aspect. Correspondingly, there is a short frontal step on the sphenoid. The frontals and parietal are not emarginated

around the orbital foramen, which is rather small; thus, only a short gap separates the ventral borders of the frontals and the anteroventral parietal edge at the orbital foramen.

Basicranial Region. The parasphenoid portion of the sphenoid is roughly triangular, with long, gradually converging sides stemming from the basisphenoid (i.e., no narrow cultriform process with relatively straight sides; see Cadle, 1996:448, 450). Ventrally, the parasphenoid bears a deep median groove extending the entire length of the parasphenoid. Anteriorly, the parasphenoid ends in a single point. In MCZ 181165, the fibrous tissue beneath the orbit and lateral to the sphenoid is slightly calcified, giving the appearance of bony flanges ventral to the orbits.⁸ The ventral surface of the sphenoid is without pronounced ridges except those bordering the posterior portion of its median ventral groove. The anterior Vidian foramina are barely within the lateral margin of the sphenoid. The trigeminal foramina are double on each side, separated by a prootic flange.

Hemipenial Morphology of Malagasy *Geodipsas*

I studied everted hemipenes of four species of Malagasy *Geodipsas* (*laphystia*, *zeny*, *boulengeri*, *infralineata*) and a retracted organ of *Geodipsas* species inquirenda (discussed in the species account for *boulengeri*). Thus, the only hemipenis left un-

⁸ I have observed such calcified tissue in skulls of many colubrids and suspect it may be widespread. However, most preparations that are thoroughly cleaned do not show this feature. When present, such calcified tissue appears as translucent flanges lateral to the parasphenoid, and not part of the parasphenoid proper, which has a very distinct lateral border. In other colubrids, however, the parasphenoid has well-ossified lateral flanges underneath the orbits that are an integral part of the bone (e. g., *Xenodon severus*, MVZ 163319; *Psammophis sibilans*, MCZ 53438). Whether or not these two types of parasphenoid flanges are homologous is unclear, but my impression is that the latter type is usually situated somewhat more posteriorly than the former.

studied is that of *G. vinckei*, a species known only from the type. I describe the organs of the first four species here. That of *Geodipsas* species inquirenda will be described in a separate report dealing with that species; however, its hemipenis is very similar to the hemipenis of *Geodipsas bou-lengeri*, with which it has been confused.

With a view toward broadening the basis of comparisons of these snakes with their African congeners, I also studied hemipenes of all three African species of *Geodipsas*. I first present descriptions of the Malagasy species, followed by a summary of their similarities and differences *inter se*. This is followed with a similar treatment for the African species. Finally, I compare the morphology of hemipenes of the Malagasy and African species.

Geodipsas laphystia (MCZ 181152, *Everted*; Fig. 14). (See also the discussion of hemipenial spine mineralization in the *Remarks* appended to the description of *laphystia*.) The hemipenis is single (non-bilobed), noncapitate, acalyculate; proximally nude on the sulcate side (proximally spinose on asulcate side), with a midsection bearing enlarged hooked spines on the sulcate and "lateral" sides (small spines on asulcate side), and spinulate distal tip; sulcus spermaticus centrolateral and forked distally. The everted organ has a total length of 10 mm and a somewhat bulbous midsection and is slightly tapered at each end. The sulcus spermaticus is a deep furrow that forks 7 mm from the base (hence, forked approximately 3 mm, or about 30% its length). The branches are broad open grooves bordered with spinules; the tip of each branch stops short of the apex of the everted organ, which is entirely covered with long spinules.

The sulcate surface is proximally nude, with spines beginning approximately $\frac{1}{3}$ of the way toward the tip, and continuous thereafter. Proximal spines are large, hooked, and robust, but they quickly grade into much smaller, narrow, straight spines or spinules. Beginning at approximately the point of sulcus division the spines

gradually become longer toward the tip (those at the apex longer than many of the small hooked spines around the midsection).

Between the sulcate and asulcate surfaces, the "lateral" surfaces of the organ bear small spines proximally and a dense battery of enlarged hooked spines on the lower midsection; these latter grade gradually into small straight spines distally.

The asulcate surface bears two very large hooked spines basally; these are positioned mesially on the asulcate surface and are the largest spines on the organ. These two spines are surrounded by a sparse array of small, slightly hooked spines. The small spines lengthen gradually and become straighter distally, occupying the entire asulcate surface except for a "lateral" series of three to four enlarged hooked spines on the lower midsection (these comprise the line of "lateral" hooked spines closest to the asulcate side).

Geodipsas zeny (MCZ 181161, *Everted*; Fig. 15). The hemipenis is single (non-bilobed), noncapitate, acalyculate; proximally nude, with a spinose midsection, and distally spinulate; sulcus spermaticus centrolateral and forked distally. The everted organ has a total length of 7 mm a somewhat bulbous midsection and is slightly tapered at each end. The sulcus spermaticus is a deep furrow that forks 5 mm from the base and has a total length of 6 mm (hence, forked approximately 1 mm, or about 17% of its length). The branches are broad open grooves bordered with spinules; each branch stops well short of the apex of the everted organ, which is covered with spinules.

On the midsection of the sulcate side is a battery of spines (but not a dense array), including a pair of enlarged spines proximally, with more distal spines only about $\frac{1}{2}$ as large. The spines grade into spinules, which densely cover the tip of the organ, beginning slightly proximal to the level at which the sulcus forks. The distal spinules are longer than proximal ones. The base of

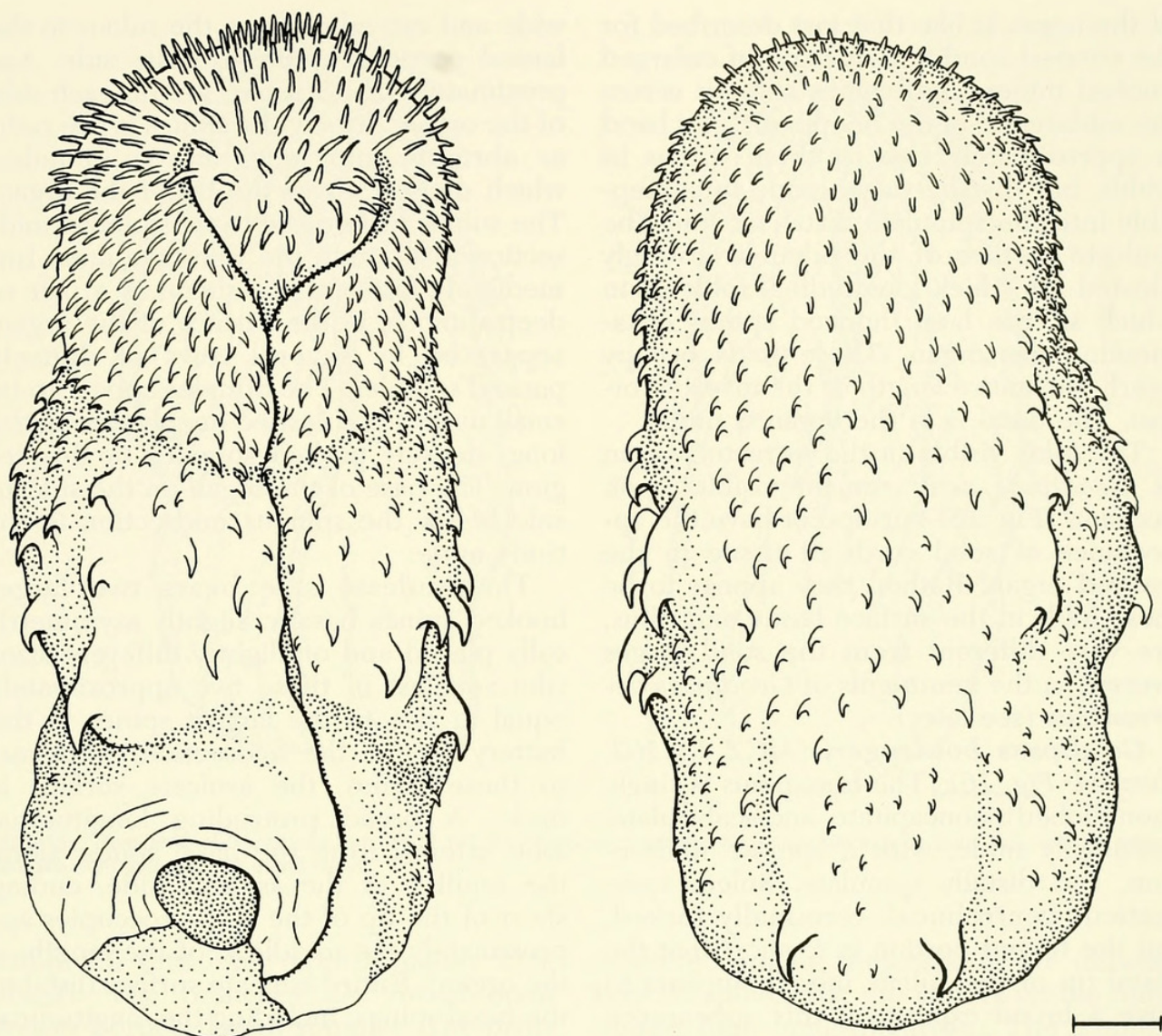


Figure 14. Hemipenis of *Geodipsas laphystia* (MCZ 180342; specimen from the RNP). Fully everted organ in sulcate (left) and asulcate (right) views.

the organ on the sulcate side is largely nude.

On the base of the asulcate side is a pair of enlarged, hooked spines, somewhat irregularly placed; other smaller spines occupy a median raised longitudinal lobe. Intervening spaces among these spines are nude or with minute hooked spines. The surface tissue of the asulcate side is slightly folded into several irregular longitudinal folds such that a couple of the enlarged spines appear to sit upon a flap comprising these folds. Distally the organ is densely spinulate, with spinules arrayed indistinctly in longitudinal rows; they become grad-

ually longer and denser toward the tip. The distal tip of the organ is flexed toward the sulcate side and bears long, straight spinules.

Geodipsas zeny (BMNH 95.10.29.62, *Retracted*). The retracted hemipenis of BMNH 95.10.29.62 was studied through a previous incision. The organ extends to the middle of the sixth subcaudal; the sulcus spermaticus divides at the middle of the fifth subcaudal and the branches extend virtually to the apex of the organ. The major retractor muscle of the hemipenis is divided for approximately 1 mm at its attachment to the organ. The ornamentation

of the organ is like that just described for the everted condition. A band of enlarged hooked mineralized spines extends across the midsection of the hemipenis; this band is approximately two to three spines in width, but distally these grade imperceptibly into the spinulate distal section. The asulcate surface of the organ is strongly pleated into thick longitudinal folds upon which sit the large hooked spines ornamenting the organ. These folds occupy nearly the entire length of the inverted organ. The basal $\frac{1}{3}$ of the organ is nude.

The folds visible in the retracted organ of *Geodipsas zeny* remain visible upon eversion (Fig. 15) but do not have the appearance of solid cords of tissue in the everted organ. Rather, they appear to be loose folds in the surface tissue and, thus, are very different from the solid ridges present in the hemipenis of *Geodipsas depressiceps* (see later).

Geodipsas boulengeri (MCZ 181163, *Everted*; Fig. 16). The hemipenis is single (nonbilobed), noncapitate, and acalyculate; proximally nude, with a spinose midsection, and distally spinulate. Sulcus spermaticus centrolineal, terminally forked, but the forked portion is so short that the distal tip of the sulcus merely appears to have a broad expansion; this appearance results from the sulcus ending distally essentially at the point of branching, hence somewhat broader than the more proximal portion. The sulcus is approximately 6 mm in length, the terminal division <1 mm. The tips of the sulcus branches stop well short of the apex of the everted organ (2 mm from the apex), which is covered densely with spinules. The everted organ has a total length of 9 mm. The distal tip of the organ is flexed toward the sulcate side.

A large protruding hemispherical lobe is present basally (Fig. 16). The distal surface of the lobe is covered sparsely with tiny spines; the proximal surface is nude.

The midsection of the organ bears a battery of moderately sized, hooked spines arrayed in a band approximately three spines

wide and extending from the sulcus to the lateral portions of the asulcate side. Approximately 12–15 spines are on each side of the organ; distally the spines grade rather abruptly into long, narrow spinules, which densely cover the tip of the organ. The sulcus forks distal to the spinous midsection just within the spinulate area. Immediately distal to the sulcus is a pair of deep dimples in the surface of the organ, separated by several rows of densely packed spinules. The dimples appear to be small nude areas nestled deeply among the long, densely packed spinules in this region. The base of the organ on the sulcate side below the spinous midsection is entirely nude.

The asulcate side bears two large, hooked spines basally, slightly asymmetrically placed and of slightly different sizes (the smallest of these two approximately equal in size to the largest spines in the battery around the midsection). Proximal to these spines, the asulcate surface is nude. A broad protruding longitudinal lobe extends from the basal spines along the midline of the asulcate side, ending short of the tip of the organ (occupies approximately the middle $\frac{1}{2}$ of the length of the organ). Entire asulcate surface distal to the basal spines, including the longitudinal lobe, ornamented with small hooked spines, distally grading gradually into spinules. The spinules are much longer on the sulcate than on the asulcate side.

Geodipsas infralineata (MCZ 181153, *Everted*; Fig. 17). The hemipenis is single (nonbilobed), noncapitate, and acalyculate; proximally more or less nude, having a spinose midsection, and distally spinulate; sulcus spermaticus centrolineal and forked distally. The everted organ is strongly flexed toward the sulcate side (probably due to contraction of the major retractor muscle internally) and has a total length of approximately 23–24 mm measured along the outer (long) flexure. The sulcus spermaticus is a deep furrow with a total length of approximately 12 mm; it forks distally, each branch of the fork approxi-

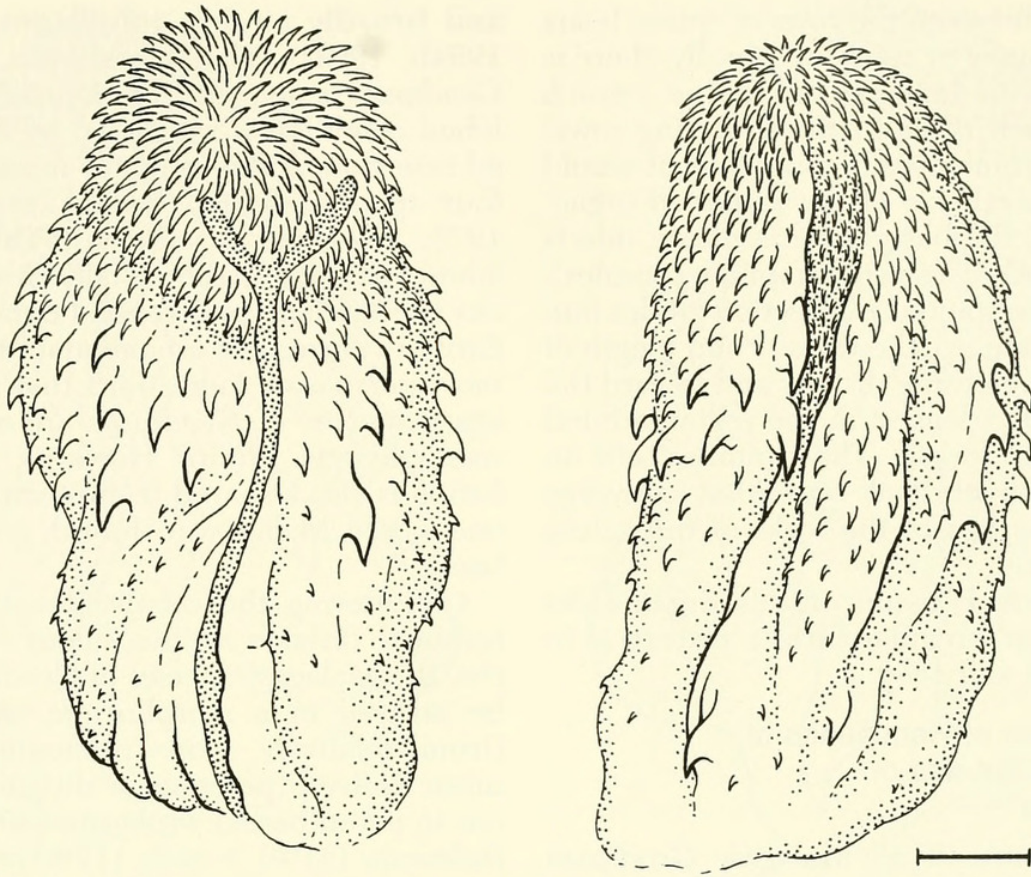


Figure 15. Hemipenis of *Geodipsas zeny* (MCZ 181161 [holotype]; specimen from near Midongy du Sud). Fully everted organ in sulcate (left) and asulcate (right) views.

mately 2.5 mm long (approximately 21% forked). The branches are broad open grooves bordered with spinules. The proximal undivided portion of the sulcus and the proximal portion of the forks is a closed canal formed by the appressed lips of the sulcus. The distal tips of the forks are open grooves that are somewhat flared and rounded distally (in form rather like elongate teardrops).

To investigate the nature of the major retractor muscle, the contralateral everted organ of MCZ 181153 and a single everted organ each of MCZ 181154 and MCZ 181157 were incised. The retractor muscle is terminally divided at its internal attachment to the organ.

The midsection of the sulcate and "lateral" sides bears a battery of moderately sized hooked spines, approximately 15–20 on each side, that increase gradually in size from the sulcate toward the asulcate side.

Scattered among these spines are minute hooked spines that are clearly visible only under high magnification. The spines grade into long, narrow spinules, which densely cover the tip of the organ beginning slightly proximal to the level at which the sulcus forks. The distal spinules are longer than proximal ones. The base of the organ below the spinous midsection is largely nude, but minute spinules border the proximal portion of the sulcus spermaticus.

The midsection of the asulcate side bears two longitudinal rows of greatly enlarged, hooked spines, the rows slightly diverging and each having four spines. Within each row the two proximal spines are the largest, the third is somewhat smaller, and the distal spine is about $\frac{1}{2}$ the size of the third. The distal spine is approximately the same size as the adjacent spines of the battery extending from the sulcate side.

The area between the rows of spines bears minute spines or spinules. Basally, there is a single moderate-sized spine (much smaller than those in the diverging rows) placed asymmetrically toward what would be the lateral side of the retracted organ; otherwise, the base of the asulcate side is mostly nude (scattered minute spinules). Distally the spinous midsection grades into the spinulate tip, the density and length of spinules increasing distally and toward the sulcate side (densest in the region around the sulcus forks). The spinules are in roughly longitudinal rows that converge around the tips of the forks of the sulcus spermaticus.

The surface tissue of this organ lacks pleats or an irregular surface texture as in *boulengeri* and *zeny*.

Comparison of Hemipenes of Malagasy Species of *Geodipsas*

Hemipenes of all Malagasy *Geodipsas* (hemipenis of *G. vinckei* unknown) are nonbilobed, noncapitate, and acalyculate. Other common features include enlarged hooked spines on at least the midsection (nude or with minute spines proximally); long, densely arranged spinules distally; a centrolineal sulcus spermaticus that divides distally; and a major retractor muscle that has a very short division at its insertion.

Of these shared characters, two are putatively derived and distinguish *Geodipsas* from most other Malagasy colubrids: (1) a simple (nonbilobed) hemipenis and (2) relatively distal or terminal division of the sulcus spermaticus. The alternative plesiomorphic states for these characters are a divided (bilobed) organ and a more deeply divided sulcus spermaticus (see Myers and Cadle, 1994:27–28, for discussion and further references). Each derived state has apparently arisen independently many times within colubrids, as indicated by their restricted presence in diverse clades worldwide (e.g., in some genera of neotropical “xenodontines” [Cadle, 1984a]

and broadly among colubrids [Cadle, 1984b, 1994]). That the simple organ of *Geodipsas* is derived from a primitively bilobed condition is suggested by the divided insertion of the retractor muscle in the four species studied herein (see Myers, 1973, 1974, for discussion). The nonbilobed hemipenis, the distally divided sulcus spermaticus, and general detailed similarity in form and ornamentation are the most persuasive indications that the Malagasy species of *Geodipsas* are a broadly monophyletic group. However, nonbilobation is also a shared feature with at least one other Malagasy colubrid genus (see later).

Considering the relative length of the terminal division of the sulcus spermaticus, the Malagasy species of *Geodipsas* can be arrayed in a morphocline, as follows (from relatively more plesiomorphic to more derived; percentage division of sulcus in parentheses): *laphystia* (30%) > *infralineata* (21%) > *zeny* (17%) > *boulengeri* and *Geodipsas* species inquirenda (< 17% each; in both species the sulcus appears barely divided [see Fig. 16], but accurate measurement is difficult on such small organs).

Cadle (1996:442–443) called attention to an unusual structure of the sulcus spermaticus in species of *Liopholidophis* and Malagasy *Geodipsas*. In both of these genera, the sulcus is very broad and deep in comparison to the sulcus in other colubrids examined (primarily Neotropical, but also representatives of most genera of Malagasy colubrids). In form it resembles an open trough rather than a discrete groove or line on the surface of the organ, as in other colubrids. Quantifying the difference is difficult because accurately measuring sulcus depth is problematical. However, some comprehension of the *Geodipsas* condition is offered by the observation that the sulcus in the specimen of *zeny* examined is nearly 1 mm deep on an organ whose overall diameter at the widest point is only about 3 mm. In the retracted organ, the sulcus is deep, with a smooth bottom,

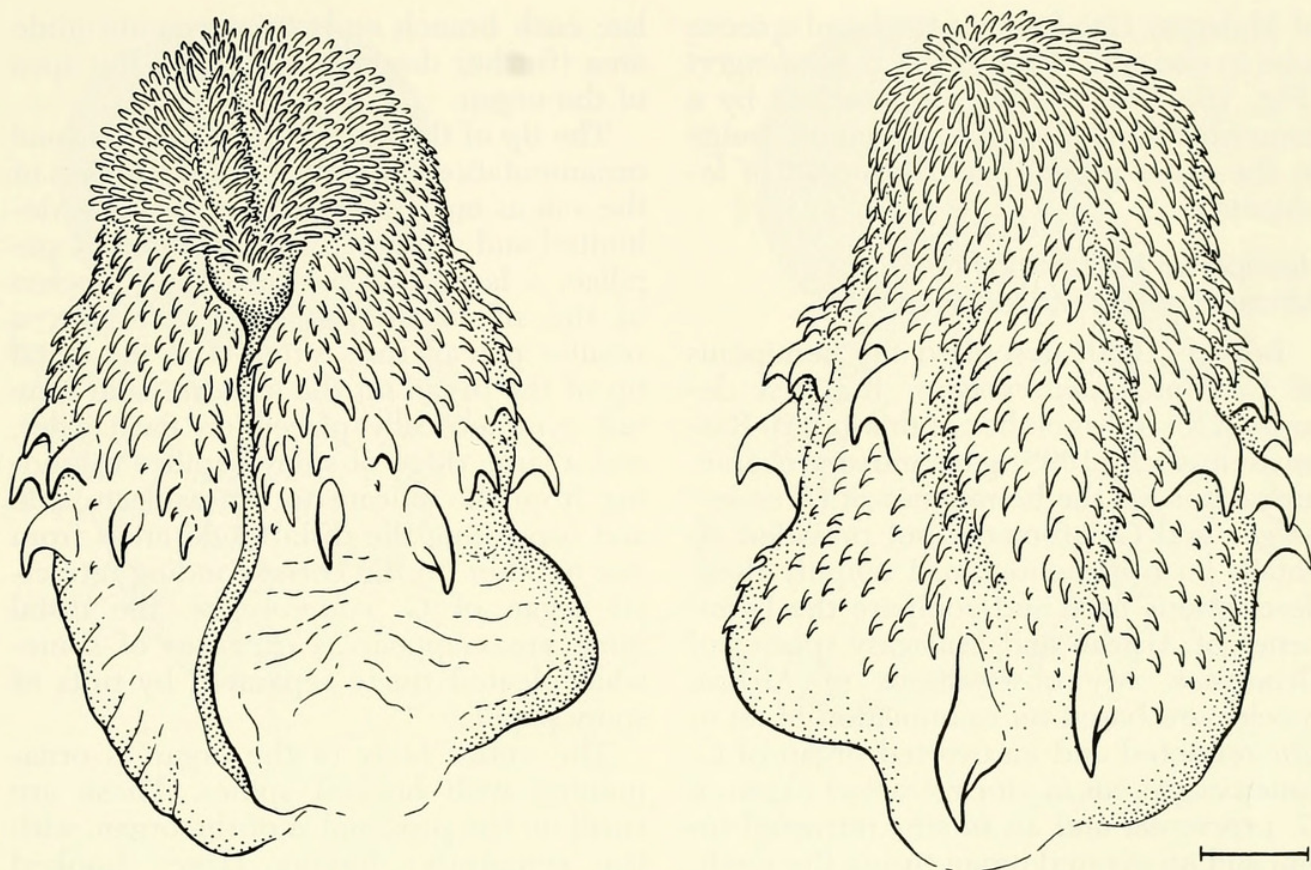


Figure 16. Hemipenis of *Geodipsas boulengeri* (MCZ 181163; specimen from the RNP). Fully everted organ in sulcate (left) and asulcate (right) views.

and surrounded by thickened fleshy ridges. The taxonomic and functional significance of this structure is, as yet, unclear.

Details of hemipenial morphology of all four described species of Malagasy *Geodipsas* are very similar. Although the organ of *infralineata* is strongly flexed (Fig. 17), and therefore appears different in configuration than the other species, this could be a preparation artifact. Aside from this, the ornamentation of the *infralineata* organ is similar to the other species. At first glance, the prominent diverging rows of greatly enlarged spines on the asulcate surface in *infralineata* seems unique among the species of *Geodipsas*. However, they also are manifested in the organs of *laphystia*, *zeny*, and *boulengeri*, although in these species the spines are much less prominent and they number only two or three in a row (Figs. 14–16). Thus, the distinctiveness of the asulcate spine arrange-

ment is not as apparent as it is in *infralineata*.

In having two enlarged basal spines on the asulcate side (Figs. 14–16), the hemipenes of *laphystia*, *boulengeri*, and *zeny* differ from those of *infralineata*, which has only a single spine. This does not seem to be an artifact of the organ of *infralineata* described because the contralateral organ of the same specimen, as well as both organs of three other specimens, had a single spine; however, one specimen of *infralineata* (MCZ 181157) did have a second minute basal spine on both organs in the same position as the second spine in organs of the first three species. The basal spine “missing” in *infralineata* compared to the other three species would be mesial in position in the retracted organ.

Aside from minor ornamentation differences, the only seemingly unique feature of the hemipenes among the four species

of Malagasy *Geodipsas* is the basal spinose lobe to one side of the sulcus in *boulengeri* (Fig. 16). This may be approached by a somewhat similar-appearing spinose bulge in the same position on the organ of *laphystia*.

Hemipenial Morphology of African Species of *Geodipsas*

Bogert (1940) described the hemipenis of *Geodipsas depressiceps*, the first described for any member of this genus. Rasmussen et al. (1995) gave cursory characterizations for the hemipenes of *G. vauerocegae* and *G. procterae* but provided no details on ornamentation. I amplify these descriptions here and compare the hemipenes of African and Malagasy species of *Geodipsas*. My observations of African species are based on examination of an *in situ* retracted and an everted organ of *G. vauerocegae*, an *in situ* retracted organ of *G. procterae*, and an *in situ* retracted organ and an everted organ (using the method of Pesantes [1994]) of *Geodipsas depressiceps*.

Geodipsas vauerocegae (MCZ 23289 and MCZ 23281, *Everted and Retracted, respectively*). The hemipenis is nonbilobed, acalyculate, and with large hooked spines from near the base to the tip of the organ. The sulcus spermaticus divides approximately at or slightly distal to the midpoint of the everted organ, with the branches extending to the tip on the same side of the organ (centrolineal in orientation). The retracted organ extends to the suture between subcaudals 8–9. The sulcus divides at approximately the suture between subcaudals 4–5 (thus, approximately 50% divided). The tips of the branches in the retracted organ end virtually at the apex. The everted organ is 9–10 mm total length, the sulcus dividing 5 mm from the base.

The sulcus spermaticus is bordered by prominent fleshy lips. Beyond the point of branching, the individual branches continue as deep grooves partly obscured by overhanging tufts of spines or spiny papil-

lae; each branch ends in a separate nude area (further described later) on the apex of the organ.

The tip of the hemipenis has an unusual ornamentation. The tips of the branches of the sulcus end in separate nude areas delimited and separated by tufts of spiny papillae: a large tuft between the branches of the sulcus on the sulcate surface, a smaller pair of tufts situated at the distal tip of the organ on the asulcate side (one tuft symmetrically placed on each side), and a large ridge of spiny papillae extending from the sulcate to the asulcate side and separating the distal nude areas from one another. In the corresponding retracted organ of *G. vauerocegae*, the distal nude areas appear as expanses of somewhat pleated tissue separated by tufts of spiny papillae.

The entire body of the organ is ornamented with hooked spines. These are small on the proximal $\frac{1}{3}$ of the organ, with the remainder having larger hooked spines. The spines are robust, have thick fleshy-looking bases, and on the body of the hemipenis are arrayed in rather regular oblique rows. Spines in large patches (each containing 25–30 spines) on either side of the sulcus spermaticus and “sides” of the organ are larger than those on most of the asulcate side. A patch containing seven to eight enlarged spines is placed mesially at the base of the asulcate side. Aside from these differences there is little proximodistal or sulcate/asulcate difference in the density of spine distribution (except apically), although there is slightly greater basad extension of the enlarged spines on the sulcate and asulcate than on the “lateral” sides. The area between the forks of the sulcus is occupied by large spines overhanging from the apical tuft of spines in this region.

Geodipsas procterae (MCZ 20188, *Retracted*). The hemipenis is nonbilobed, acalyculate, and with large hooked spines from near the base to the tip of the organ. The retracted organ extends to the suture between subcaudals 10–11. The sulcus

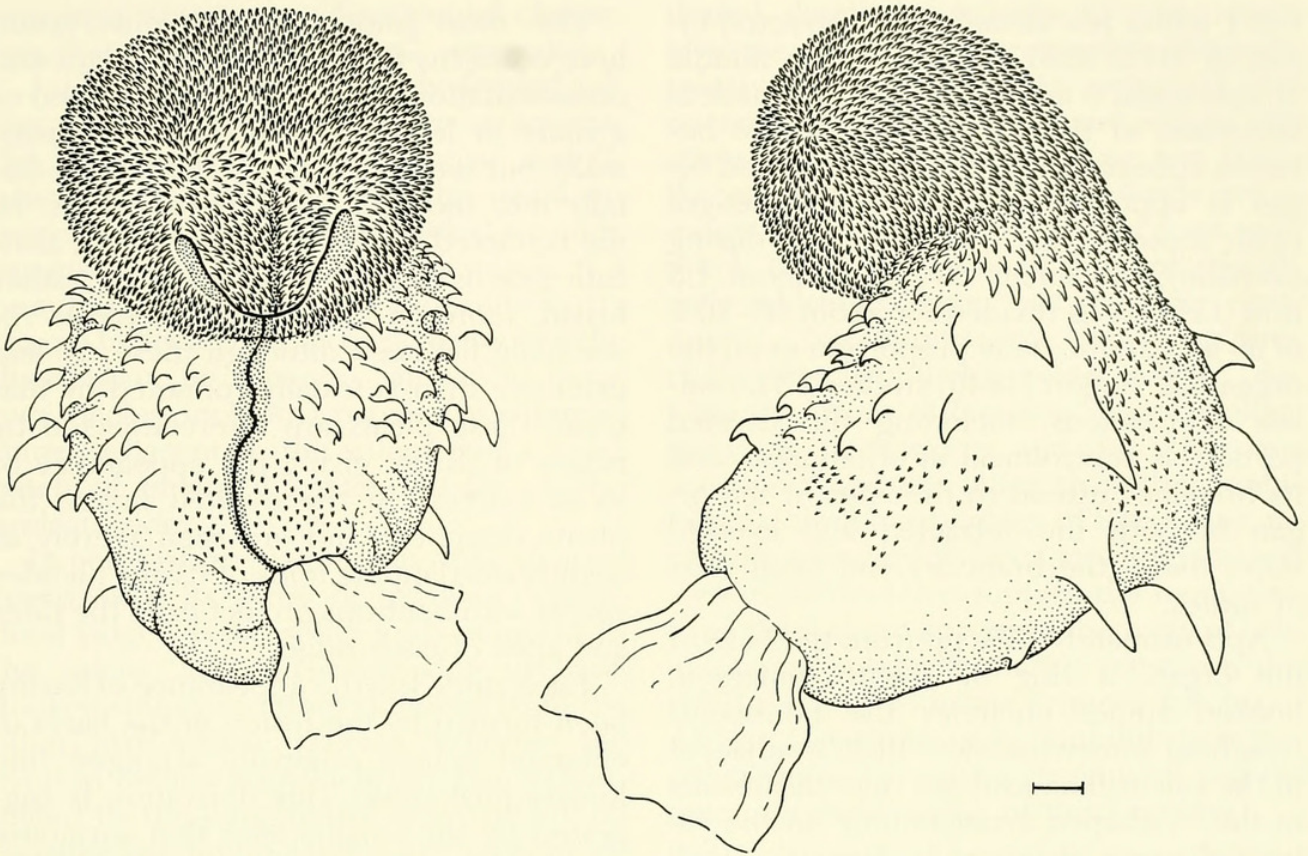


Figure 17. Hemipenis of *Geodipsas infralineata* (MCZ 181153; specimen from the RNP). Fully everted organ in sulcate (left) and asulcate (right) views. The asulcate view is shown in three-quarters view to accommodate the strong flexure of this particular organ. The flared tissue at the base of the organ is simply the tissue below the ligature tying off the base.

spermaticus divides at the suture between subcaudals 4 and 5 (approximately 65% divided) and extends distally in the lateral wall of the retracted organ (centrolineal in orientation); the branches extend to separate nude areas on the apex of the organ. The spines are much denser on the sulcate than on the asulcate side, are present between the branches of the divided sulcus, and appear to be arranged roughly into longitudinal rows. The form of the spines and the relative distribution of spine sizes appears similar to that described for *G. vauerocegae*, including the presence of a patch containing seven to eight enlarged spines basally on the asulcate side. As in *G. vauerocegae*, the sulcus branches end in nude areas separated by tufts of spines, although the nude portions seem less extensive than in *vauerocegae* (but perhaps would be equivalent upon eversion). The distal ornamentation, spine size and distri-

bution, and overall appearance of the hemipenis of *G. procterae* are probably very similar to that of *G. vauerocegae* in the everted state.

Geodipsas depressiceps (MCZ 9261, *Retracted and Everted*). Bogert's (1940: 38) description of the hemipenis of *G. depressiceps* (based on a specimen from the Congo) is here repeated in its entirety: "Not bifid [i.e., nonbilobed], extending to the seventh caudal, but with the sulcus bifurcating at the second. Near the base are about thirteen slightly enlarged basal hooks in a V-shaped arrangement, with the apex distally at the sulcus immediately anterior to its division. From each basal hook there extends a ridge surmounted with spinules, the ridges becoming less apparent at the distal end, which is ornamented with slender spines."

My observations of MCZ 9261 (from Cameroon) agree essentially with Bogert's,

but I add a few details. The retracted organ of MCZ 9261 extends to the middle of subcaudal 6 and the sulcus spermaticus bifurcates at the level of the suture between subcaudals 2 and 3. The everted organ is approximately 6.2 mm in length (with some of the base damaged during eversion); the sulcus divides at about 1.5 mm (i.e., sulcus divided for about 65–70% of its length, the same proportion as on the organ that Bogert [1940] studied). The sulcus spermaticus, including the divided portion, is centrolineal in orientation, and its branches extend to the apex of the organ in both the retracted and everted state; there, the branches end amid tufts of spines.

Approximately 25% up from the base of the organ, a ring of slightly enlarged, hooked spines encircles the hemipenis (reaching somewhat more distally adjacent to the sulcus than asulcate side; this results in the "V-shaped arrangement" in the retracted organ observed by Bogert). Small spines ornament the portion of the organ proximal to this ring. The body of the organ is ornamented with thickened ridges that bear small spines at their apexes; these ridges mostly extend from the slightly enlarged basal spines, as observed by Bogert. There are approximately 10 such ridges in MCZ 9261. Three of the ridges are more prominent than the others: the pair bordering the outer edges of the sulcus spermaticus, and the ridge separating the branches of the sulcus from its point of division to the apex. Although single for most of its length, the latter ridge distally divides into two portions that parallel the respective sulcus branches. Dense arrays of long, narrow spines occupy the longitudinal strips of tissue between the ridges; these are more or less straight or have bent tips. Adjacent to the base of the sulcus is a discrete series of three or four short folds of tissue that are covered with a dense array of small hooked spines. Similar spines generally cover the base of the organ proximal to the encircling ring of enlarged hooked spines.

The most important new observation here concerns the nature of the ridges and ornamentation. Each ridge is composed of a more or less solid cord of tissue proximally but tends to become subdivided distally into more or less oblique pleats. In the retracted organ, one ridge on the asulcate side is distally produced into rather broad, more or less transverse pleats resembling flounces, although these are less extensive than is usually connoted by that term; these pleats are interconnected by ridges of tissue, giving the appearance of loose calyces. In the everted organ, the pleats disappear and are seen merely as slightly overlapping folds of tissue. Slender spines with bent tips project from the sides and apex of each ridge.

Each ridge has the appearance of having been formed by the fusion of the bases of enlarged spines originally arranged into longitudinal rows. This derivation is suggested by the small spines that surmount the ridges, as if only the tips of originally separated elongate spines are exposed above the fused tissue comprising the ridges. Moreover, with high magnification and proper lighting, the bases of individual spines comprising the ridges can be seen as denser areas of tissue. In addition to the spines on the ridges, long, narrow spines occupy the longitudinal strips of tissue between the ridges.

Comparison of Hemipenes of African Species of *Geodipsas*

The hemipenes of all three African species of *Geodipsas* are nonbilobed, acalyculate, and ornamented with spines from the base to the tip. The sulcus spermaticus is deeply divided in all three species (50% in *Geodipsas vauerocegae*, 65–70% in *G. procterae* and *G. depressiceps*). The branches of the divided portion of the sulcus in all three species diverge slightly and end at the apex of both retracted and everted organs; the orientation is centrolineal. *Geodipsas vauerocegae* and *G.*

procterae share more hemipenial characters than either does with *G. procterae*.

Aside from the more deeply divided sulcus spermaticus in *Geodipsas procterae*, the hemipenes of *G. vauerocegae* and *G. procterae* are very similar. The distal ornamentation of the lobes, including nude expanses separated by tufts of spines, is a peculiar, probably derived, similarity shared by these two species. Moreover, the distribution of spines is similar in these two species, including patches of enlarged spines adjacent to the sulcus and a small patch of enlarged spines basally on the asulcate side.

In contrast, the hemipenis of *G. depressiceps*, with its series of peculiar longitudinal ridges, basal spiny folds adjacent to the sulcus, and encircling ring of basal hooked spines, is rather different from the other two African species. Whereas the everted hemipenis of *depressiceps* is dominated by the longitudinal spiny ridges, no features resembling those are seen in either *vauerocegae* or *procterae*. I detected no detailed similarities in ornamentation between *depressiceps* on the one hand, and the two east African species of *Geodipsas* on the other, that suggest a special relationship between these two groups of species.

The overall form of individual spines also differs between *vauerocegae* and *procterae* on the one hand and *depressiceps* on the other hand. Except for the basal ring of spines, in *depressiceps* the spines are long, narrow, and either more or less straight or (more frequently) bent at the tip. In the former two species, the spines are short, thick, and strongly hooked and have thick, somewhat fleshy-appearing bases. The differences in spine morphology alone result in quite different superficial appearances of the hemipenes of *vauerocegae* and *procterae* compared to *depressiceps*.

The special hemipenial similarities (i.e., apical morphology and patterns of spine distribution) shared by *Geodipsas vauerocegae* and *G. procterae*, as well as their

shared detailed similarity in spine morphology and their biogeographic proximity relative to *depressiceps*, suggest that *vauerocegae* and *procterae* are closest relatives. Of course, whether or not these three species of African colubrids are a monophyletic group remains an open, and much larger, question that is not specifically addressed here (but see later comments). No hemipenial characters preclude this hypothesis being correct, despite the strong differences in morphology between *depressiceps* and the other two species. However, other than the nonbilobed overall morphology of the organs, no clearly apomorphic hemipenial characters were identified that support the monophyly of these three species. Discovery of other African colubrids sharing putatively derived features with one or more species of African *Geodipsas* (e.g., nonbilobation, peculiar ridges, or apical structures) will require reconsideration of this question.

Comparison of Hemipenes of African and Malagasy Species of *Geodipsas*

The hemipenes of African *Geodipsas* are similar to the Malagasy species in being nonbilobed (simple) and having a divided sulcus spermaticus that is centrolineal in orientation. Otherwise, the details of structure and ornamentation are rather different in the two geographic groups.

In the Malagasy species, enlarged, hooked spines are sparsely distributed basally and around the midsection of the organ, but distally these grade abruptly into long, more or less straight spinules that densely cover the distal tip of the organ. Thus, the distal ornamentation of the organs in the Malagasy species is quite different from the more proximal ornamentation (see Figs. 14–17), resulting in a distinctively ornamented head region. In the African species, enlarged hooked spines cover the entire surface of the hemipenis (*vauerocegae* and *procterae*), or the body of the organ is covered with longitudinal, spine-bearing ridges (*depressiceps*). Al-

though in *vauerocegae* and *procterae* the tip of the hemipenis bears nude regions where the branches of the sulcus terminate, no distinctively ornamented head region occurs.

The African and Malagasy species of *Geodipsas* also differ in several aspects of the morphology of the sulcus spermaticus. The terminal divided portion is shorter in the Malagasy species ($\leq 30\%$ the length of the sulcus) than in the African species ($\geq 50\%$) (see preceding descriptions for details). More basal division of the sulcus spermaticus appears to be plesiomorphic within many clades of colubrids (reviews in Myers, 1973, 1974; Myers and Cadle, 1994). Increasingly distal division, or shortening of the individual branches to give the appearance of more distal division, is a derived state compared with basal sulcal division. Thus, in this respect the Malagasy species of *Geodipsas* are more derived than their African congeners.

Perhaps correlated with shorter sulci spermatici in the Malagasy species, the distal tips of their sulci invariably fail to reach the apex of the everted hemipenis (apparently a result of differential expansion of apical tissues upon eversion, as the sulci of retracted organs reach virtually to the apex). In all Malagasy species, the apex of the organ is densely covered with spinules; the tips of the sulcus spermaticus in everted organs stop well short of the apex. In contrast, the tips of the sulcus spermaticus in the the African species always reach the apexes of both retracted and everted organs.

Finally, the African species of *Geodipsas* do not exhibit the unusual "trough-like" morphology of the sulcus spermaticus shown by the Malagasy species (see *Comparison of Hemipenes of Malagasy Species of Geodipsas*). In *vauerocegae* and *procterae*, the relative depth of the sulci appears more or less "normal," although in both species well-developed lips border it. The structure of the sulcus in *procterae* is unusual in having prominent longitudinal ridges bordering it and another ridge sep-

arating its branches. In none of the African species does the sulcus appear as deep as in the Malagasy species.

At first glance, one feature of retracted organs of *Geodipsas depressiceps* and *G. zeny* appears similar: the retracted hemipenes of both species appear to have longitudinal ridges. The similarity is only superficial, however. The ridges in *depressiceps* are more solid and remain evident on the everted organ (especially those surrounding the sulcus). The "ridges" in *zeny* largely disappear in the everted hemipenis; they are created in the retracted state by simple folding of the expansible tissue of the organ.

Thus, there are few shared similarities between hemipenes of African and Malagasy species of *Geodipsas* that could be construed as synapomorphies. However, a problem in interpreting the morphology of these animals is the lack of a broader context insofar as most other snakes pertinent to the problem of *Geodipsas* monophyly is concerned. In comparing the hemipenial morphology of African and Malagasy species of *Geodipsas*, I was specifically concerned with identifying characters potentially interpretable as synapomorphies. This proved difficult because many of the hemipenial descriptions of African and Malagasy snakes in the literature are insufficiently detailed to be informative in a broad comparative context (a statement that applies equally or greater to some other character sets, such as osteological ones). This situation should improve as basic descriptive studies are completed; several papers by Domergue (1983, 1986, 1987) and Cadle (1996) are steps in this direction for Malagasy colubrids. Nonetheless, an enormous amount of this basic work remains to be done before the phylogenetic relevance of many hemipenial characters in these snakes becomes apparent. In the next section I try to put the hemipenial data available on African and Malagasy *Geodipsas* into perspective when considered in conjunction with other characters and taxa.

Relationships of *Geodipsas*

In this section I raise the issue of whether *Geodipsas sensu lato* is monophyletic and review characters that have been used to define the genus. I conclude that no strong evidence favors monophyly of the genus in the broad sense. I do not intend here to rigorously estimate the relationship of included species to other Malagasy and African snakes. Knowledge of most colubrid genera from these areas must substantially improve before such a critical assessment can take place. What follows is a provisional interpretation of similarities between the Malagasy and African species of *Geodipsas* and between the former and other species of Malagasy colubrids.

Analysis of the relationships of Malagasy species of *Geodipsas* is clearly complicated by the inclusion of three African species in the genus, although that seems to be largely for historical and rather arbitrary nomenclatural procedures (see later). The three African taxa involved are *Tropidonotus depressiceps* Werner (1897), *Geodipsas vauerocegae* Tornier (1902), and *G. procterae* Loveridge (1922). Their inclusion in *Geodipsas* seems almost accidental when the literature associating them with *Geodipsas* is examined. The basis for including both African and Malagasy species in the same genus (or even species within either of these geographic units) seems never to have been carefully considered. But the issue of whether *Geodipsas sensu lato* is monophyletic is of broader importance than simply resolving a taxonomic issue. *Geodipsas* is widely cited in distributional summaries of the Malagasy fauna as a "shared element" with Africa (e.g., Brygoo, 1987; Cadle, 1987). Yet, in the absence of strong evidence for the monophyly of the genus, it is not clear what such a statement means or, indeed, whether it has any meaning at all. In the following historical summary, I attempt to reconstruct the reasoning that led to inclusion of African and Malagasy species in *Geodipsas* and then evaluate whether that

broad concept of the genus seems well supported.

Status of African Species. Boulenger (1896) erected *Geodipsas* for the two Malagasy species known at that time, *infralineata* and *boulengeri*. Both species were originally described in the Neotropical genus *Tachymenis* Wiegmann (1834) (type species, *T. peruviana*), from which they differ, among other things, in having hypapophyses on the posterior trunk vertebrae. The first African species of *Geodipsas* described, *G. depressiceps* (Werner, 1897), was originally placed in the genus *Tropidonotus*. Subsequently, Andersson (1901) described the first African snake assigned to *Geodipsas* as *G. mapanjensis* (currently a synonym of *depressiceps*). Andersson (1901:20) commented that [*G. mapanjensis*] "seems to come nearest to *Geodipsas Boulengeri*, (Peracca), from which however it is distinguished by the keeled scales, the single loreal, the two praeoculars, the colour, and the geographical distribution . . ." Andersson's generic assignment was probably based solely on using Boulenger's (1896) key. So, too, was Tornier's (1902) generic assignment for *Geodipsas vauerocegae*, which was accomplished with the simple comment "[c]lose to *Geodipsas infralineata* Blgr., but no diastema between the grooved teeth and the solid maxillary teeth" (Tornier, 1902:703). Sternfeld (1908) recognized that *G. mapanjensis* was a synonym of *Tropidonotus depressiceps* and first used the combination *Geodipsas depressiceps*; however, his comments on this point and the generic status are as follows (Sternfeld, 1908:410; my translation):

Through examination of the type specimens of the Berlin Museum I was able to ascertain that *Tropidonotus depressiceps* Werner is identical with *Geodipsas mapanjensis* Andersson. In fact, we are dealing with a *Geodipsas* species, as examination of the dentition shows. It may well be closest to *G. vauerocegae* described by Tornier from the Usambara [mountains]; however, it is sharply separated by the keeled scales in 19 rows (17 in *G. vauerocegae*).

Thus, Sternfeld's assignment presumably was based almost solely on the presence of grooved rear teeth. And although Loveridge (1922) stated, without presenting evidence, that *G. procterae* was "closely allied" with Malagasy *Geodipsas*, he prefaced his description with the less definitive phrase "[i]f included in this genus [*Geodipsas*]. . . , the generic description will have to be enlarged to include snakes with single as well as double subcaudals" (emphasis added).

All of these authors apparently assigned the African species to *Geodipsas* by using Boulenger's (1896) key and generic diagnosis (Loveridge [1922] did so explicitly) and therefore based their assessment on shared features of posterior hypapophyses, grooved rear fangs, undifferentiated anterior maxillary and mandibular teeth, smooth scales, round pupil, and cylindrical body (but see discussion of pupil shape herein). Thus, the monophyly of *Geodipsas sensu lato* has never been critically evaluated relative to other Malagasy and African colubrid genera. Most authors (e.g., Guibé, 1958; Underwood, 1967; Brygoo, 1987; Cadle, 1987; Rasmussen et al., 1995) have implicitly accepted its monophyly. However, it seems equally, or perhaps more, plausible that the Malagasy species of *Geodipsas* are more closely related to other Malagasy colubrids than they are to their African congeners.

Furthermore, the characters that "support" recognition of *Geodipsas sensu lato* actually constitute rather weak evidence of relationship. All of the shared features that have historically been used to link the African species with those of Madagascar are arguably plesiomorphic character states (posterior hypapophyses, homogeneous dentition), have evidently evolved multiple times within colubrids (grooved rear fangs), or are dubious indicators of relationship at this level (smooth scales, cylindrical body).

Only with Bogert's (1940) description of the hemipenis of *Geodipsas depressiceps* was knowledge of the internal anatomy of

these animals advanced (see also Underwood, 1967). Nevertheless, hemipenial characters have not been used as evidence supporting the monophyly of *Geodipsas sensu lato* (e.g., Rasmussen et al., 1995) despite their general importance in colubrid systematics. Hemipenial morphology of all described species of *Geodipsas sensu lato* except *G. vinckei* is now known (see earlier; Bogert, 1940; Rasmussen et al., 1995), and the monophyly of *Geodipsas* can now be addressed using hemipenial characters.

As already suggested, one putatively derived hemipenial character—single (nonbilobed) organs—is shared by the African and Malagasy species of *Geodipsas*. It seems not to have been used as evidence supporting the monophyly of *Geodipsas* by any author, although it is perhaps less equivocally a derived character than any of the characters already listed. Nonetheless, nonbilobed hemipenes have evolved many times within colubrids (for reviews and additional references, see Myers, 1974; Myers and Cadle, 1994). Without additional corroborating synapomorphies, the nonbilobed hemipenial morphology shared by African and Malagasy species of *Geodipsas* is weak evidence of monophyly. Moreover, this character, among others, is shared with at least one other genus of Malagasy colubrids, *Alluaudina* (discussed later). Thus, by itself the nonbilobed character of hemipenes of African and Malagasy species of *Geodipsas* does not unambiguously support its monophyly.

Several other aspects of hemipenial morphology show no special resemblance between the African and Malagasy species of *Geodipsas*. First, the sulcus divides more distally (a derived condition) in the Malagasy species than in their African congeners. Second, the details of ornamentation of hemipenes of Malagasy species of *Geodipsas* are quite similar among the Malagasy species, and these are quite different from the African species (see relevant sections, earlier). The African species, in fact, fall into two groups based on hem-

ipenial morphology and it is questionable whether or not any aspects of hemipenial morphology support the hypothesis that they themselves are monophyletic.

Thus, the case for considering *Geodipsas* in the broad sense monophyletic seems especially weak, essentially supported only by the derived condition of overall hemipenial morphology (single, as opposed to bilobed). This character is further undermined as a potential synapomorphy for *Geodipsas sensu lato* because it is found in at least one other Malagasy colubrid genus, *Alluaudina* (discussed later). The phyletic unity of the Malagasy species of *Geodipsas*, on the other hand, is supported by detailed similarity in several aspects of hemipenial morphology and by their sharing (again, with *Alluaudina* among other Malagasy colubrid genera) of a broadly elliptical pupil, an unusual (? derived) pupil morphology (see later).

I conclude that improved clarity of the uncertainty surrounding relationship of the Malagasy species of *Geodipsas* to those of Africa is best served by removing the African species to another genus, the Malagasy *Geodipsas infralineata* being the type species of *Geodipsas* (Loveridge, 1957). At the least, this would require that a hypothesized "link" between the Malagasy and African reptile faunas based on species of *Geodipsas sensu lato* be specifically justified by phylogenetic inference, rather than by recourse to what appears, at present, to be a taxonomic artifact. However, no other name seems to be currently available for the African species, and I defer specific nomenclatural action to a future report so as to be able to provide a more rigorous diagnosis for the new taxon that must be defined. This conservative course for the present seems also dictated by the questionable monophyly of the three African species, as implied by strong differences in hemipenial morphology between the east and central African species. I next consider evidence suggesting that the Malagasy species of *Geodipsas* are monophyletic *inter se*.

Monophyly of the Malagasy Species of Geodipsas and Comparisons with Other Malagasy Colubrid Genera. The Malagasy species of *Geodipsas* are a superficially disparate assemblage of snakes. *Geodipsas la-phystia* and *G. infralineata* are highly arboreal snakes,⁹ whereas *G. zeny* and *G. boulengeri* are not (of the two specimens of *zeny* with collection data, one was on the ground, the other in a shrub). *Geodipsas boulengeri*, especially, has a body form typical of terrestrial or cryptozoic snakes (short tail ending in a sharp point, small head little distinct from neck). Thus, consideration of the evidence indicating monophyly of the Malagasy species of *Geodipsas* is worthwhile.

The strongest indications of monophyly of the species of *Geodipsas* are the two putatively derived hemipenial characters described earlier: (1) simple (nonbilobed) organs and (2) distal or terminal division of the sulcus spermaticus. Moreover, the detailed similarity of ornamentation of the hemipenes is corroborative evidence of the monophyly of the five species for which the hemipenes are known (all except *vinckei*), even though character polarity for these features is problematic. These details include (1) midsection with enlarged, hooked spines; (2) enlarged bas-

⁹ The macrohabitat of *Geodipsas vinckei* is difficult to infer from the only known specimen, which is rather desiccated, thus making exact interpretation impossible. My examination of the specimen leads to slightly different conclusions than Domergue (1988). Domergue (1988:140) reported the body form as "cylindrical." My impression is that the body is somewhat compressed and with angulate ventrals. Both characters are found in many arboreal colubrids, but the relatively small head and short tail are not generally characteristic of arboreal snakes.

I augment Domergue's (1988) description of the type with the following comments. The type is a male, as suspected by Domergue (verified by gonad inspection through a previous slit in the body wall). It has 18 prediastemal maxillary teeth (not 12, as stated by Domergue), a diastema approximately 1.5× the width of the preceding tooth, and two deeply grooved fangs. The scale row reduction is by loss of row 4 or fusion of 3 + 4 at the level of ventrals 100 (left side) and 102 (right).

al asulcate spine or spines; (3) "head" of the organ with long spinules, distinctly different in ornamentation than more proximal portions; (4) tips of the sulcus branches falling short of the apex on the everted organ; and (5) deep, trough-like morphology of the sulcus.

Casual inspection of hemipenial morphology of other Malagasy colubrids (Cadle, 1996; Domergue, 1984, 1986; unpublished observations for *Dromicodryas*, *Ithyocyphus*, *Lycodryas*, *Liophidium*, *Madagascarophis*, *Pseudoxyrhopus*) reveals no others with detailed similarity comparable to that shared among species of *Geodipsas*. On the basis of the two shared derived hemipenial characters, plus the detailed similarities in overall ornamentation (pending their examination in *Geodipsas vinckei*), I conclude that the Malagasy species of *Geodipsas* are a monophyletic group.

The two putatively derived hemipenial characters shared by species of Malagasy *Geodipsas* are unknown in Malagasy snakes other than *Geodipsas* and *Alluaudina*. According to McDowell (1987:40), *Alluaudina* [*bellyi*] has a nonbilobed, entirely spinose hemipenis, but the sulcus spermaticus is more deeply forked than species of *Geodipsas* with the exception of *G. depressiceps*, which has the most deeply forked sulcus of any species of *Geodipsas* (see earlier descriptions). *Alluaudina* differs from *Geodipsas* in having a high number (25) of strongly keeled dorsal scale rows and perhaps some subtle differences in body proportions. One additional difference noted in most of the literature on these snakes is pupil shape: round in *Geodipsas* and vertically elliptical in *Alluaudina* (e.g., Guibé, 1958:234). That difference is actually nonexistent insofar as Malagasy species of *Geodipsas* are concerned, as both they and *Alluaudina* have broadly elliptical pupils (see *Pupil Shape* in *Geodipsas*).

It seems clear that at least the nonbilobed hemipenial morphology shared by *Geodipsas* and *Alluaudina* is a potential

synapomorphy suggestive of a relationship between these two genera—at least as suggestive in this case as for the monophyly of the Malagasy and African species of *Geodipsas*. Moreover, *Alluaudina* shares with Malagasy *Geodipsas* a broadly elliptical pupil, which seems to be a less common state in colubrids than the round condition seen in African *Geodipsas*. I have not personally studied the hemipenial morphology of *Alluaudina*, and no detailed descriptions are in the literature. Thus, I cannot comment on the details of ornamentation in that genus or how they might compare with *Geodipsas*. However, the species of Malagasy *Geodipsas* have a derived condition of the sulcus spermaticus—division occurring on the distal half of the organ—that is not seen in *Alluaudina* according to McDowell's (1987) observations. More detailed study and comparison of *Alluaudina* with *Geodipsas* should help clarify whether, indeed, there is a relationship between these two.

Relationships among Species of Malagasy Geodipsas. Tentatively accepting the monophyly of the six Malagasy species of *Geodipsas* based on shared details of hemipenial morphology, as already documented, I offer some speculations on relationships among them. It seems possible to adduce evidence that two sets of species pairs are clades relative to the remaining two species.

Geodipsas laphystia and *G. infralineata* share a suite of characters associated with arboreality, including (1) prehensile tail; (2) compressed body with angulate ventrolateral edge; (3) body attenuation, with a narrow "neck" and relatively greater mass shifted posteriorly; (4) tail relatively long; and (5) head relatively broad and very distinct from neck. They also share high numbers of ventral and subcaudal scales and are unusual among *Geodipsas* in being highly polymorphic in dorsal ground color, with the range of colorations being similar in the two species. These two species are also similar in having the most plesiomorphic condition of the sulcus spermaticus.

cus, which divides more proximally in these than in the other species. If we assume that arboreality is a derived ecology in this genus, then the morphological correlates of that macrohabitat would be synapomorphies for a clade comprising these two species.

Geodipsas boulengeri and the species referred to herein as *Geodipsas* species inquirenda share two highly unusual aspects of color pattern (see Fig. 8): (1) a large, light-colored postmandibular spot on the neck and (2) discrete light spots (often dark-bordered) on each upper and lower labial scale. They both also show the most derived condition of the sulcus spermaticus: in both species the division is terminal, so that the tip of the sulcus appears merely expanded (branches extremely short; see Fig. 16). In fact, their hemipenes overall appear nearly identical (unpublished observations). Because of their highly unusual nature, I consider the two color pattern features derived, as is the terminal division of the sulcus. Thus, three synapomorphies support a clade containing these two species. The other two species, *Geodipsas zeny* and *G. vinckei*, are not so easily placed based on present knowledge.

Geodipsas zeny shares with *G. boulengeri* a low number of ventrals and subcaudals and small body size. Its color pattern is a curious mosaic of that in three other species. In having a fine network of dark lines anteriorly that tend to form diagonals separated by two scale rows (Figs. 4–5), *zeny* is similar to the pattern in *infralineata*, in which the diagonals usually are present over the whole body (Fig. 10). All three specimens of *zeny*, and some specimens of *infralineata*, have dark lateral nape blotches (cf. Figs. 4–5, 10). In having dark longitudinal lines posteriorly on scale rows 3–4 and 5–6, and the vertebral row, *zeny* is similar to *laphystia*. Finally, as indicated in the description of *zeny*, two of three specimens (MCZ 181161, BMNH 95.10.29.62) have light spots on the upper and lower labials. Neither manifestation of

labial spots is as striking in *zeny* as in either *boulengeri* or *Geodipsas* species inquirenda (although they are quite discrete in the BMNH specimen), but the appearance of such spots in *zeny* might be construed as an incipient manifestation of the more well-developed condition in the other two species. Moreover, all three specimens of *zeny* have a dusky gular region with light maculations, as in *boulengeri*. In hemipenial morphology, *zeny* is most similar to *boulengeri* but hemipenial differences among the species of Malagasy *Geodipsas* in general are slight. Thus, *zeny* seems to be an amalgam of characters expressed more individually in the other species.

Geodipsas vinckei has a somewhat compressed body (see footnote 8) and an angulate ventrolateral body edge, both features shown by *G. laphystia* and *G. infralineata*. However, the body form of *vinckei* does not appear as modified for arboreality as are the other two species (e.g., it has a relatively small head not very distinct from the neck, and it has a relatively short tail; see Domergue, 1988). *Geodipsas vinckei* also has light spotting on the upper labials reminiscent of those in *boulengeri*; however, the spots are not as consistently present on the supralabials in *vinckei*, and they are also present on the loreals, preoculars, and some of the postoculars, unlike in *boulengeri*. *Geodipsas vinckei*, *laphystia*, and *infralineata* are the largest species of *Geodipsas*, with males reaching 600 mm or greater total length (<400 mm for all other species). The incipient arboreal adaptations (if inferred correctly from the dessicated type) are possibly weak evidence associating *vinckei* with the clade containing *laphystia* and *infralineata*, but any such inference seems tenuous.

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from the RNP and one of the few known for this rare taxon; I thank whatever nymph distracted her upward gaze for our strepsirhine cousins and fixed it upon the ground at the propitious moment the snake crawled by, as well as the muse that guided her hand to grab the animal. I am grateful to the Chicago Zoological Society and the Douroucoul Foundation for providing financial assistance for the fieldwork. The William F. Milton Fund of Harvard University also supported some of the final stages of the work reported herein. Several people found snakes or contributed observations, especially Talata Pierre, Rajeriarason Emile, Steve Zack, Ron Altig, and the RNP guides. Laszlo Meszoly prepared the illustrations of hemipenes. Agnes Pilot enthusiastically shared her remarkable language skills, helped me understand subtle nuances of German prose, and transformed my feeble translation efforts into readable English. Charles Domergue kindly clarified data for specimens obtained by him and now in the MNHN. I thank Charles W. Myers for discussing these and other snakes with me through the years; his insights and incredible breadth are constant sources of inspiration. Louise Emmons provided a list of mammals of the RNP; Maria Rutzmozer and Terry McFadden permitted me to examine mammals in the MCZ. For loan of specimens I am grateful to F. Andreone (MZUT); E. N. Arnold and C. McCarthy (BMNH); and I. Ineich and A. Dubois (MNHN). As always, many Malagasy friends gave their unerring support. I am especially grateful to M. Benjamin Andriamihaja, Mme. Berthe Rakotosamimanana (MINISUP), Mme. Celestine Ravaoarinaromanga (MPAEF), and M. Philemon Randrianarijaona (Directeur des Eaux et Forêts). A grant from the Ernst Mayr fund of the MCZ permitted examination of types and other material at the BMNH and the MNHN. Harry Greene commented on an early version of the manuscript. Charles W. Myers and an anonymous reviewer provided detailed and helpful com-

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SPECIMENS EXAMINED

The following abbreviations of collections are used in the text and in the list of specimens examined. As all specimens are from Madagascar, localities begin with the province. Coordinates are given for those localities that could be reliably localized. Bracketed information in localities are inferred political units (province and, where possible, fivondronana), coordinates, or updated names for towns. A useful reference for names of smaller political units within provinces (fivondronanas) is Brygoo (1971:36, map 4), although some must now be updated to reflect current name usage.

- BMNH British Museum (Natural History), London
- MCZ Museum of Comparative Zoology, reptile collection, Harvard University, Cambridge
- MNHN Muséum National d'Histoire Naturelle, Paris
- MVZ Museum of Vertebrate Zoology, University of California, Berkeley
- MZUT Museo Zoologica dell'Università di Torino [now incorporated as part of the Museo Regionale di Scienze Naturali di Torino], Torino

Geodipsas boulengeri (Peracca)

[**TOAMASINA:** *Fivondronana Moramanga*]: "Valle dell'Umbi (Andrangoloka)" [Valley of the Umbi River (Andrangoloka)] [= Andrangoloaka] [19°02'S, 47°55'E], MZUT R-1874 (*holotype*). [**FIANARANTSOA:** "Pays Zafiminy" [east of Ambositra *fide* C. A. Domergue, in litt., who obtained the specimens from Dr. H. Pinon; approximately 20°30'S, 47°30'E; the Zafiminy [=Zafimaniry] are one of the Tanala tribes], MNHN 1986.1373-78. *Fivondronana Ifanadiana*: Talataky, Ranomafana National Park, 1,000 m [21°16'S, 47°25'E], MCZ 181163. [*Fivondronana Ikongo*]: Along the Sahandrato River, upstream from Tsianovoha [= Tsianivoho; 21°57'S, 47°21'E], 600 m

(Angel, 1936:125), MNHN 1936.19 (holotype of *G. heimi* Angel).

Geodipsas infralineata
(Günther)

NO SPECIFIC LOCALITIES: [[?] **FIANARANTSOA**]: "Eastern Betsileo." BMNH 1946.1.7.20 (erroneously noted as holotype of *infralineata*, as explained in the text; thus, the correct locality for this specimen is "Eastern Imerina"). [[?] **TOAMASINA**]: "Eastern Imerina," BMNH 95.10.29.52 (inferred correct *holotype*, as explained in the text, in which case the correct locality data are "Eastern Betsileo"). [**ANTSIRANANA**]: Fivondronana Andapa]: Marojezy, alt. 300 m [14°26'S, 49°44'E], MNHN 1986.1391. [**ANTANANARIVO**]: Fivondronana Manjakatampo]: Manjakatampo [19°20'S, 47°26'E], MNHN 1957.731. [[?] *Fivondronana Anjozorobe*]: Forêt NE d'Anjozorobe [[?] approx. 18°24'S, 47°52'E; the particular "Anjozorobe" of three identified is assumed to be the largest, most accessible town of that name], MNHN 1986.1392. [**FIANARANTSOA**]: *Fivondronana Ifanadiana*: Ambodimahirira, Ranomafana National Park, 1,200 m [approximately 21°18'30"S, 47°26'E], MCZ 181154. Ivalohoaka, Ranomafana National Park, approx. 1,040 m [21°17'50"S, 47°26'20"E], MCZ 181153. Along main course of Menarano River south of Ivalohoaka, Ranomafana National Park, 1,130 m [approx. 21°18'30"S, 47°26'20"E], MCZ 181155–56. Approx. 2.2 km (airline) SE Sahavondrona along Andranoroa River, 1,170 m [21°17'10"S, 47°21'20"E], MCZ 181157. Talatakely, Ranomafana National Park, 900–1000 m [21°16'S, 47°25'E], MCZ 181147, 181149. [*Fivondronana Ikongo*]: Vallée de la Sahandratao [= Sahandrato = Sahandranto; 22°12'S, 47°28'E], MNHN 1936.20. *Fivondronana Midongy du Sud*: Approx. 7 km SW (airline) Midongy du Sud [Midongy Atsimo], near Rianambo ("high waterfall") on Alapo River, 670 m elev. [23°35'S, 47°01'E], MCZ 181160. [**TOAMASINA**]: *Fivondronana Moramanga*] R[oute] N[ational] 2 (route Tamatave), MNHN 1978.91. Vers PR 60, route de Tamatave, MNHN 1978.93. Perinet [= Andasibe; 18°56'S, 48°25'E], MNHN 1978.90, 1978.92, 1978.94. Environs of Perinet, Anamalazaotra Forest [18°56'S, 48°25'E], BMNH 1930.2.2.14. Forêt d'Analamazaotra (E) [18°56'S, 48°25'E], MNHN 1947.7. [**TOLIARA**]: *Fivondronana Tolanaro*]: Region de Fort Dauphin ["mountains north of Fort Dauphin" *fide* tag attached to specimen; approx. 24°30'S, 47°00'E], MNHN 1986.1390.

Geodipsas vinckei Domergue

[**TOAMASINA**]: *Fivondronana Moramanga*]: Station de Pisciculture de Perinet-Analamazaotra [= Andasibe; approx. 900 m; 18°56'S, 48°25'E], MNHN 1977.818 (*holotype*).

Geodipsas species inquirenda

(These specimens were referred to *Geodipsas "heimi"* [= *boulengeri*] in their respective museum catalogs, but I consider them to represent a distinct species; see comments under *Distribution* in the *Geodipsas boulengeri* species account).

[**ANTSIRANANA**]: *Fivondronana Antsiranana*]: Joffreville [= Ambohitra; 12°29'S, 49°12'E], MNHN 1986. 1379. Montagne d'Ambre (forêt basse) [= Ambohitra; 12°30'S, 49°10'E], MNHN 1978. 2786, 1986. 1380. Montagne d'Ambre [= Ambohitra; 12°30'S, 49°10'E], USNM 149836.

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