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A Revision of the Dwarf *Zonosaurus* Boulenger (Reptilia: Squamata: Cordylidae) from Madagascar, including Descriptions of Three New Species

By

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CONTENTS

ABSTRACT Surveys in Madagascar led to the discovery of three new species of dwarf *Zonosaurus*. One is endemic to limestone karst formations in the north, the second is endemic to limestone karst formations in the west, and the third is endemic to the low elevation humid forests in extreme south-eastern Madagascar. The two new karst-inhabiting species are the first species of *Zonosaurus* known to be confined to rocky habitats. The northern karst-inhabiting species and *Zonosaurus subunicolor* have

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fragile skin. This seems to be an antpreditor mechanism, and within the Cordylidae is uniquely evolved. The holotype of *Zonosaurus aeneus* is redescribed, and data are presented for *Z. brygooi* and *Z. subunicolor*, based on our recently collected material. A key is provided for all seven dwarf species. Biogeographic patterns show a clear predominance for allopatry, with all species are restricted to primary forest, or forest edge. The new species from southeastern Madagascar is of greatest conservation concern, and further strengthens the importance of the Andohahela Reserve, where it is know to occur.

Key words: Reptilia; Squamata; Cordylidae; *Zonosaurus; New* species; Systematics; Taxonomy; Biogeography; Madagascar.

INTRODUCTION

In Madagascar the family Cordylidae (Plated Lizards) is currently represented by two endemic genera containing 15 species— 13 *Zonosaurus* and two *Tracheloptychus*. The most recent review of the Madagascan Cordylidae was made by Brygoo (1985a). Since then two additional taxa were described: *Zonosaurus brygooi* Lang and Böhme, 1989, and a new subspecies *Z. madagascariensis haraldmeieri* Brygoo and Böhme, 1985. The latter is now considered to be a full species by most authors (e.g. Lang, 1991; Glaw and Vences, 1994; Raxworthy and Nussbaum, 1994a). In addition, *Z. subunicolor* was recently resurrected by Glaw and Vences (1994) and Vences et al. (1996). This taxon previously was considered to be a junior synonym of *Z. rufipes* by Brygoo (1985a), Lang and Böhme (1989) and Lang (1990). Herein we follow Brygoo (1985a) and Branch (1988) in considering the family Cordylidae to include the subfamilies Cordylinae and Gerrhosaurinae, while other authors have preferred to give both family rank: Cordylidae and Gerrhosauridae (Lang, 1991; Pough et al. 1998). These two subfamilies/families have been consistently considered as sister groups, and morphological data supports the monophyly of each group (Lang, 1991). All Malagasy species fall into the gerrhosaurid clade (Lang, 1991).

Two distinct groups of *Zonosaurus* can be recognized on body size alone— dwarf species with adult snout-vent lengths (SVL) of less than 100 mm (maximum known size 93 mm), and larger species with adult SVLs of 100-230 mm. Furthermore, the dwarf *Zonosaurus* previously were characterized as having three supralabials anterior to the subocular (compared to four or more in the other species) and two or three well-defined antehumeral mite pockets (compared to none or a single mite pocket) (Lang, 1991). This phenetic group was referred to as the *Zonosaurus aeneus* group by Vences et al. (1996), and included four species— *Z. aeneus, rufipes, brygooi,* and *subunicolor.* Characters of the type material for this group are given in Table 1.

During herpetofaunal surveys between 1989 and1996 we discovered three new species of dwarf *Zonosaurus;* two are rock-dwellers in northern and western Madagascar, and the third a low elevation humid adapted species in extreme southeastern Madagascar. During the course of describing these species it was necessary to examine the holotype of *Zonosaurus aeneus*, which we redescribe here, and we also present data on our recent collections of *Z. subunicolor* and *Z. brygooi*.

Table 1. Characteristics of the type specimens of dwarf *Zonosaurus*

	Type Specimens				
Character	*Z. aeneus* holotype	*Z. brygooi* holotype[1]	*Z. brygooi* paratypes[1]	*Z. rufipes* lectotypes[1]	*Z. subunicolor* lectotype[1] paralectotype[1]
Interparietal scale absent	yes	yes	yes	no	yes
Scale rows around midbody	20	22	20–23	26	25[2]
Ventral scales (chin–cloaca)	51[3]	44	43–48	48	45–46
Femoral pores (left/right)	15/15[4]	19/19	16–19/16–19	13/14	10–11/10–11
Scales under 4th toe	18–19	18	17–19	22	20–22
Dorsolateral anterior line on body	yes unbroken	yes broken	yes broken	no	no
Throat stripes	no	no	no	yes	no

[1] Data from Lang and Böhme (1989).
[2] Paralectotype only.
[3] 47 in Brygoo (1985a).
[4] 15/16 in Brygoo (1985a).

ACKNOWLEDGMENTS

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MATERIALS AND METHODS

All measurements were taken from preserved specimens collected by us during the last 11 years. Specimens were collected using field methods described by Raxworthy and Nussbaum (1994a). Specimens were initially fixed in 10% buffered formalin and later stored in 75% ethanol. A ruler was used to measure the snout-vent length (SVL) and body and tail lengths to the nearest mm, and electronic dial calipers were used for all other measurements to the nearest 0.1 mm. Scale characters are based largely on terminology used by Brygoo (1985a) and Lang (1991). All specimens examined are in the Museum of the Zoology, University of Michigan (UMMZ) and the Université d'Antananarivo, Département de Biologie Animale (UADBA). Other museum acronyms are MNHN (Museum National d'Histoire Naturelle) and ZFMK (Zoologisches Forschunginstitut und Museum Alexander Koenig).

SYSTEMATICS

TAXONOMIC PROBLEMS REGARDING *ZONOSAURUS AENEUS* AND *Z. BRYGOOI*

In the diagnosis of *Zonosaurus brygooi*, Lang and Böhme (1989) listed five characters of scutellation (interparietal scale absent or present, number of scale rows around midbody, number of scales between chin and cloaca, number of femoral pores, and number of subdigital lamellae on 4th toe) and two features of coloration (throat stripes present or absent, and tongue entirely or partly covered by dark pigment) to distinguish *Z. brygooi* from all other species of *Zonosaurus*. However, the only character that separates *Z. brygooi* from *Z. aeneus* is the tongue pigmentation (e.g. see Table 1, figures 1–4; Lang and Böhme, 1989). Although tongue color is the critical character given in the diagnosis, it is omitted in the description of the holotype of *Zonosaurus brygooi* and in the discussion of variation in the paratypes. Lang and Böhme (1989) also did not describe tongue coloration for the series of *Zonosaurus aeneus* and *Z. rufipes* that they examined. More recently, tongue coloration was either ignored in diagnosing these species (e.g. Glaw and Vences, 1994), or considered difficult to evaluate in specimens not in a good state of preservation (Vences et al. 1996).

In their key, Glaw and Vences (1994) separated the two species as follows: *Zonosaurus aeneus*, 12–19 femoral pores, dorsolateral bands on body present, and first upper labial posterior to subocular not divided; *Z. brygooi*, 15–19 femoral pores, dorsolateral bands on body rudimentary, in the form of a series of spots on neck, and first upper labial posterior to subocular divided. The diagnosis of *Z. aeneus* was further modified by Vences et al. (1996) to include the presence of continuous dorsolateral stripes, which begin on the head and continue at least on the anterior third of the body (absent in all other species in the *Z. aeneus* group), and the presence of an undivided first supralabial behind the subocular (absent in all other *Zonosaurus*).

However, the condition of the holotype of *Zonosaurus aeneus* (MNHN 7634) has been a continuing problem. The state of preservation was considered to be so bad as not to be worthy of a redescription (Vences et al. 1996), moreover, the holotype is a juvenile (SVL 35 mm) that is uniform dark brown (Brygoo, 1985a). Glaw and Vences (1994) suggested that the lack of body lines was due to its juvenile condition, and Vences et al. (1996) claimed only meristic characters could be used to diagnose the holotype because of its poor condition and juvenile coloration.

Our observations do not indicate that juvenile *Zonosaurus* have uniform coloration compared to adults. In contrast, we observed that juveniles of all dwarf species of *Zonosaurus* have markings that are similar to, or bolder than those of the adults. Among the following juveniles (SVL 33-39 mm) of *Zonosaurus aeneus*: UMMZ 192213, 192215, and 207179–80, none is uniform in color, and all have the same markings as the adults. We consider it far more likely that the markings of the juvenile holotype of *Z. aeneus* have faded over the past 120 years. This idea is substantiated by Grandidier's (1872) original description of the holotype which included statements of the species having darker flanks and a greenish dorsolateral

line. Because of the importance of coloration in the diagnosis of *Z. aeneus* and the lack of a recent detailed description of the holotype, we redescribe the holotype and present new data from recently collected material.

REDESCRIPTION OF *ZONOSAURUS AENEUS*

Zonosaurus aeneus (Grandidier)
Figures 1, 2, 3

Gerrhosaurus aeneus Grandidier, 1872: 8
Zonosaurus aeneus —Boulenger, 1887:127. First use of combination.

Holotype.—MNHN 7634, juvenile, reported by Mocquard (1895) as collected from "Malaimbandy, pays des Sakalaves," Madagascar.

Specimens examined.—All from Madagascar: MNHN 7634, UADBA 395–97, Ambohimitombo, Ambositra Fivondronana, Fianarantsoa Province, 30 September 1994, J. B. Ramanamanjato and A. P. Raselimanana; UADBA 398–406, Ankeniheny forest, Moramanga Fivondronana, Toamasina Province, 9–22 December 1993, N. Rabibisoa, J. B Ramanamanjato, and O. Ramilison; UADBA 407–09, Fiherenana region, Amboasary Fivondronana, Toamasina Province, 19–23 September 1994, N. Rabibisoa, J. B Ramanamanjato, and O. Ramilison; UADBA 4124–35, 4137–41, Andohahela National Park, 24°38′ S, 46°46′ E, 440–1450 m elevation, Tolagnaro Fivondronana, Toliara Province, 18 October–14 November 1995, J. B. Ramanamanjato and A. P. Raselimanana; UMMZ 192206, Nahampoana, 24°58′ S, 46°58′ E, 250 m elevation, Tolagnaro Fivondronana, Toliara Province, 29 December 1989, C. J. Raxworthy; UMMZ 196437, 196449, 196454, Manantantely, 24°59′ S, 46°55′ E, 140–300 m elevation, Tolagnaro Fivondronana, Toliara Province, 4–24 November 1990, R. A. Nussbaum, J. B. Ramanamanjato, A. P. Raselimanana, and C. J. Raxworthy; UMMZ 196462–4, Manangotry, 24°45′ S, 46°52′ E, 500 m elevation, Tolagnaro Fivondronana, Toliara Province, 15 December 1991, J. B. Ramanamanjato, A. P. Raselimanana, and C. J. Raxworthy; UMMZ 196465–8, Ampamakiesiny, 24°32′ S, 46°51′ E, 450–700 m elevation, Tolagnaro Fivondronana, Toliara Province, 18–29 December 1990, J. B. Ramanamanjato, A. P. Raselimanana, and C. J. Raxworthy; UMMZ 196470, Manangotry, 24°45′ S, 46°52′ E, 500 m elevation, Tolagnaro Fivondronana, Toliara Province, 4 January 1991, J. B. Ramanamanjato, A. P. Raselimanana, and C. J. Raxworthy; UMMZ 196471–78, Mantady National Park, 18°51′ S, 48°27.5′ E, 1000–1100 m elevation, Moramanga Fivondronana, Toamasina Province, 28 March–11 April 1991, J. B. Ramanamanjato, A. P. Raselimanana, and C. J. Raxworthy; UMMZ 207327–36, 22°13′ S, 47°01′ E, and 22°14′ S, 47°00′ E, 650–800 m elevation at Andringitra National Park, Ivohibe Fivondronana, Fianarantsoa Province, 17–29 November 1993, N. Rabibisoa, C. J. Raxworthy, and A. Razafimanantsoa; UMMZ 214927–34, Andohahela National Park (as UADBA 4124–35); UMMZ 215812, , 18°11′ S, 47°07′ E, 1580 m elevation at Ambohitantely Special Reserve, Ankazobe Fivondronana, Antananarivo Province, 4 February 1995, C. J. Raxworthy; UMMZ 221902–03, UADBA Field tags RAN 57021, 57076, 23° 27′S, 46° 29′E, 1100–1240 m elevation at Kalambatritra Special Reserve, Iakora Fivondronana, Fianarantsoa Province, 29 October–9 November 1996, J. Rafanomezantsoa and J. B. Ramanamanjato.

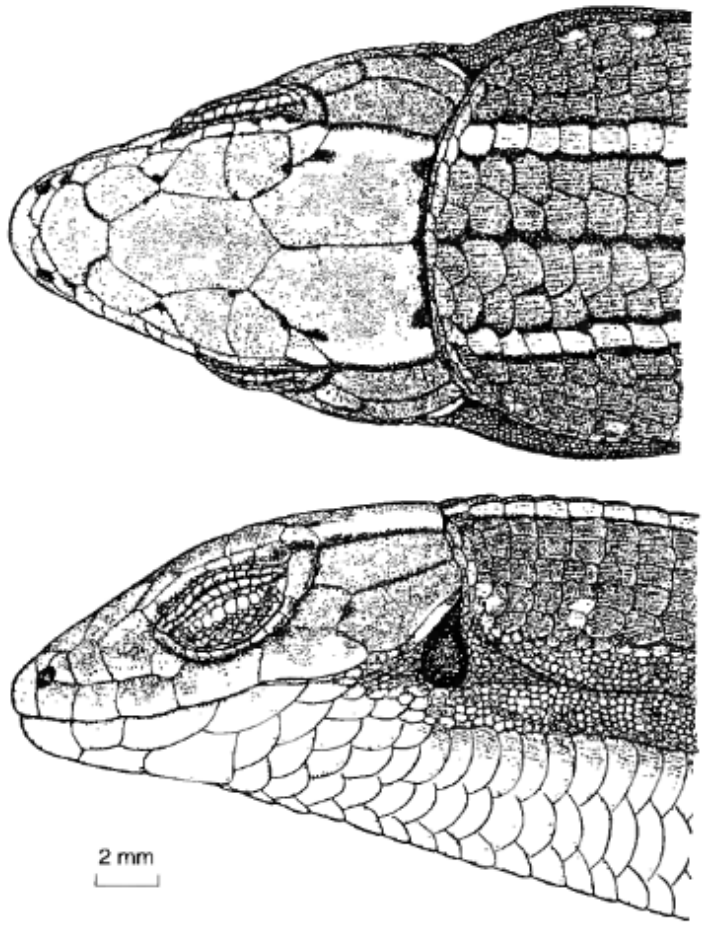


Fig. 1. Lateral and dorsal head views of *Zonosaurus aeneus*, UMMZ 207336.

Diagnosis.— A small, slender *Zonosaurus* (maximum SVL 75 mm) with 51–59 ventral scale rows between chin and cloaca; 2–3 supralabials anterior to subocular, 1–2 supralabials posterior to subocular; throat without dark longitudinal lines; and a pale dorsolateral line on neck and anterior third of body, typically unbroken. No other species of *Zonosaurus* with an adult SVL <100 mm has more than 50 ventral scale rows between chin and cloaca, and no other species of *Zonosaurus* with a dorsolateral line on neck and anterior third of body has a single supralabial posterior to subocular.

Description of holotype.—Juvenile, in good condition, with tail missing 5 mm posterior to cloaca, a ventral incision in the abdomen, and a hole in the throat; SVL 30 mm;

tail length 5 mm; axilla-groin length 14 mm; head length 8 mm; head width 5 mm; head depth 5 mm; snout length (distance between the anterior limit of eye and snout tip) 3.5 mm; horizontal eye diameter 2.8 mm.

Scutellation (left/right): 3/3 supralabials anterior to subocular; 1/1 supralabials posterior to subocular; 5/5 infralabials, the posterior two much smaller than the anterior infralabials; 4/4 supraoculars; posteriormost supraocular in contact with superiormost temporal; suture between two right posteriormost supraoculars incomplete; 1/1 preoculars; 1/1 postoculars; 4/4 supraciliaries; 4/4 temporals; nostril bordering rostral, first supralabial, nasal, and postnasal; nasals not meeting medially, separated by 0.2 mm; 2/2 loreals; anteriormost loreal smallest, higher than long, and in contact with first supralabial; interparietal scale absent; prefrontal scales separated by contact of frontal and frontonasal scales; parietals as long as frontal, longer than frontonasal; pair of postmentals in contact medially; post-postmentals separated by intrusion of two gulars; 51 rows of ventrals between chin and cloaca; 52 rows of dorsals between parietal and level above vent; 20 rows of scales around midbody; subdigital scales on Fingers I–V: 4-7-11-11-7/4-7-10-11-6; on Toes I-V: 5-8-13-18-9/5-8-13-19-10; femoral pores 15/15; dorsal scales keeled; ventral scales of fore- and hind limbs weakly keeled; ventral scales of body, manus and pes smooth.

Dorsal coloration of head, body, limbs, and tail brown, with a thin, faint, unbroken, pale brown dorsolateral line between posteriormost supraocular and a point just posterior to front limb insertion; pale dorsolateral line fading to same coloration as that of the body posterior to forelimb; pale dorsolateral line bordered ventrally by flanks that are slightly darker brown than middorsal region of body; supralabials and supraciliaries with pale brown spots; a row of pale brown spots ventral to lateral body fold of throat and body; ventral surface of throat, body, limbs, and tail pale brown.

Variation.—Measurements and scale counts for the holotype and other specimens examined are given in Table 2. Five of the 78 specimens have two supralabials posterior to the subocular on one side of the head; four specimens have this condition on both sides of the head. Variation in the number of supralabials anterior to the subocular also is evident; two individuals have a pair of supralabials, rather than three. No obvious sexual dimorphism in size was noted. The dorsolateral line on the neck and anterior third of body is broken in one or several places in 19% of the specimens (Table 2), but it still forms a distinct line, rather than a series of spots.

In life, the typical coloration is: head, body, limbs, and tail golden brown dorsally, with a thin, unbroken, pale yellow dorsolateral line from the posteriormost supraocular or posterior margin of the parietal scale to a point posterior to the insertion of the front limb. Posterior to the insertion of the front limb the pale yellow dorsolateral line is broken, and fades to pale brown at the base of the tail. The pale dorsolateral line is bordered dorsally by a broken or continuous thin black line. Often a thin, black, broken vertebral line is present on the anterior third of the body. The body flanks are dark brown below the dorsolateral line, with small black and pale yellow spots. Limbs dorsally marked with a few pale yellow spots, tail with black spots on dorsal and lateral surfaces. Head with a few pale white spots on the supralabials, and a pale yellow spot anterior to tympanum; supraoculars, frontal, and parietals are marked with black spots; throat yellow, orange, blue, or white without longitudinal stripes or spots; ventral body and tail pale blue.

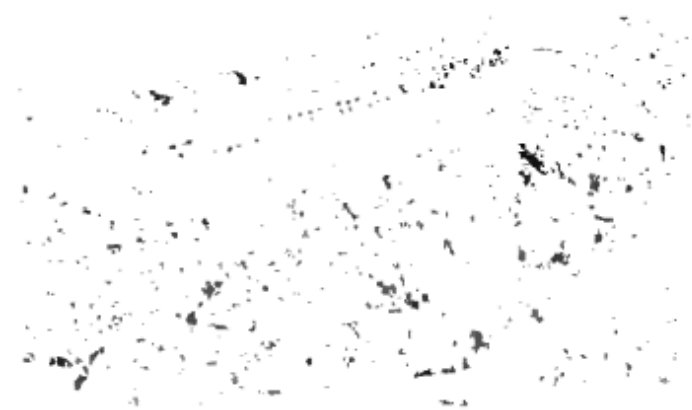
The color of the throat is highly variable within populations, such as at Andohahela and Ambohimitombo. From photographs and observations made in the field (throat color of living individuals is not maintained in preservative) we suspect that the yellow and orange throats are typical of males in reproductive condition, and that blue and white throats are restricted to juveniles, females, or males not in reproductive condition. Some geographic variation is evident in the coloration of the flanks. Indi-

Table 2. Summary of variation in *Zonosaurus aeneus*.

Character	Holotype	Other specimens		Total
		UADBA UMMZ	Vences et al (1996)	
Total *N*	1	77	14	92
Male	0	36+	?	36+
Female	0	21+	?	21+
Juvenile	1	12	?	12+
Maximum SVL (mm)	30	75	72	75
Supralabials anterior to subocular (left/right)				
2/2	0	1	0	1
2/3 or 3/2	0	1	0	1
3/3	1	75	14	90
3/4 or 4/3	0	0	0	0
4/4	0	0	0	0
Supralabials posterior to subocular (left/right)				
1/1	1	68	14	83
1/2 or 2/1	0	5	0	5
2/2	0	4	0	4
Ventral scales (chin-cloaca)	51	51-59	?	51-59
Scale rows around midbody	20	18-24	18-21	18-24
Scales under 4th toe	18-19	16-22	17-20	16-22
Femoral pores	15	12-18	13-18	12-18
Dorsolateral anterior lines				
Broken	0	9	0	9
Unbroken	1	52	14	67
Broken + unbroken	0	4	0	4
Mutilated	0	12	0	12

Zonosaurus aeneus, UMMZ 207336, adult, Andringitra National Park.

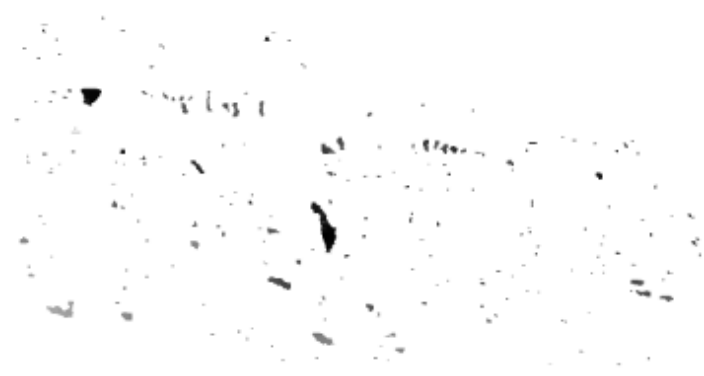
Zonosaurus aeneus, UMMZ 207336, adult, Andringitra National Park.



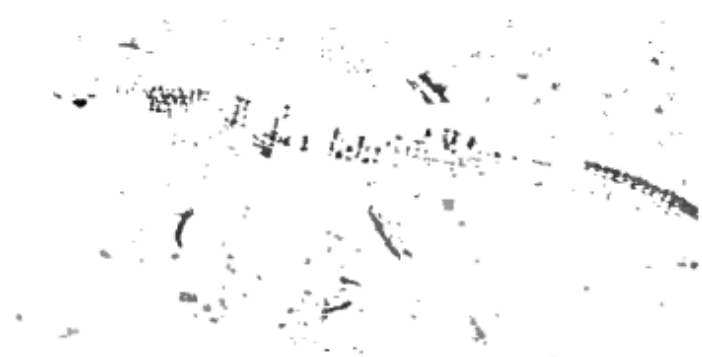
Zonosaurus brygooi, adult, Zahamena Strict Reserve.

Zonosaurus anelanelany, adult, Sainte-Luce strand forest.

Zonosaurus rufipes, adult, Lokobe National Park, Nosy Be.



Zonosaurus subunicolor, adult, Lokobe National Park, Nosy Be.



Zonosaurus tsingy, adult, Ankarana National Park.

Zonosaurus bemaraha, UADBA, adult, Bemaraha National Park.

Fig. 2. The seven species of dwarf *Zonosaurus*.

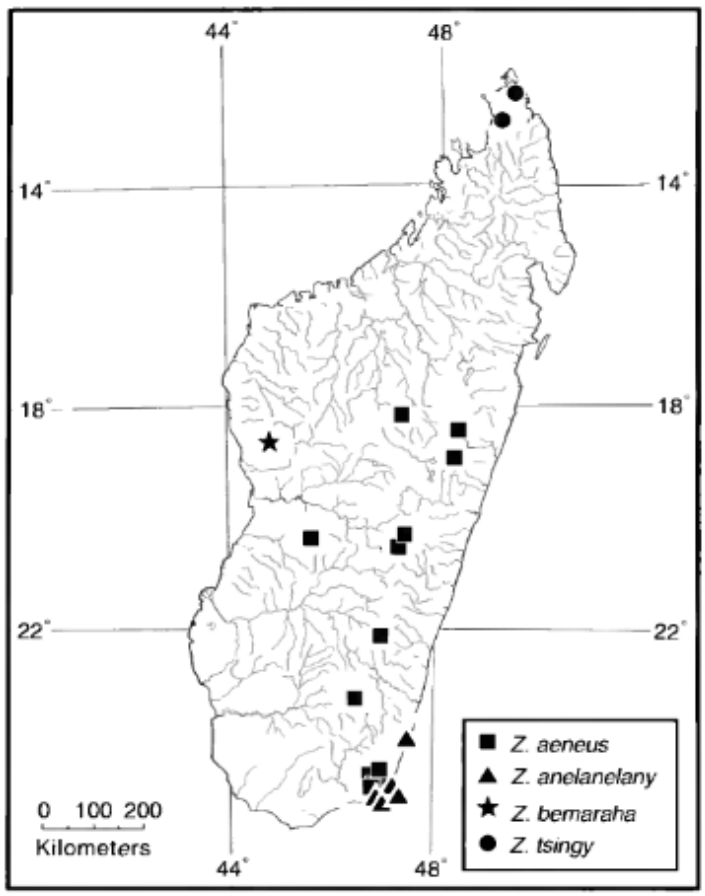


Fig. 3. Localities noted in the text for the three new species of dwarf *Zonosaurus*, and *Z. aeneus*.

viduals from the Mantady and Andringitra (East-Central Region) have pale spots, which most frequently form two or three longitudinal lines above the lateral fold, whereas specimens from Manantantely and Ampamakiesiny (Southeast Region) have fewer pale spots that are arranged irregularly. The anterior limit of the pale dorsolateral line is at the posteriormost supraocular scale (e.g., at Mantady and Andringitra; Figs 1 and 2) or at the posterior margin of the parietal scale (e.g., at Manantantely and Ampamakiesiny).

Distribution and habitat.—*Zonosaurus aeneus* is distributed across the High Plateau and Eastern Escarpment of Madagascar between Ambohitantely and Manantantely (18°–25° S latitude) at elevations of 140–1580 m. We have not found this species farther to the north despite intensive surveys at sites such as Zahamena (17°44′ S, 48°59′ E), Ambatovaky (16°51′ S, 49°16′ E), and Masoala (15°19° S, 50°14′ E).

All specimens of *Zonosaurus aeneus* were collected in, or in close proximity to, the primary low or midelevation humid forest that is typical of the Eastern Escarpment, and the central High Plateau. However, this species appears to prefer forest-edge habitats with good exposure to sun (such as along major river courses, trail edges, and road verges). It was never found in complete shade in deep forest.

The type locality is not mentioned in Grandidier's species description, but Mocquard (1895) listed the type locality without explanation as Malaimbandy (20°21′ S, 45°36′ E). Therefore, this locality was considered doubtful by Vences et al. (1996). Brygoo (1985b) suggested that Mocquard's locality might be confused with the type locality of *Eupreps sakalava*. Another possible reason to doubt this locality is its western location, which was noted (although accepted) by Brygoo (1985a). Malaimbandy lies between the Eastern and Western Domains (as recognized by Humbert, 1955), with areas of High Plateau above 1000 m elevation only 20 km to the east. Because *Zonosaurus aeneus* occurs on the High Plateau, we do not consider this locality to be dubious, as have other authors.

A single specimen of *Zonosaurus aeneus* (ZFMK 14365) is recorded from Nosy Be in northwestern Madagascar; this locality was considered to be doubtful by Vences et al. (1996) because they were unable to confirm the presence of this species during a survey of the island. We also were unable to confirm the presence of *Zonosaurus aeneus* at Lokobe Special Reserve, Nosy Be (13°25′ S, 48°19 ′E) during our month-long intensive survey of the reserve. Because *Zonosaurus aeneus* is currently unknown at any other site north of 18° S, we consider it unlikely that this species actually occurs on Nosy Be Island.

Remarks.—Other dwarf species of *Zonosaurus* have been confused with *Zonosaurus aeneus* for many years. This is evident, for example, in the series of *Zonosaurus aeneus* in the MNHN (Table 2; Brygoo 1985a), which includes *Zonosaurus brygooi*. (Fig. 2c, Table 3).

DESCRIPTIONS OF NEW SPECIES

Zonosaurus ***anelanelany*** new species

Figures 2, 4

Holotype.—UMMZ 192205, adult female, collected 24 October 1989 at Sainte-Luce strand forest, 24°49′ S, 47°09′ E, 20 m elevation, Tolagnaro Fivondronana, Toliara Province, Madagascar, by C. J. Raxworthy.

Paratopotypes.—UMMZ 192203–04, 21–24 October 1989 by C. J. Raxworthy.

Paratypes.—All from Toliara Province, Madagascar: UMMZ 192207, Nahampoana, 24°58′ S, 46°58′ E, 100–300 m elevation, Tolagnaro Fivondronana, 29 December 1989, C. J. Raxworthy; UMMZ 196435, 196448, 196450–51, Manantantely, 50–450 m elevation, 24°59′ S, 46°55′ E, Tolagnaro Fivondronana, 31 October–15 November 1990, R. A. Nussbaum, C. J. Raxworthy, A. P. Raselimanana, and J.B Ramanamanjato; UMMZ 196453, Nahampoana, 24°58′ S, 46°58′ E, 100–300 m elevation, Tolagnaro Fivondronana,

Table 3. Summary of variation in *Zonosaurus brygooi*.

Character	Types[1]	UADBA, UMMZ[2]	MNHN[1]	Total
Total *N*	10	35	11	56
Male?	24	?	24+	
Female	?	11	?	11+
Juvenile	?	0	?	0+
Maximum SVL (mm)	76	76	71	76
Supralabials anterior to subocular (left/right)				
2/2	0	0	0	0
2/3 or 3/2	0	0	0	0
3/3	10	35	11	56
3/4 or 4/3	0	0	0	0
4/4	0	0	0	0
Supralabials posterior to subocular (left/right)				
1/1	0	0	0	0
1/2 or 2/1	0	0	0	0
2/2	10	35	11	56
Ventral scales (chin–cloaca)	43–48	45–50	?	43–50
Scale rows around midbody	20–23	20–24	22[3]	20–24
Scales under 4th toe	17–19	16–21	16–19	16–21
Femoral pores	16–19	16–20	15–17	15–20
Dorsolateral anterior lines				
Broken	10	35	11	56
Unbroken	0	0	0	0
Broken + unbroken	0	0	0	0
Mutilated	0	0	0	0

[1] Based on Vences et al. (1996).
[2] UADBA 377, 380–81, 383–87, UMMZ 192208–12,192214, 207165–78, 207181–87.
[3] Single specimen.

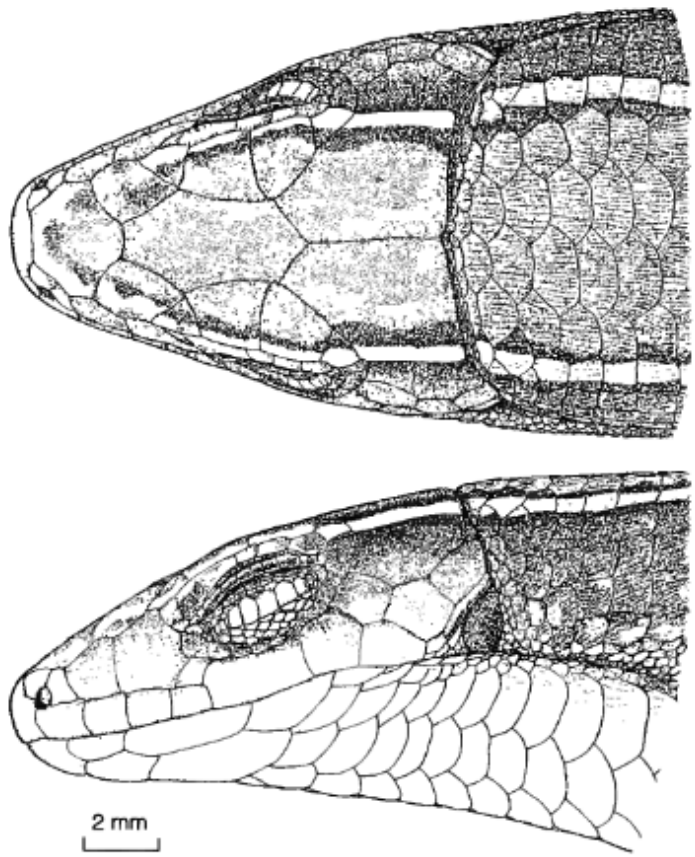


Fig. 4. Lateral and dorsal head views of the holotype of *Zonosaurus anelanelany*, UMMZ 192205.

23 November 1990, R. A. Nussbaum, C. J. Raxworthy, A. P. Raselimanana, and J. B. Ramanamanjato; UMMZ 196461, Marovony, 24°05′ S, 47°20′ E, 50-150 m elevation, Tolagnaro Fivondronana, 3 December 1990, G. Raharimanana.

Referred specimens.—UADBA 378–79, 2189–94, 2196, 2202 (as UMMZ 196435); 2198–2200, 2203–05 (as UMMZ 196453); 4121, 18 October 1995, Andohahela National Park, 24°39′ S, 46°47′ E, 200 m elevation, Tolagnaro Fivondronana, Toliara Province, Madagascar by J. B. Ramanamanjato and A. P. Raselimanana.

Diagnosis.—A robust dwarf *Zonosaurus* (maximum SVL 93 mm) with fewer than 51 ventral scale rows between chin and cloaca; 17–20 lamellae under 4th toe; typically four supralabials anterior to subocular (three supralabials on both sides of the head occurred once in a series of 27 specimens); two supralabials posterior to subocular; 13–16 femoral pores; pale dorsolateral line between head and anterior insertion of front limbs, typically not broken (or broken on one side only); throat without dark longitudinal lines.

All other species of dwarf *Zonosaurus* have a maximum adult SVL of less than 89 mm. *Zonosaurus subunicolor*, *rufipes*, and *tsingy* lack pale dorsolateral lines between the head and the anterior insertion point of the front limbs (Figures 2e, 2f, 2g). *Zonosaurus aeneus* has a greater number of ventral scale rows between the chin and cloaca (51–59), 2–3 supralabials anterior to the subocular, and typically one supralabial posterior to subocular. *Zonosaurus brygooi* has 3 supralabials anterior to the subocular, and the dorsolateral line between the head and the insertion of the forelimbs is always broken. *Zonosaurus bemaraha* (Fig. 2h) has more lamellae under the 4th toe (22–23), typically 3 supralabials anterior to the subocular, and a maximum SVL of 75 mm.

Description of holotype.—Adult female, in excellent condition, with original tail for first 11 mm; left ovary 5 mm long, containing 7 eggs, the largest 3 mm in diameter; SVL 80 mm; tail length 81 mm; axilla–groin length 39 mm; head length 19 mm; head width 11.5 mm; head depth 9.4 mm; snout length (distance between anterior limit of eye and snout tip) 6.9 mm; horizontal diameter of eye 4.3 mm.

Scutellation (left/right): 4/4 supralabials anterior to subocular; 2/2 supralabials posterior to subocular; 5/5 infralabials, posterior two much smaller than anterior infralabials; 4/4 supraoculars, posteriormost supraocular not in contact with superiormost temporal; 1/1 preoculars;

2/2 postoculars; 5/5 supraciliaries; 4/4 temporals; nostril bordering rostral, first supralabial, nasal, and postnasal; nasals not meeting medially, separated by 1.4 mm; 2/2 loreals, anteriormost loreal smallest, as high as long, just touching first supralabial; interparietal scale absent; prefrontal scales separated by contact of frontal and frontonasals; parietals same length as frontal and longer than frontonasal; pair of postmentals in contact medially; post-postmentals separated by intrusion of two gulars; 46 rows of ventrals between chin and cloaca; 46 rows of dorsals between parietal and level above vent; 24 rows of scales around midbody; subdigital scales on Fingers I–V: 3-7-10-10-5/3-7-10-10-6; on Toes I-V: 5-8-13-19-10/5-8-12-19-10; femoral pores15/15; dorsal scales keeled; ventral scales of forelimbs weakly keeled; ventral scales of hindlimbs and body smooth; ventral scales of manus and pes smooth.

In life, the dorsal surfaces of the head, body, limbs, and tail are brown. An unbroken, pale yellow dorsolateral line extends from the supraoculars to the anterior insertion of the forelimbs (level with the ninth dorsal scale row) before fragmenting and fading at midbody. The pale dorsolateral line is bordered dorsally by a broken thin black line. A black, broken, vertebral line is present on the anterior third of body. The flanks are slightly darker brown than the dorsum and have small dark and pale brown spots below dorsolateral line. A few pale yellow spots are present on the dorsal surfaces of the limbs. Throat, body and tail pale-gray, with some faint darker spots on ventrolateral regions.

In preservation, the pale yellow markings are pale brown, and overall contrast in the makings is reduced. The pale gray ventral surfaces are yellowish-brown.

Variation.—Measurements and scale counts are given in Table 4. One of the 27 specimens examined has three supralabials anterior to the subocular on both sides of the head, and five have the formula either 4/3 or 3/4. Females appear to be larger than males; the maximum SVL in males is 86 mm, compared to 93 mm in females. The head is either uniform brown or brown with darker spots especially, on the parietals. The anterior, pale yellow, dorsolateral line was broken on one side in 8% of specimens (Table 4).

Etymology.—The specific name *anelanelany* (pronounced aneal-aneal-any) means intermediate in Malagasy; the name is used here because this new species shares characteristics exhibited by both the dwarf and larger species of *Zonosaurus* .

Distribution and habitat.—*Zonosaurus anelanelany* is confined to lowland rainforest in extreme southeastern Madagascar, south of 24° S (Fig. 3). This species is present in closed canopy littoral forest and in humid rainforest of the Anosy and Vohimena Massifs, at elevations of 20–450 m.

Table 4. Summary of variation in *Zonosaurus anelanelany*.

Character	Holotype	Paratypes	UADBA	Total
Total *N*	1	9	17	27
Male0	5	11	16	
Female	0	3	5	9
Juvenile	0	1	1	2
Maximum SVL (mm)	80	90	93	93
Supralabials anterior to subocular (left/right)				
2/2	0	0	0	0
2/3 or 3/2	0	0	0	0
3/3	0	0	1	1
3/4 or 4/3	0	4	1	5
4/4	1	5	15	21
Supralabials posterior to subocular (left/right)				
1/1	0	0	0	0
1/2 or 2/1	0	0	0	0
2/2	1	9	17	27
Ventral scales (chin–cloaca)	46	45–50	45–49	45–50
Scale rows around midbody	24	22–24	20–23	20–24
Scales under 4th toe	19–19	17–20	17–20	17–20
Femoral pores	15	13–16	13–16	13–16
Dorsolateral anterior lines				
Broken	0	0	0	0
Unbroken	1	9	12	22
Broken + unbroken	0	0	2	2
Mutilated	0	0	3	3

Remarks.—Andreone and Randriamahazo (1997) referred a single specimen of *Zonosaurus* from rainforest at Andohahela (290-320 m elevation) to *Zonosaurus* c.f. *madagascariensis*. Subsequently, Vences et al. (1999) considered this specimen as *Zonosaurus* c.f. *brygooi*. The number of ventral scales (45), the four supralabials anterior to subocular, two supralabials posterior to the subocular, and the size of this specimen (SVL either 82.7 or 85 mm, Andreone and Randriamahazo, 1997; Vences et al. 1999) suggest that it is *Zonosaurus anelanelany*. Their photograph shows a male with a bright orange throat and a dorsolateral line that is broken anteriorly. The reported 17/16 femoral pores is slightly higher than the range of specimens that we examined.

The distribution of *Zonosaurus anelanelany* is confined to southeastern Madagascar, and is similar to those of several other reptiles that also are endemic to that region (*Phelsuma antanosy, Paragehyra gabriellae, Pseudoxyrhopus kely*, and *P. sokosoko*).

Zonosaurus ***bemaraha*** new species

Figures 2, 5

Holotype.—UMMZ 217174, adult female, collected 12 March 1996 at Antranopasasy, Bemaraha National Park, 18°41.5′ S, 44°43.0′ E, 100 m elevation, Antsalova Fivondronana, Toliara Province, Madagascar, by J. B.

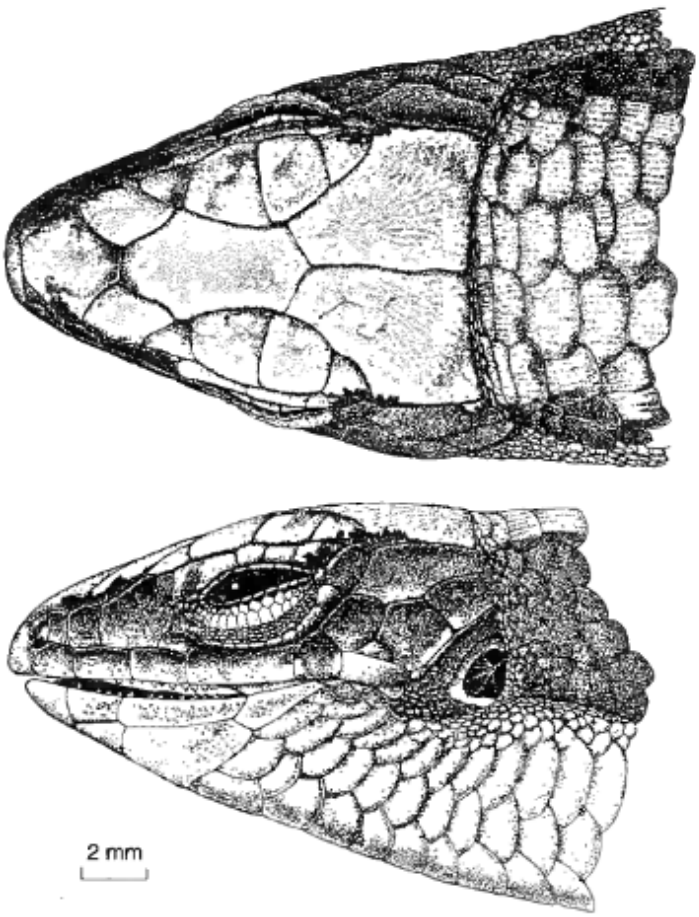


Fig. 5. Lateral and dorsal head views of the holotype of *Zonosaurus bemaraha*, UMMZ 217174.

Ramanamanjato, A. P. Raselimanana, C. J. Raxworthy, Angeluc Razafimanantsoa, and Angelin Razafimanantsoa.

Paratopotypes.— UADBA 5382-89, UMMZ 217170–73, collected 8–12 March 1996 by J. B. Ramanamanjato, A. P. Raselimanana, C. J. Raxworthy, Angeluc Razafimanantsoa, and Angelin Razafimanantsoa.

Diagnosis.—A small *Zonosaurus* (maximum SVL 75 mm) with fewer than 49 ventral scale rows between chin and cloaca, a pale broken or unbroken dorsolateral line between head and anterior insertion point of forelimbs, 22–23 lamellae under 4th toe, 11–15 femoral pores, throat without dark longitudinal lines, three supralabials typically anterior to subocular (four supralabials on one side of head occurred once in a series of 13 specimens), two supralabials posterior to subocular. All other species of *Zonosaurus* with a maximum adult SVL < 94 mm and a pale dorsolateral line have either more than 50 ventral scales (*Z. aeneus*), or fewer than 22 lamellae under the 4th toe (*Z. brygooi* and *Z. anelanelany*). *Zonosaurus brygooi* also may be distinguished by its greater number of femoral pores (15–20) and *Z. anelanelany* by its larger maximum adult SVL (93 mm).

Description of holotype.—Adult female, in excellent condition, with partially regenerated tail (18 mm) detached from body at base, and a small area of irregular scales (probably scar tissue) dorsally on left side posterior to the forelimb; left ovary 7.5 mm long, containing 7 developing eggs, largest egg 1 mm diameter; SVL 67 mm; tail length 84 mm; axilla–groin length 33 mm; head length 15 mm; head width 11.5 mm; head depth 11.0 mm; snout length (distance between anterior limit of eye and snout tip) 6.5 mm; horizontal diameter of eye 4.4 mm.

Scutellation (left/right): 3/3 supralabials anterior to subocular; 2/2 supralabials posterior to subocular; 4/5 infralabials, posterior two much smaller than anterior supralabials; 4/4 supraoculars, posteriormost supraocular not in contact superiormost temporal; 1/1 preoculars; 2/2 postoculars; 5/5 supraciliaries; 4/4 temporals; nostril bordering rostral, first supralabial, nasal, and postnasal; nasals not meeting medially, separated by 0.9 mm; 2/2 loreals, anteriormost loreal smallest, as high as long, contacting first supralabials; tiny interparietal present; prefrontals separated by contact of frontal and frontonasals; parietals shorter than frontal, but longer than frontonasal, left parietal with irregular fissures; pair of postmentals in contact medially; post-postmentals separated by intrusion of two gulars; 45 rows of ventrals between chin and cloaca; 45 rows of dorsals between parietal and level above vent; 24 rows of scales around midbody; subdigital scales on Fingers I–V: 3-7-11-10-7/4-8-12-11-7; on Toes I-V: 5-8-16-23-12/4-8-16-23-12; femoral pores (left/right) 14/12; dorsal scales keeled; ventral scales of fore- and hindlimbs, and body smooth; ventral scales of manus and pes smooth.

In life, the dorsal coloration of head, body, limbs, and tail are brown, with scattered dark brown spots middorsally. A broken, pale yellow, dorsolateral line extends from the lateral edge of parietals and to the base of the tail, the stripe gradually fades posteriorly. The pale dorsolateral line is bordered laterally by darker brown on the flanks, darkest two scale rows below the pale dorsolateral line. The lateral surface of the head is darker brown than the dorsal surface. The flanks are dark brown with small pale yellow spots below the dorsolateral line. Limbs marked with pale and dark brown spots on the dorsal surface. The tail has dark spots on the dorsal surfaces, and a faint pale brown, broken, dorsolateral line. The throat is pale gray with faint longitudinal stripes between the scale rows. The ventral surfaces of the body and tail are pale gray.

Variation.—Measurements and scale counts are given in Table 5. One of the 13 specimens examined has four supralabials anterior to the subocular on one side of the head. The dorsolateral line in this species is either broken or unbroken on the anterior region of the body between

Table 5. Summary of variation in *Zonosaurus bemaraha*.

Character	Holotype	Paratopotypes	Total
Total *N*	1	12	13
Male	0	5	5
Female	1	2	3
Juvenile	0	5	5
Maximum SVL (mm)	67	75	75
Supralabials anterior to subocular (left/right)			
2/2	0	0	0
2/3 or 3/2	0	0	0
3/3	1	11	12
3/4 or 4/3	0	1	1
4/4	0	0	0
Supralabials posterior to subocular (left/right)			
1/1	0	0	0
1/2 or 2/1	0	0	0
2/2	1	12	13
Ventral scales (chin–cloaca)	45	43–48	43–48
Scale rows around midbody	24	22–24	22–24
Scales under 4th toe	23–23	22–23	22–23
Femoral pores	12–14	11–15	11–15
Dorsolateral anterior lines			
Broken	1	6	7
Unbroken	0	2	2
Broken + unbroken	0	1	1
Mutilated	0	3	3

the forelimb insertion and the parietals (Table 5). The line is broken in 80% of the specimens.

Etymology.—The specific name is a noun in apposition and refers to the type locality of this species.

Distribution and habitat.—*Zonosaurus bemaraha* currently is known only from one site in the Bemaraha karst system in western Madagascar (Fig. 3). During our survey of Bemaraha, two other sites farther to the south were also visited—Ambalarano (18°59′ S, 44°45.5′ E); and Manambolo (19°08′ S, 44°50′ E)— but this species was not observed at either of these sites. The habitat of *Z. bemaraha* is western deciduous forest growing on karst limestone substrate, where an abundance of rocky outcrops exist. This species was active on the forest floor and on the rock substrate. Apparently suitable habitat for this species also exists at Ambalarano and Manambolo, and we were surprised that it was not found at these sites, despite our specific searches to find this species.

Remarks.—*Zonosaurus bemaraha* is phenetically similar to *Z. brygooi* and *Z. anelanelany*. However, *Z. bemaraha* has more subdigital scales under the 4th toe than the other two species. Possibly the increased number of subdigital scales is an adaptation for climbing rocky substrates.

The only other record of a dwarf species of *Zonosaurus* from this region of western Madagascar is Brygoo's (1985a) report of a single specimen of *Z. aeneus* (MNHN 1984.404) collected in 1957 by A. Robinson from "forêt d'Andobo (Antsingy, sous-préfecture d'Antsalova)". Antsingy is a name previously used for the Bemaraha karst system, but we have been unable to locate the Andobo Forest. Vences et al. (1996) reported a SVL of 33 mm, and 18 subdigital scales under the 4th toe in this specimen. These authors listed this specimen as *Zonosaurus brygooi* but wrote that the specific identity is not certain. The Antsingy locality suggests MNHN 1984.404 is *Zonosaurus bemaraha;* however, the subdigital scale count is much lower than the type material.

Zonosaurus ***tsingy*** new species

Figures 2, 6, 7.

Holotype.—UMMZ 217422, adult male, collected 28 April 1996 at Lac Vert, Ankarana National Park, 12°52′ S, 49°06′ E, 100 m elevation, Ambilobe Fivondronana, Antsiranana Province, Madagascar, by J. B. Ramanamanjato.

Paratopotypes.—UMMZ 201494–97 and 207326, 2–4 February 1992, A. P. Raselimanana, C. J. Raxworthy, A. Razafimanantsoa, and A. Razafimanantsoa; UMMZ 217423–34, 25–28 April 1996, at 100–200 m elevation, J. B. Ramanamanjato, A. P. Raselimanana, A. Razafimanantsoa, and A. Razafimanantsoa.

Paratype.—UMMZ 217435, at Montagne de Français, 12°18′ S, 49°19′ E, 50 m elevation, Antsiranana Fivondronana, Antsiranana Province, 10 May 1996, J. B. Ramanamanjato, A. P. Raselimanana, and A. Razafimanantsoa.

Referred specimens.—UADBA 6033 from the locality as holotype, 21 January 1996, A. Ravoninjatovo and F. Rabemananjara; UADBA 6681–85; UADBA 6686–96 (as UMMZ 217423–34); UADBA 6697–99 (as UMMZ 217435).

Diagnosis.—A small *Zonosaurus* (maximum SVL 85 mm), without pale dorsolateral stripes on the anterior or posterior part of the body; dorsal body skin fragile (scales readily shed in life when restrained); throat lacking dark longitudinal lines; 2–4 supralabials anterior to subocular; 1–2 supralabials posterior to subocular; and 14–20 femoral pores.

The only other species of *Zonosaurus* with an adult SVL < 94 mm that lacks anterior light dorsolateral body lines are *Z. rufipes* and *Z. subunicolor*. *Zonosaurus rufipes* can be distinguished by the dark longitudinal lines on the throat, and the dorsal skin, which is not fragile. *Zonosaurus subunicolor* can be distinguished by the lower number of femoral pores (8–13), and the pale and dark dorsolateral lines in the pelvic region (Table 6).

Description of holotype.—Adult male, in excellent condition, with partly regenerated tail (93 mm), and

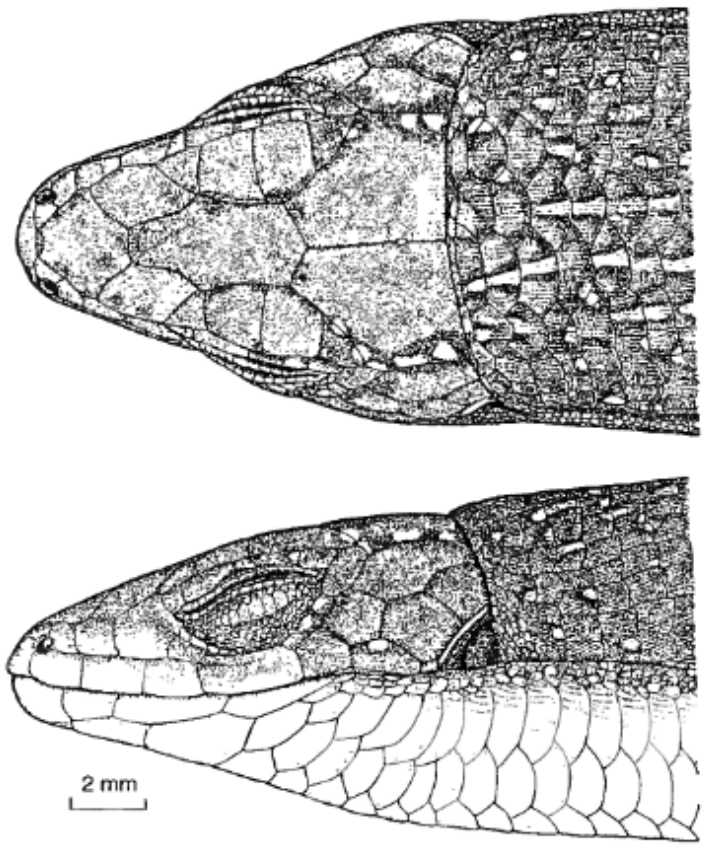


Fig. 6. Lateral and dorsal head views of the holotype of *Zonosaurus tsingy*, UMMZ 217422.

everted hemipenes; left testes is white, length 4 mm, width 1 mm; hemipenes both 6 mm long, without calyces, with a bilobed apex and transverse ridges on the lateral and asulcal side of each apical lobe; SVL 75 mm; tail length 129 mm; axilla–groin length 34 mm; head length 18 mm; head width 13.3 mm; head depth 10.3 mm; snout length (distance between the anterior limit of eye and snout tip) 6.2 mm; horizontal diameter of eye 3.8 mm.

Scutellation (left/right): 3/3 supralabials anterior to subocular; 2/2 supralabials posterior to subocular; 5/5 infralabials, posterior 2 much smaller than anterior supralabials; 4/4 supraoculars, posteriormost supraocular not in contact with superiormost temporal; 1/1 preoculars; 1/1 postoculars; 5/5 supraciliaries; 4/4 temporals; nostril borders rostral, first supralabial, nasal, and postnasal; nasals not meeting medially, separated by 0.7 mm; 2/2 loreals; interparietal scale tiny; prefrontal scales separated by contact of frontal and frontonasals; parietals shorter than frontal but longer than frontonasal; pair of postmentals contact medially; post-postmentals separated by intrusion of two gulars; 46 rows of ventrals between chin and cloaca; 41 rows of dorsals between parietal and level above vent; 22 rows around midbody; scales of body are readily shed

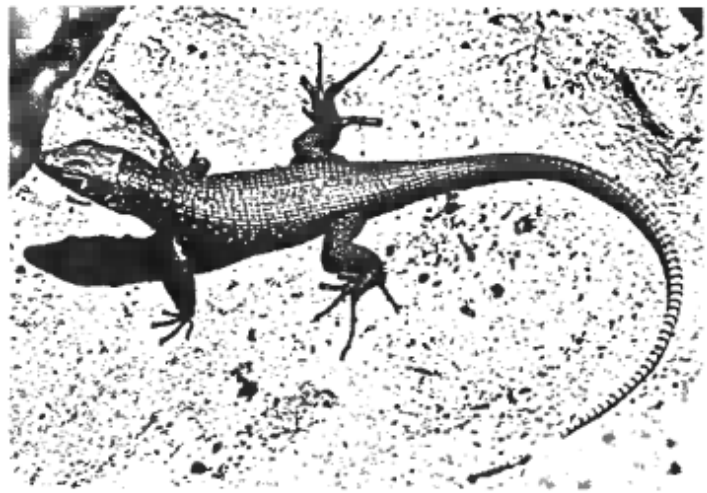


Fig. 7. *Zonosaurus tsingy*, juvenile, Ankarana National Park

when restrained alive; subdigital scales on Fingers I-V: 5-8-12-12-7/5-8-11-12-7; on Toes I-V: 6-8-14-21-13/6-10-14-21-13; femoral pores 17/18; dorsal scales keeled; ventral scales of fore- and hindlimbs, and body smooth; ventral scales of manus and pes smooth.

In life, the dorsal surfaces of the head, body, limbs, and tail are brown. Lateral surfaces of head gray. Dorsal and lateral surfaces of body with pale yellow and dark brown spots, the former being most frequent on the anterior half of body. Flanks with bluish-gray spots. Ventral surfaces of hindlimbs and tail pale gray. Throat and ventral surfaces of body and forelimbs pale yellow. Throat without longitudinal stripes or spots. Ventral surfaces of manus and pes pale brown. In preservative, the coloration has remained unchanged, except that some pale yellow and blue pigments have faded to pale brown.

Variation.—Morphometric variation is presented in Table 6. There is no sexual dimorphism in size. Live adults vary in ventral coloration; they are either yellow or grayish-blue on the throat and body. The dark brown dorsal markings may extend to the tail or form a vertebral line on the body. The specimens from Montagne de Français have pale yellow spots that are slightly more concentrated in the dorsolateral region of the anterior body, compared to those from Ankarana. The pale body spots are absent on regenerated scales.

Etymology.—The specific name *tsingy* is the Malagasy name for the karst rock formation where this species occurs.

Distribution and Habitat.—*Zonosaurus tsingy* is only known from northern Madagascar in Ankarana and Montagne de Français (Fig. 3). This species is strictly rock–dwelling as an adult; it lives in tsingy, a karst rock formation that has eroded to form sharp points and ridges, with deep vertical and horizontal cracks. The vegetation asso-

Table 6. Summary of variation in *Zonosaurus tsingy* and *Z. subunicolor*.

Character	*Zonosaurus tsingy*				*Zonosaurus subunicolor*		
	Holotype	Paratypes	UADBA	Total	UMMZ	Vences et al (1996)	Total
Total *N*	1	18	20	39	13	10	23
Male	1	3	3	7	4	?	4+
Female	0	4	3	7	8	?	8+
Juvenile	0	11	14	25	1	?	1+
Maximum SVL (mm)	75	85	81	85	84	86	86
Supralabials anterior to subocular (left/right)							
2/2	0	0	0	0	0	0	0
2/3 or 3/2	0	0	1	1	0	0	0
3/3	1	15	14	30	11	10	21
3/4 or 4/3	0	2	5	7	1	0	1
4/4	0	1	0	1	1	0	1
Supralabials posterior to subocular (left/right)							
1/1	0	0	0	0	0	0	0
1/2 or 2/1	0	1	0	1	0	0	0
2/2	1	17	20	38	13	10	23
Ventral scales (chin–cloaca)	46	44–49	44–49	44–49	43–48	45–49	43–49
Scale rows around midbody	22	21–24	21–24	21–24	22–26	22–25	22–26
Scales under 4th toe	21	20–25	20–25	20–25	18–22	19–22	18–22
Femoral pores	17–18	15–20	14–20	14–20	8–12	8–13	8–13

ciated with tsingy in the area is deciduous open canopy forest growing on rock. Juveniles occur both on tsingy, and on nearby leaf litter. Adults are never found more than a few meters from a tsingy crevice refuge. Intensive herpetofaunal surveys made by ourselves at other tsingy areas (Bemaraha, Namoroka, and Analamera) did not reveal populations of *Z. tsingy*; this suggests that this species is endemic to Ankarana and Montagne de Français.

Remarks.—Fragile body scales like those of this species also occur in *Zonosaurus subunicolor*, which is phenetically most similar to *Z. tsingy*. Fragility in both species may serve as an antipredator mechanism, and in many ways resembles the condition found in the Madagascar endemic gecko genus *Geckolepis*, which readily sheds scales when restrained. Integumentary fragility also has been reported for other Madagascan geckos—*Phelsuma breviceps*, *P. seippi*, *P. guttata*, and *P. madagascariensis* (Raxworthy and Nussbaum, 1994b).

During our first visit to Ankarana in early February 1992, only adult *Zonosaurus tsingy* were observed, but during late April 1996 many newly-hatched juveniles also were encountered. Hatching seems to be timed for the latter part of the rainy season (March-April).

IDENTIFICATION KEY FOR THE DWARF *ZONOSAURUS*

All dwarf *Zonosaurus* are small, with an adult SVL < 94 mm and 2–4 supralabials anterior to the subocular (Table 7). All other species of *Zonosaurus* are larger (adult SVL 132–230 mm, Brygoo 1985a) and typically have 4 or 5 supralabials anterior to the subocular.

1. Pale dorsolateral line on anterior half of body, broken or continuous 2

   No pale dorsolateral line on anterior half of body 5

2. Ventral scale rows in 43–50 rows between chin and cloaca; always two supralabials posterior to subocular on both sides of head; 3–4 supralabials anterior to subocular 3

   Ventral scale rows in 51–59 rows between chin and cloaca; typically one supralabial posterior to subocular (4 of 92 specimens with 2 on both sides of head); 2–3 supralabials anterior to subocular .... *Zonosaurus aeneus*

3. Lamellae under 4th toe 16–21; femoral pores 13–20; maximum SVL 93 mm 4

   Lamellae under 4th toe 22–23; femoral pores 11–15; maximum SVL 75 mm ..... *Zonosaurus bemaraha*

4. Always three supralabials anterior to subocular; maximum SVL 76 mm; always a broken pale dorsolateral line on neck and anterior third of body ..... *Zonosaurus brygooi*

   Typically 4 supralabials anterior to subocular (26 of 27 specimens with 4 supralabials on one side of head);

Table 7. Summary of diagnostic characters for the dwarf *Zonosaurus* species.

Character	*Z. aeneus*	*Z. brygooi*	*Z. bemaraha*	*Z. anelanelany*	*Z. rufipes*[1]	*Z. subunicolor*	*Z. tsingy*
Maximum SVL (mm)	75	76	75	93	88	86	85
Supralabials anterior to subocular (left/right)							
2/2	+	–	–	–	+	–	–
2/3 or 3/2	+	–	–	–	+	–	+
3/3	+	+	+	+	+	–	+
3/4 or 4/3	–	–	+	+	+	+	+
4/4	–	–	–	+	+	+	+
Supralabials posterior to subocular (left/right)							
1/1	+	–	–	–	–	–	–
1/2 or 2/1	+	–	–	–	–	–	+
2/2	+	+	+	+	+	+	+
Ventral scales (chin–cloaca)	51–59	43–50	43–48	45–50	44–51	43–49	44–49
Scale rows around midbody	18–24	20–24	22–24	20–24	22–29	22–26	21–24
Scales under 4th toe	16–22	16–21	22–23	17–20	18–24	18–22	20–25
Femoral pores	12–18	15–20	11–15	13–16	8–14	8–13	14–20
Fragile body scales	–	–	–	–	–	+	+
Dorsolateral anterior lines							
Absent	–	–	–	–	+	+	+
Broken	+	+	+	–	na	na	na
Unbroken	+	–	+	+	na	na	na
Broken + unbroken	+	–	+	+	na	na	na
Dorsolateral posterior lines	–	–	–	–	–	+	–
Throat stripes	–	–	–	–	+	–	–

[1] Based on data from Brygoo (1985a) and Vences et al. (1996).

maximum SVL 93 mm; typically unbroken pale dorsolateral line on neck and anterior third of body (broken on one side in 2 of 25 specimens) ..... *Zonosaurus anelanelany*

5. Throat with obvious bold black longitudinal lines; skin on dorsum of body not fragile ..... *Zonosaurus rufipes*

Throat lacking obvious bold black longitudinal lines; skin on dorsum of body fragile (very easily broken if restrained during handling) 6

6. Femoral pores 8–13; obvious dorsolateral lines (both dark and pale brown) between level of insertion of hindlimbs and base of tail ..... *Zonosaurus subunicolor*

Femoral pores 14–20; no obvious dorsolateral lines (dark or pale brown) between level of insertion of hind-limbs and base of tail ..... *Zonosaurus tsingy*

DISCUSSION

Our discovery of three new species of dwarf *Zonosaurus* can be attributed partly to the prior taxonomic confusion within the group. The recognition and description of *Zonosaurus tsingy* required the resolution of the *Z. subunicolor-rufipes* complex, which was discussed by Angel (1942), Mertens (1967), Brygoo (1985a), and Lang and Böhme (1989), but only resolved recently by Vences et al. (1996). Another taxonomic problem for this group of *Zonosaurus* was the lack of data published on the juvenile (and faded) holotype of *Zonosaurus aeneus* , especially in relation to the diagnosis of *Zonosaurus brygooi* (Lang and Böhme, 1989).

Biogeographic understanding for the group has been hampered by limited geographic sampling and, in a few cases, by dubious localities. The most recent example concerns the locality for six of the types of *Zonosaurus brygooi* reportedly collected by R. Seipp from "Loucoubé, Nosy-Bé "(= Lokobe, Nosy Be). *Zonosaurus brygooi* has not been found again at this northwestern locality despite intense surveys by Vences et al. (1996) and ourselves (over a period of one month), and the closest known other localities are 280–290 km to the southeast (Nosy Mangabe, Vences et al. 1996; and Ankavanana River, Masoala, 15° 18.5′ S, 50°14′ E [UMMZ 207165-78]). At least one of the *Zonosaurus brygooi* specimens from Lokobe was "terrarium kept" (Lang and Böhme, 1989), which may explain how localities (associated with live terrarium animals) became confused.

The phylogenetic relationships among the dwarf *Zonosaurus* species are currently under investigation (Raselimanana, in prep.). The only prior cladistic study is that of Lang (1990), who reported *Z. aeneus* as basal to the

Z. brygooi + *Z. rufipes* clade; the only synapomorphy for this clade is the fully pigmented blue tongue. Phenetic similarity suggests to us two obvious groups of dwarf *Zonosaurus*: 1) *Z. brygooi* + *Z. bemaraha*, and 2) *Z. subunicolor* + *Z. tsingy*. These groups and species fall into different biogeographic regions of Madagascar: *Z. aeneus* on the central High Plateau, the *Z. brygooi* group at low elevations on the East and West coastal regions, the *Z. subunicolor* group in the North, *Z. anelanelany* in the extreme Southeast, and *Z. rufipes* in the North, Northeast and Northwest. Sympatry among these species is rare, the exception is *Zonosaurus rufipes*, which occurs with *Z. subunicolor* and *Z. brygooi*.

Five of the dwarf species of *Zonosaurus* are ground-dwelling in humid forests (*Z. aeneus*, *brygooi*, *anelanelany*, *rufipes*, and *subunicolor*). Two species in particular (*Z. aeneus* and *Z. rufipes*) also are found frequently at forest edge, such as along streams or paths where there is more exposure to sun; they seem to avoid the deeply shaded areas of the forest. The only dwarf species within this group that occur in drier deciduous forest are *Z. tsingy* and *Z. bemaraha*. Both are rock-dwelling specialists, and they are restricted to the limestone karst systems of western and northern Madagascar.

The discovery of these rock-dwelling species of *Zonosaurus* further broadens the ecological adaptations seen within the genus. Most of the larger species of *Zonosaurus* inhabit the forest floor, but *Z. boettgeri* is arboreal (observed by us to a height of 10 m, and by Thorstrom [pers. com] to a height of 25 m in forest canopy) and *Z. maximus* is semiaquatic; the latter lives along river banks. The only other *Zonosaurus* we have encountered frequently on rocks is *Z. laticaudatus*, but most populations of this species (especially in western and northwestern Madagascar) occupy forests without rocky substrates. Neither of the two species of *Tracheloptychus* (the only other cordylid genus in Madagascar) are restricted to rocky substrates. By contrast, both species can be found in sandy areas. Rock-dwelling also is rare among African species of the Gerrhosaurinae (which includes *Zonosaurus*); this habitat is only known for two species— *Gerrhosaurus major* and *G. validus* (Branch, 1988). By contrast, rock-dwelling is the typical condition in the Cordylinae, including the genera *Cordylus*, *Cordylosaurs*, *Platysaurus*, and *Pseudocordylus* (Branch, 1988). Typically, the bodies are flattened in these rock-dwelling species, but this condition is not obvious in the rock-dwelling Malagasy cordylids.

The fragility of the skin of *Zonosaurus tsingy* and *Z. subunicolor* is otherwise unreported for the Cordylidae. Skin-loss as an antipredator behavior was recently reviewed for lizards by Bauer and Russell (1992), and it is known for two scincid genera and at least 10 gekkonid genera. Because the dorsal scales of all *Zonosaurus* are completely juxtaposed, skin loss in *Z. tsingy* and *Z. subunicolor* results in fractures forming on the scale sutures; typically whole square-shaped sections of scales are removed together. The complete scales (epidermis and some dermis) readily separate from the underlying dermis when subjected to any type of lateral pressure, such as when the animal is gripped. The precise mechanism for the fracture is unknown (presumably there are weakened layers within the dermis), but it is clearly facilitated by the body being thrown into lateral undulations. A similar type of movement is seen in geckos of the genus *Geckolepis*, which also readily shed scales when seized. The frequency of skin loss in the two species of *Zonosaurus* is unknown, but all individuals we observed in the field showed no signs of fresh skin damage. The scar tissue that develops in the area of scale loss is unable to reproduce the regular arrangement of the original scales.

All three new species of *Zonosaurus* occur in protected areas; therefore, their conservation status is not of immediate concern. *Zonosaurus tsingy* occurs in Ankarana National Park, a small protected area (18,225 ha) that is becoming increasingly visited by tourists. The impact of the increased tourism is not known, but much of the tsingy habitat occupied by *Z. tsingy* is extremely difficult to enter. Montagne des Français, the other site where *Z.tsingy* occurs, is protected as a classified forest. *Zonosaurus bemaraha* is currently known from a single site at Bemaraha National Park; however, the large size of this reserve (152,000 ha) and the natural protection offered by the karst limestone suggest that this species is not threatened. *Zonosaurus anelanelany* is known from Parcel One of the Andohahela National Park, and it appears to be restricted to humid forest up to 450 m elevation in extreme southeastern Madagascar. The low elevation distribution of this species is of some concern, as low elevation forest is one of the most vulnerable habitat types in this region of Madagascar. Rapid destruction of forest was underway at three sites where we found this species (Manantantely, Nahampoana, and Marovony), and the strand forest at Sainte-Luce is potentially vulnerable to a proposed mining program. Protection of the low elevation forested areas of Parcel One, Andohahela National Park, is necessary to conserve populations of *Z. anelanelany* for the long-term future.

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