

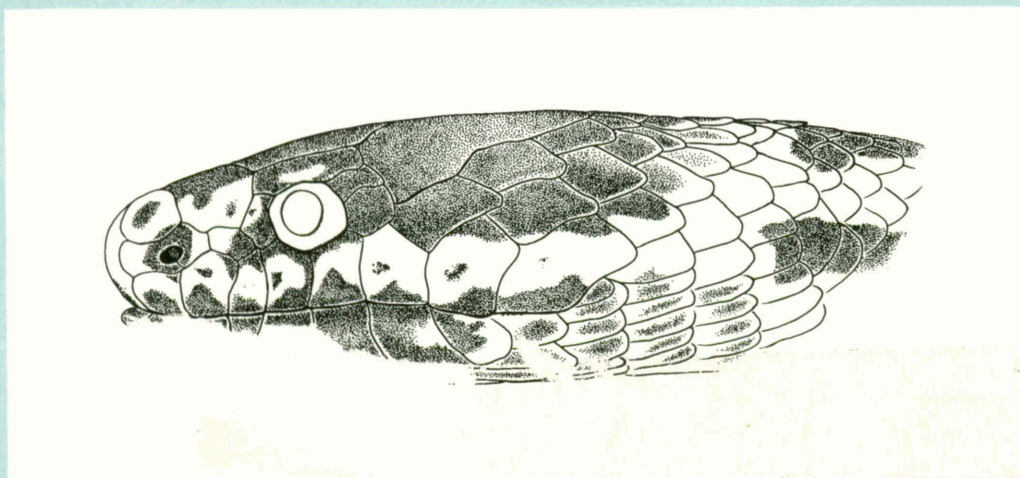
**A REVIEW OF THE MADAGASCAN  
SNAKE GENERA *PSEUDOXYRHOPUS*,  
*PARARHADINAEA*, AND *HETEROLIODON*  
(SQUAMATA: COLUBRIDAE)**

BY

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AND

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**MISCELLANEOUS PUBLICATIONS**

**MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 182**

Ann Arbor, July 30, 1994  
ISSN 0076-8405

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 182

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**A Review of the Madagascan Snake Genera  
*Pseudoxyrhopus*, *Pararhadinaea*, and  
*Heteroliodon* (Squamata: Colubridae)**

by

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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 182

Ann Arbor, July 30, 1994

## ABSTRACT

Raxworthy, C.J. and R.A. Nussbaum. 1994. A review of the Madagascan snake genera *Pseudoxyrhopus*, *Pararhadinaea*, and *Heteroliodon* (Squamata: Colubridae). *Misc. Publ. Mus. Zool. Univ. Michigan*, 182: 1-37, 25 figs. The colubrid genus *Pseudoxyrhopus*, the largest endemic Madagascan snake genus, is revised as a result of recent collections. A synopsis is provided for all species, which includes new biogeographic data and field observations for *P. ambreensis*, *P. heterurus*, *P. microps*, *P. quinquelineatus* and *P. tritaeniatus*. Three new species of *Pseudoxyrhopus* are described, two collected close to Tôlaïaro (Fort Dauphin) and a second from the Betsileo region. Based on the new material, *P. dubius* is demonstrated to be a junior synonym of *P. tritaeniatus*. *Pseudoxyrhopus occipitalis* is transferred to the genus *Heteroliodon*, and *H. torquatus* is recognized as a junior synonym of this species.

A synopsis is also presented for the genera *Heteroliodon* and *Pararhadinaea*, both previously confused with, and probably closely related to, *Pseudoxyrhopus*. An identification key is provided for all 12 species of *Pseudoxyrhopus*, *Pararhadinaea*, and *Heteroliodon*; comments on phylogenetic relationships, biogeography and conservation are also included.

Key words: *Reptilia*, *Squamata*, *Colubridae*, *Pseudoxyrhopus*, *Pararhadinaea*, *Heteroliodon*, *Madagascar*, *systematics*, *new species*.

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## INTRODUCTION

The island of Madagascar has three families, 19 genera and 66 species of snakes, including one genus and three species of boids, two genera and nine species of typhlopids, and 16 genera and 54 species of colubrids. Endemicity of Madagascan snakes is high, with just six genera (*Boa*, *Typhlops*, *Geodipsas*, *Liophidium*, *Ithycyphus*, *Lycodryas*) and four species (*Ramphotyphlops braminus*, *Ithycyphus miniatus*, *Lycodryas gaimardi*, *Liophidium vaillanti*) occurring outside Madagascar (the latter three species possibly accidentally introduced to other Indian Ocean Islands from Madagascar). The endemic colubrid genera *Heteroliodon*, *Pararhadinaea* and *Pseudoxyrhopus*, with one, two and eight currently recognized species, form an apparently closely related group with similarities in dentition, color pattern, eye size, head shape, and behavior. They are among the most poorly known Madagascan snakes. Although they have been collected from many scattered regions of the island, they are documented by very few specimens, and several species are known only from small geographic areas and are probably locally endemic.

The scarcity of museum specimens of *Pseudoxyrhopus* is striking. Guibé (1958), in his monograph of the Madagascan snakes, presented data for just 20 specimens of *Pseudoxyrhopus* representing eight species. Most of the museum material was collected during the last century, and the most recently described species was by Mocquard in 1904.

From 1989 to 1993 we collected 28 *Pseudoxyrhopus* specimens representing seven species. These specimens represent significant range extensions, clarify some aspects of ecology and behavior, and contribute to the recognition of two new synonyms and three new species. A herpetological survey of the forests in the Tôlañaro (Fort Dauphin) Fivondronana, southeastern Madagascar, yielded two new species. A third new species of *Pseudoxyrhopus* was present in the collections of the British Museum. In this paper, we describe these new species, summarize new information for the other species, and present a synopsis and revised key for the genus. One species, *P. occipitalis*, is transferred to the genus *Heteroliodon*.

A synopsis is provided for *Heteroliodon* and *Pararhadinaea*, both of which were previously confused with *Pseudoxyrhopus*. These snakes, like *Pseudoxyrhopus*, are also poorly represented in museums, and this is reflected in the most recent reviews of each genus: Guibé (1958) presented data for a single *Heteroliodon* specimen, and Domergue (1984) summarized data for four *Pararhadinaea* specimens. We present data on new museum material, including three *Heteroliodon* and three *Pararhadinaea* specimens collected by us between 1989 and 1993.

## ACKNOWLEDGMENTS

We especially thank Jean-Baptiste Ramanamanjato and Achille Raselimanana for their help in collecting some of the snakes described in this paper, and for their enthusiasm in the field. We thank David Bay for photographic assistance and Margaret Van Bolt for drawing Figures 1, 4, 5, 8, 10, 11, 15, 21, 23, and 25. We also thank E.N. Arnold, B. Clark, A. Dubois, C. McCarthy, C.J. McCoy and P. Freed for access to Museum specimens, D. Reid for donation of

specimen UMMZ 200059, M. Podestà for searching for the *Pseudoxyrhopus heterurus* type, and V. Wallach and two anonymous reviewers for comments. The expedition to Ambatovaky was funded by the following sponsors: Royal Geographical Society, Fauna and Flora Preservation Society, International Council for Bird Preservation, Conservation Foundation, Loke Wan Tho Memorial Fund, Gilchrist Educational Trust, Elmgrant Trust, Percey Sladen Trust, British Museum (Natural History), British Ornithologists' Union, and the Biological Council. The surveys made in the Tôlañaro region were funded by Quebec Iron and Titanium Inc. in cooperation with L'Office Militaire National pour les Industries Stratégiques (Madagascar) and the Canadian International Development Agency. The Montagne d'Ambre survey was supported by Earthwatch and World Wide Fund for Nature, the Masoala Survey by CARE, and the Zombitsy survey by World Wide Fund for Nature. We also wish to acknowledge the Ministère des Universités, the Ministère des Eaux et Forêts, and the Ministère de la Recherche Scientifique, whose cooperation made this research program possible.

This research was supported in part by NSF grant BSR-90-24505.

## MATERIALS AND METHODS

A total of 68 *Pseudoxyrhopus*, seven *Heteroliodon*, and three *Pararhadinaea* specimens were examined, representing almost all of the known material. All specimens in the Museum of Zoology, University of Michigan were collected in Madagascar between 1989 and 1993. Photographs of these specimens were taken soon after capture to record natural coloration. All measurements were taken on preserved material, using a ruler to the nearest millimeter. Standard colubrid scale counts were used throughout. Dentary and maxillary teeth were examined by removing the exterior gum surfaces of the *in situ* jaw for representatives of each species collected by us. Tooth sockets were included in the counts in cases of tooth loss. Tooth counts were not made of other museum material unless already displayed by dissection. Snout-vent length is abbreviated to SVL. The following museum abbreviations are used: BM, British Museum (Natural History); CM, Carnegie Museum; MNHN, Muséum National d'Histoire Naturelle, Paris; MSNM, Museo Civico di Storia Naturale di Milano; SMF, Natur-Museum und Forschungs-Institut Senckenberg; SMNS, Staatliches Museum für Naturkunde in Stuttgart; UMMZ, University of Michigan, Museum of Zoology.

## TAXONOMIC HISTORY OF PSEUDOXYRHOPUS

In 1863 Jan described *Homalocephalus heterurus*, a colubrid snake collected from an unknown locality in Madagascar. This species was placed in a new monotypic genus, which Jan defined by the following characters: rostral wider than high; divided nasal; loreal small and elongated; one preocular and two postoculars, both in contact with the parietal; temporal formula 1 + 2; eight supralabials, eight infralabials; the fifth upper labial below and in contact with the eye; smooth scales in 21 dorsal rows; divided anal; subcaudals single on the anterior section of the tail, double on the rest of the tail. Günther (1881) stated that *Homalocephalus* was preoccupied in entomology and, therefore, replaced the name with *Pseudoxyrhopus*. He also described a second species which he named *Pseudoxyrhopus micros*. Williams and Wallach (1989) recently pointed out that Günther erroneously believed *Ho-*

*malocephalus* was preoccupied by the dipteran genus *Homalocephala* Zetterstelt 1833. Smith et al. (1992) petitioned the International Commission on Zoological Nomenclature (ICZN) to conserve *Pseudoxyrhopus* and suppress *Homalocephalus*, a proposal we support, because *Pseudoxyrhopus* has been used continuously for the last 110 years. In anticipation of this recommendation being endorsed by the ICZN, we continue to use *Pseudoxyrhopus*.

The type species of *Pseudoxyrhopus* is *Homalocephalus heterurus* by originally monotypy (Brygoo, 1983; Jan, 1863). Welch (1982) erroneously considered *Pseudoxyrhopus microps* to be the type species.

Boulenger (1890) redefined the genus as follows: 16–18 maxillary teeth, the two posterior teeth strongly enlarged and separated by a space from the anterior teeth; anterior dentary teeth much larger than the posterior, and increasing in size to the fifth, sixth or eighth; head scarcely distinct from neck; eye small, pupil round; cylindrical body; smooth dorsal scales without pits in 17 to 25 rows; short tail with subcaudals in two rows, or partly in two rows. Boulenger (1893) further modified this definition to include: ventrals rounded, hypophyses developed throughout the vertebral column.

Based on the character of the enlarged dentary teeth, Boulenger (1890) moved *Liophis quinquelineatus*, *Coronella microps* and *Xenodon punctatus* into *Pseudoxyrhopus*. He considered *Liophis imerinae* to be a junior synonym of *Coronella microps*, based on their similar morphology, but because *Pseudoxyrhopus microps* was preoccupied *Pseudoxyrhopus imerinae* was conserved. *Xenodon punctatus* (not *Liophis punctatus*, as shown by Welch, 1982) had been described by Peters (1880) and was collected in Brazil. However, Boulenger (1890), after having viewed a sketch of the dentary teeth sent by Dr. Matschie in which the fourth and fifth teeth were drawn enlarged, thought this was a *Pseudoxyrhopus* species and that its origin would prove to be Madagascar. The following *Xenodon punctatus* features were also shared with the *Pseudoxyrhopus* species: supraocular not more than half the width of the frontal, loreal longer than deep, one preocular, two postoculars, temporals 1+2, and divided anal. Mocquard (1909) noted that the teeth were not mentioned in the original description and he questioned Boulenger's decision to place this species in *Pseudoxyrhopus*.

Hoge (1958) examined the holotype of *Xenodon punctatus* and found it differs from all *Pseudoxyrhopus* in that the anterior dentary teeth are not enlarged. In addition, Guibé (1958) noted that, in the original description, the specimen was reported to have three supralabials in contact with the eye, a condition not known in any specimen of *Pseudoxyrhopus*. Hoge (1958) placed *Pseudoxyrhopus punctatus* in the genus *Sordellina* Procter 1923 and considered *S. brandon-jonesii* Procter 1923 and *S. pauloensis* Amaral 1923 to be synonyms of *S. punctata*. *Sordellina punctata* is endemic to Brazil, and there is no evidence to support a Madagascan origin for the holotype. Hoge's (1958) findings were not cited by subsequent authors (e.g., Welch, 1982; Brygoo, 1983), although recent Madagascan colubrid lists (Blanc, 1972; Brygoo, 1983; IUCN/UNEP/WWF, 1987) do not include *Pseudoxyrhopus punctatus*.

The status of *Pseudoxyrhopus tritaeniatus* and *P. dubius* has been controversial. Boulenger (1896, 1915) considered *P.*

*tritaeniatus* and *P. dubius* to be synonyms of *P. microps* (although no justification was given). Mocquard (1909), Angel (1934), and Guibé (1958) recognized *P. tritaeniatus* and *P. dubius* as valid species. Domergue (1969) commented on the similarity of *P. tritaeniatus* and *P. dubius* to *P. microps* and suggested they may deserve subspecies recognition only.

Boulenger (1915) also placed *Rhabdotophis subcaudalis* Werner 1909 in the genus *Pseudoxyrhopus*, although this taxon was subsequently recognized by Guibé (1958) to be a junior synonym of *Pararhadinaea melanogaster* Boettger 1898. The loreal scale is absent in *Pararhadinaea*.

The genus *Pseudoxyrhopus* is currently represented by eight species: *P. ambreensis* Mocquard, *P. dubius* Mocquard, *P. heterurus* (Jan), *P. imerinae* (Günther), *P. microps* Günther, *P. occipitalis* Boulenger, *P. quinquelineatus* (Günther), and *P. tritaeniatus* Mocquard. The genus was most recently reviewed by Guibé (1958) and Brygoo (1983).

#### THE STATUS OF *PSEUDOXYRHOPUS TRITAENIATUS* AND *P. DUBIUS*

*Pseudoxyrhopus tritaeniatus* and *P. dubius* were always considered to be morphologically very similar. Angel (1934) used the condition of the anal plate (divided or entire) to separate the two species, and later Guibé (1958) used the following pair of characters: *Pseudoxyrhopus tritaeniatus*, anal divided and three longitudinal dark lines on body; *P. dubius*, anal entire and four longitudinal dark lines on body. Both snakes are very rare. *Pseudoxyrhopus tritaeniatus* is known only from the holotype, and *P. dubius* is represented currently by just five specimens in Paris (MNHN), three of which were not available to Angel or Guibé. One specimen, MNHN 1950.153, a skin of *Pseudoxyrhopus dubius* collected from Ambatomainty, which was apparently examined by Guibé (1958), could not be found in 1992. We collected a further three snakes and were given a fourth specimen that we identified as either *Pseudoxyrhopus dubius* or *P. tritaeniatus*.

The holotype of *Pseudoxyrhopus tritaeniatus*, MNHN 1891.24, has three dark longitudinal lines on the body, unlike the nine other specimens, which have four or five lines. However, the median vertebral dark line of the *Pseudoxyrhopus tritaeniatus* holotype is very broad, giving the impression it represents the fusion of the two median lines seen in the specimens referred to as *P. dubius*. The *Pseudoxyrhopus dubius* holotype, MNHN 1898.7, has four dark longitudinal lines on the body, with the two median dark lines separated by a pale vertebral line.

Three specimens intermediate in color pattern were examined: MNHN 1978.48 has two dark median lines which are nearly fused, being separated by a very thin pale vertebral line one scale wide; MNHN 1930.365 and UMMZ 203649 have five dark longitudinal lines, the additional fifth line being a thin, broken, vertebral line between the two dark median lines. These three specimens represent intermediate color forms between the *Pseudoxyrhopus dubius* holotype (a pair of well separated dark median lines) and the *P. tritaeniatus* holotype (complete fusion of the dark median lines to form a single broad vertebral line).

The condition of the anal plate is variable within the nine



specimens with the typical coloration of *Pseudoxyrhopus dubius*. Four specimens have divided anals, three specimens are undivided and two (including the holotype of *Pseudoxyrhopus dubius*, as noted by Angel, 1934) are semidivided by an incomplete median fold or suture. There is no correlation between the anal plate condition and either color pattern or sex.

With the exception of the variation in anal plate condition and the number of longitudinal lines, this sample of ten snakes is extremely homogeneous and different from all other *Pseudoxyrhopus*. We believe, therefore, that the condition of the anal plate (divided, semidivided or entire) and the number of longitudinal lines (three to five) represents variation within a single species and regard *Pseudoxyrhopus dubius* as a junior synonym of *P. tritaeniatus*.

#### THE STATUS OF *PSEUDOXYRHOPUS OCCIPITALIS*

The type of *Pseudoxyrhopus occipitalis* apparently has not been examined since this species was described by Boulenger (1896), and no other specimen has been subsequently reported in the literature. At the British Museum (Natural History), we examined the type (BM 1946.1.12.28) plus a second specimen (BM 1930.7.1.238). Both of these proved to resemble closely *Heteroliodon torquatus*, a species we are familiar with in the field.

The genus *Heteroliodon* Boettger 1913 is readily distinguished from *Pseudoxyrhopus* by the following characters: the anterior dentary teeth are not enlarged and the eye is large. The holotype of *Pseudoxyrhopus occipitalis* does not have greatly enlarged anterior dentary teeth. The middle teeth are considerably larger than the anterior and posterior teeth. The eye is large, unlike all other *Pseudoxyrhopus*. The teeth of the other specimen, BM 1930.7.1.238, had not been displayed by dissection, but the eye size is similar to that of the holotype of *P. occipitalis*, and the two resemble each other very closely in scalation and coloration. The characters of both specimens closely fit the description of the genus *Heteroliodon* given by Boettger (1913) and Guibé (1958), and, therefore, we propose to transfer *Pseudoxyrhopus occipitalis* to the genus *Heteroliodon*.

The only species currently in the genus *Heteroliodon* is *H. torquatus* Boettger 1913. The morphological characters of the holotype of *H. torquatus* are so similar to the holotype of *H. occipitalis* (see synopsis) that we conclude they represent the same species, and, therefore, based on priority, *H. torquatus* is designated a junior synonym of *H. occipitalis*.

#### SYNOPSIS

##### *Pseudoxyrhopus* Günther

*Pseudoxyrhopus* Günther, 1881:359. Type species *Homalocephalus heterurus* Jan, 1863, by monotypy.

DIAGNOSIS.—Colubrids without grooves in teeth; one or two posterior teeth of maxilla strongly enlarged and separated by a diastema from anterior teeth; anteriormost dentary teeth increase in size to fifth or sixth and are larger than

posteriormost teeth; loreal scale present; eye small, diameter less than 0.3 times head depth at midorbit.

DESCRIPTION.—Teeth without grooves; 9–18 maxillary teeth, the posteriormost one or two teeth strongly enlarged and separated by a diastema from the anterior teeth; 14–18 dentary teeth, the anteriormost teeth increase in size to the fifth or sixth and are larger than the posteriormost teeth; hypapophyses developed throughout the vertebral column; head scarcely distinct from neck; eye small, pupil round; eye diameter 0.2–0.3 times head depth at midorbit; cylindrical body; smooth dorsal scales without apical pits, in 19 to 25 longitudinal rows at midbody; short tail with 37–89 subcaudals, paired, or partly paired and partly single; anal plate divided, semidivided or entire; rostral scale much wider than high, clearly visible when viewed dorsally; 7–9 supralabials; internasals shorter than prefrontals; nasal divided or semidivided; loreal present.

CONTENT.—Nine species: *Pseudoxyrhopus ambreensis* Mocquard, *P. ankafinaensis* n. sp., *P. heterurus* (Jan), *P. imeriniae* (Günther), *P. kely* n. sp., *P. microps* Günther, *P. quinquelineatus* (Günther), *P. sokosoko* n. sp., and *P. tritaeniatus* Mocquard.

DISTRIBUTION.—Madagascar. All known localities are shown on Figure 1.

##### *Pseudoxyrhopus ambreensis* Mocquard Figures 2 and 3

*Pseudoxyrhopus ambreensis* Mocquard, 1894:4.

HOLOTYPE.—MNHN 1893.213, sex and maturity not known, from "Montagne d'Ambre, Mararaomby, Madagascar," collected by Mr. Alluaud and Mr. Belly.

MATERIAL EXAMINED.—MNHN 1893.213 (holotype); UMMZ 200061, adult male, collected 21 November 1991 by Loren Caira at Antomboka River, 12°32'E, 49°10'S, 1200 m altitude, Antsiranana (Diégo Suarez) Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar; UMMZ 200062–3, juvenile females, collected 14 December 1991 by R.A. Nussbaum at the Botanical Garden, Montagne d'Ambre National Park, 12°31'E, 49°11'S, 1000 m altitude, Antsiranana (Diégo Suarez) Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar.

DIAGNOSIS.—A *Pseudoxyrhopus* with 21 rows of dorsal scales on midbody, seven supralabials, and a pale nuchal collar.

DESCRIPTION OF HOLOTYPE.—SVL 235 mm; tail length 60 mm; 21 rows of smooth dorsal scales at midbody; body round in cross section; 146 ventrals; 49 paired subcaudals (extreme tail tip missing); anal divided; seven supralabials, third and fourth contacting eye; nine infralabials, four in contact with anterior genials; rostral wider than high, visible from above; internasals shorter than prefrontals; frontal hexagonal, as long as wide, shorter than parietals, shorter than distance between anterior margin of frontal and snout tip; one loreal, as high as wide; nasals semidivided by inferior suture; one preocular; two postoculars; temporals 1 + 2 + 3; rounded, blunt snout; eye small, diameter 0.23 times head depth at midorbit, with round pupil; head slightly distinct from neck.

Dorsum of body and tail uniform pale brown. Head



FIG. 1. Localities of *Heteroliodon*, *Pararhadinaea*, and *Pseudoxyrhopus*.

slightly darker brown than body with faint, pale nuchal collar. Supralabials marked by pale line. Venter of head, throat, body, and tail immaculate pale brown.

VARIATION.—The other examined specimens, UMMZ 200061, 200062, 200063, vary as follows (specimen data in same sequence as UMMZ numbers): SVL 333 mm, 227 mm, 238 mm; tail length 90 mm, 58 mm, 60 mm; ventrals 146, 152, 154; subcaudals 54, 54, 52. The dentition of UMMZ 200061 was examined (the teeth of the holotype could not be seen). There are 12 + 1 maxillary teeth, the posteriormost tooth considerably enlarged and separated by a gap from the

anterior 11 teeth. Sixteen dentary teeth are present, the six anterior teeth enlarged compared to the ten posterior teeth. *Pseudoxyrhopus ambreensis* is unusual compared to most other *Pseudoxyrhopus* species in that there is just a single enlarged posterior maxillary tooth rather than two.

The color in life of UMMZ 200061, 200062, and 200063 was dark brown dorsally on the head, body, and tail, with a sharp transition to white between scale rows II-III on the body and tail (Figs. 2 and 3). The tip of the snout is marked by an orangish-red spot that extends across the rostral, nasal, and first supralabial. The supralabials have a white, some-



FIG. 2. *Pseudoxyrhopus ambreensis*, UMMZ 200061.

what zigzagged line just below their dorsal borders from the first labial to the neck (Fig. 2); this line merges into a broad, pale brown nuchal collar. The anterior border of the transverse nuchal collar abuts the posterior edge of the parietals. The collar is three transverse scale rows in width and extends ventrally to the lateral white line on the neck (Fig. 2). The body is marked by a faint pale brown line on scale row V, beginning near midbody and terminating above the cloaca. The tip of the chin is dark brown fading to white by the first ventral scale. The venter of the body and tail is white with a few very fine pale brown spots on some ventral and subcaudal scales. The iris is red, and the tongue tip white.

**HABITAT AND DISTRIBUTION.**—The holotype locality is “Mararaomby,” Montagne d’Ambre. On the most recent topographic map of Montagne d’Ambre (Foiben Taosar. Mad., 1986), we found a mountain top called Maraoamby, which is probably the collecting site of this specimen. The summit is at 940 m altitude, 12°30’S, 49°11’E; and although the forest is now partly degraded, there was probably primary rainforest between 900–940 m when Alluaud and Belly visited Montagne d’Ambre.

The time of capture and habitat description of each

UMMZ specimen are: UMMZ 200061, 0900–1600 h inside a freshly opened rotten log; UMMZ 200062 and 200063, 1230 h in soil under rotten logs; a freshly killed headless body UMMZ 203643, probably of this species, was found on a path at 1600 h, 29 November 1991, at 1100 m; and a decomposing head UMMZ 203644 was found at 1500 h, 11 December 1991, on a trail at 1050 m altitude. Both UMMZ 203643–4 had probably been partly eaten by mongooses. *Pseudoxyrhopus ambreensis* was found only in primary rainforest between about 900 and 1200 m altitude.

The rainforest in the Montagne d’Ambre Mountains (frequently called Ambohitra on modern maps) is completely isolated from the otherwise continuous Sambirano/Eastern rainforest belt, and the lack of specimens from outside this area (Fig. 4) makes us believe this species is endemic to the Montagne d’Ambre Mountain Range.

**REMARKS.**—This is one of the smallest *Pseudoxyrhopus* species. The largest examined specimen, UMMZ 200061, SVL 333 mm, is a mature male with developed testes. The smallest female (UMMZ 200062, SVL 227 mm) is immature, while the other female (UMMZ 200063, SVL 238 mm), appears to be nearly sexually mature.

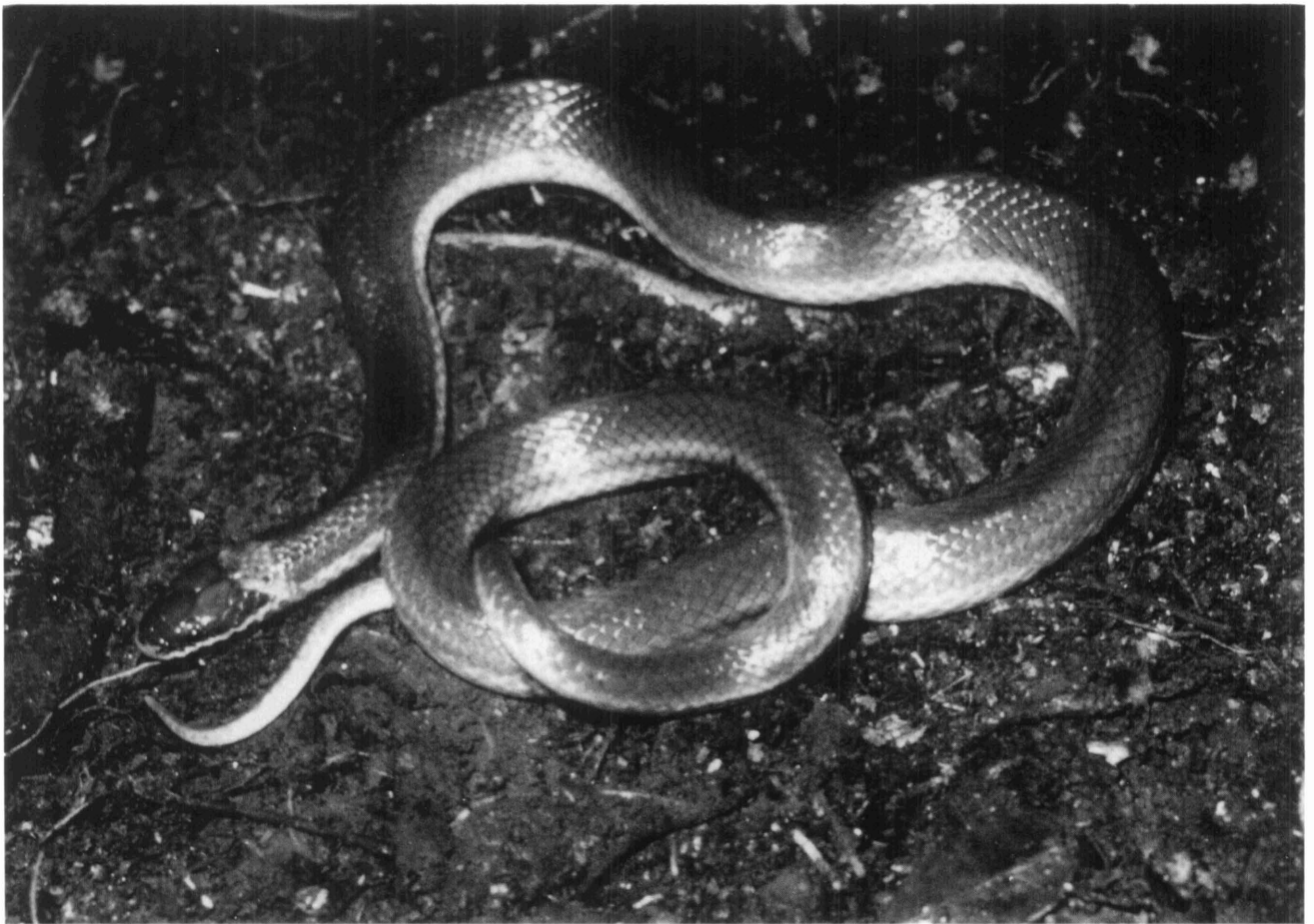


FIG. 3. *Pseudoxyrhopus ambreensis*, UMMZ 200063.

*Pseudoxyrhopus ankafinaensis* new species  
Figures 5 and 6

HOLOTYPE.—BM 1882.2.25.65, adult male, from “Ankafana, Betsileo, Madagascar” (actually Ankafina, see remarks), collected probably mid-February to mid-March 1880 (see remarks) by the Rev. W.D. Cowan.

DIAGNOSIS.—A *Pseudoxyrhopus* with 25 dorsal scale rows at midbody, short parietal scales equal in length to frontal, loreal scale almost as high as long, body dark brown dorsally, supralabials and rostral marked by a continuous white line.

DESCRIPTION OF HOLOTYPE.—Specimen poorly fixed posteriorly where it is soft but undamaged, except that tail tip is missing; SVL 945 mm; tail 119 mm (tail tip missing); 25 rows of smooth dorsal scales at midbody; body round in cross section; 206 ventrals; 46 paired subcaudals (tail tip missing); anal divided; eight supralabials, fourth and fifth contacting eye; infralabials, ten left and eight right, four in contact with anterior genials; anterior and posterior genials equal in length; rostral wider than high and visible from above; internasals shorter than prefrontals; left prefrontal has irregular border with frontal (Fig. 5); frontal almost pentagonal (notched on anterior border by left prefrontal), as long as wide, equal in length to parietals, longer than distance between anterior margin of frontal and snout tip; loreal almost

as high as long; nasal partly divided, on the left side by an inferior suture and on the right side by inferior and superior sutures that do not meet; one preocular, two postoculars; temporals 1+3+3 (left) and 1+3+4 (right); snout bluntly rounded; eye small, diameter 0.2 times head depth at midorbit, pupil round; head barely distinct from neck; 12+2 maxillary teeth (left side), two posteriormost teeth much larger and separated by diastema from anterior teeth; 18 dentary teeth, six anteriormost increasing in size to sixth, followed by 12 posterior teeth that are smaller than anterior teeth.

Coloration in alcohol dark brown dorsally on head, body, and tail. Sharply defined white line crosses all supralabials, nasals and rostral (Fig. 5). Lower edge of supralabials has brown line with denticulated upper border posterior to second supralabial. Faint trace of broken, median brown line on neck between transverse scale rows III to VII and very faint hint of slightly paler brown, diffuse transverse band forming a nuchal collar. Body and tail without dorsal longitudinal lines (Fig. 6). Chin pale grey with small irregular pale brown spots which decrease in size and density on anterior ventrals. Venter and undersurface of tail pale brown, marked by very faint slightly darker brown spots. Faint median longitudinal line on posteriormost 20 ventral scales of body and undersurface of tail.

VARIATION.—Known only from the holotype.

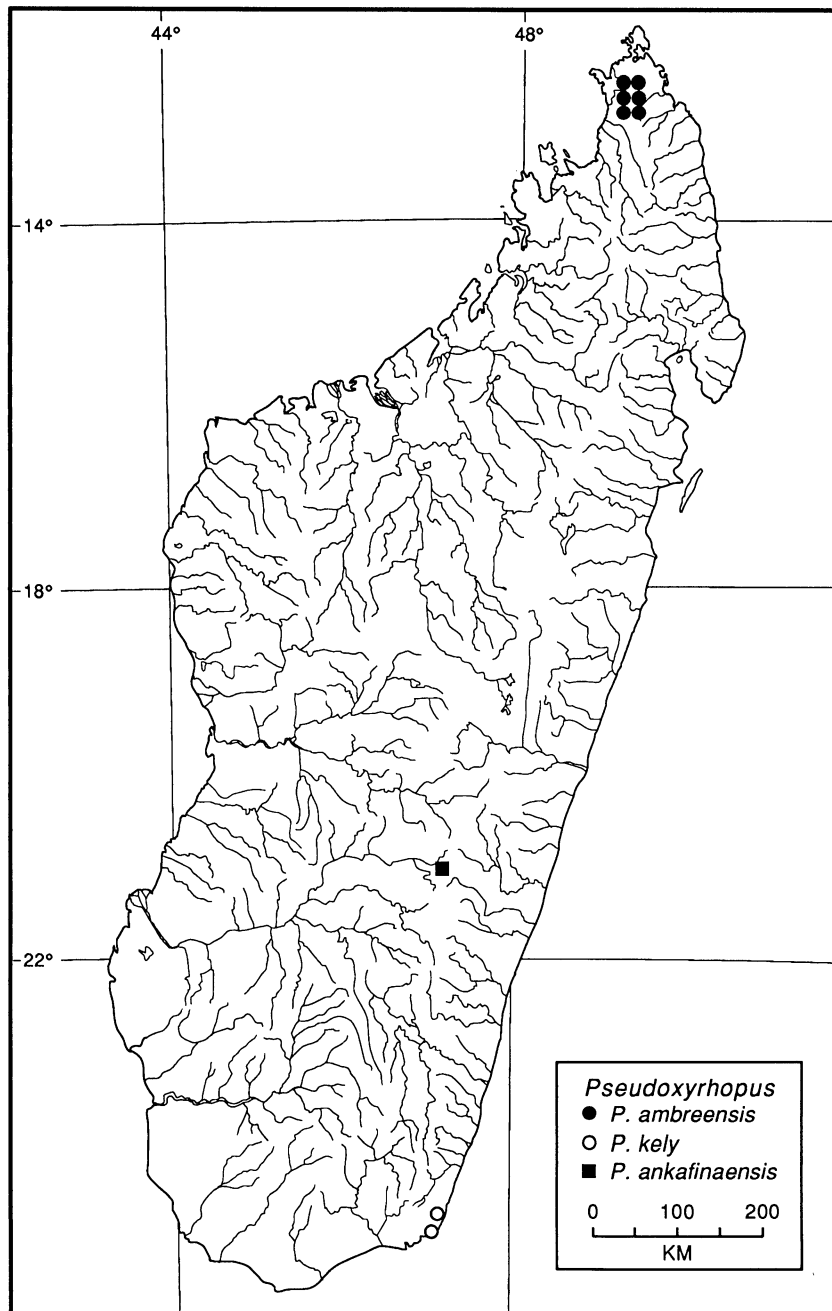


FIG. 4. Distribution of *Pseudoxyrhopus ambreensis*, *Pseudoxyrhopus kely*, and *Pseudoxyrhopus ankafinaensis*.

ETYMOLOGY.—The name “ankafinaensis” refers to the type locality, Ankafina Mountain.

JUSTIFICATION.—Only two other *Pseudoxyrhopus* species, *P. microps* and *P. tritaeniatus*, have 25 rows of dorsal scales, more than 200 ventral scales, and reach a SVL of more than 800 mm. *P. ankafinaensis* can be readily separated from both these species by its shorter parietal scales, which are the same length as the frontal (a condition that does not occur in any other *Pseudoxyrhopus* species).

*Pseudoxyrhopus ankafinaensis* also differs from *P. microps* in

the shape of the loreal scale, which is always elongated (twice as long as high) in *P. microps* compared to *P. ankafinaensis* in which the loreal is nearly as high as long (1.4 to 1.5 times as long as high). Judging from the degree of tail taper in *Pseudoxyrhopus ankafinaensis*, this species almost certainly has fewer subcaudals in the undamaged tail (probably about 55–65) than *P. microps* (70–89), although, because the tail tip is missing in the holotype, it is impossible to be precise.

*Pseudoxyrhopus ankafinaensis* also differs from *P. tritaeniatus* by having a white snout line and an unstriped dark brown

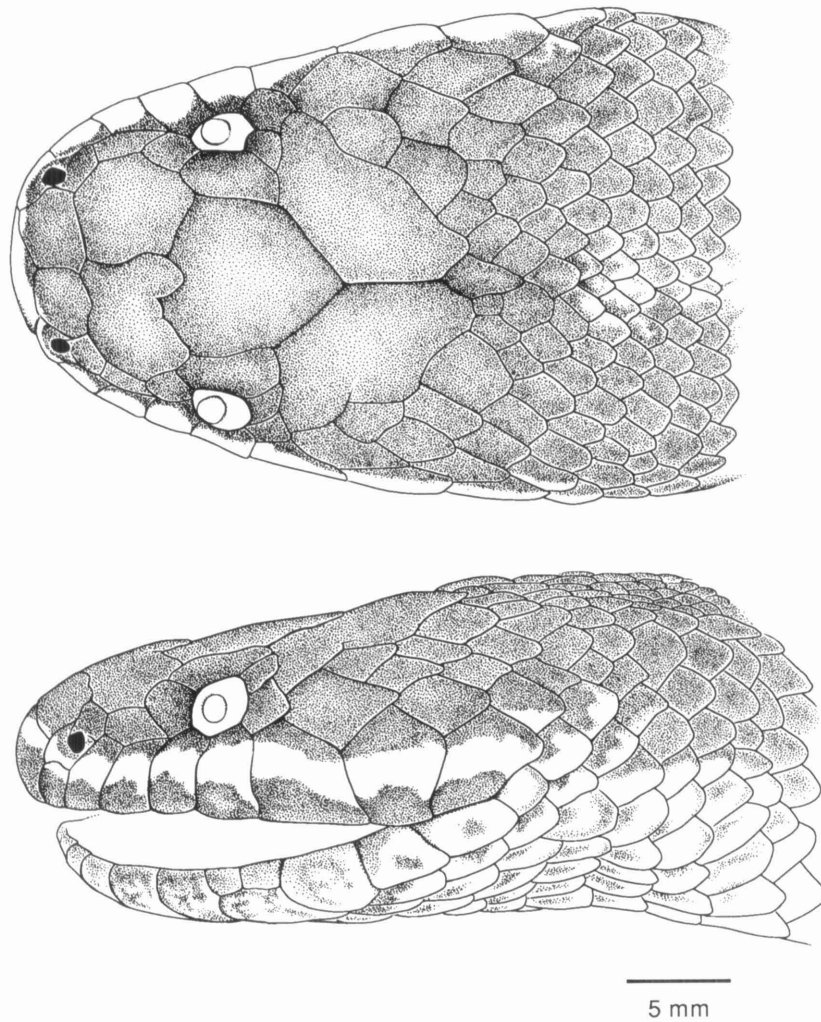


FIG. 5. Dorsal and lateral views of *Pseudoxyrhopus ankafinaensis* holotype, BM 1882.2.25.65.

body. *Pseudoxyrhopus tritaeniatus* lacks a white snout line, and the body is red with three to five dark brown longitudinal lines. About half the *Pseudoxyrhopus tritaeniatus* specimens (four of the nine known specimens) have an undivided or semidivided anal plate, which is unknown for any other *Pseudoxyrhopus* species, including *P. ankafinaensis*.

**HABITAT AND DISTRIBUTION.**—The holotype locality is “Ankafana,” a locality we were unable to trace using a Gazetteer (Dept. of Interior, 1955). However, the collector, Rev. W. Deans Cowan, also collected small mammals in Madagascar, including the types of *Microgale cowani* and *M. longicaudata*, which were deposited at the British Museum at the same time (1882) as the holotype of *Pseudoxyrhopus ankafinaensis*. MacPhee (1987) lists the type locality of both these species as “Ankafina [not Ankafana] forest, eastern Betsileo.” The mammal specimens from Ankafina were collected by Cowan between mid-February and mid-March, 1880 (MacPhee, 1987), and it seems most likely that the holotype of *Pseudoxyrhopus ankafinaensis* was also collected at that time.

Ankafina is a small forested mountain located at 21°12'S,

47°13'E, 3 km west of Tsarafidy Village, on the main route between Fianarantsoa and Antananarivo, two of the largest towns on the High Plateau (Fig. 4). The Ankafina rainforest survived as part of a strip of native forest, approximately 1–3 km wide and 10 km long, based on aerial surveys done in the 1950's and 1960's (Inst. Géog. Nat., 1973). Its current size is unknown. The altitude of the forest in this area is between 1300 and 1540 m. *Pseudoxyrhopus ankafinaensis* may also occur in other forest fragments of similar altitude in the Betsileo and possibly Merina regions of the High Plateau, although these forests are being eliminated by fire and degraded or cleared.

*Pseudoxyrhopus heterurus* (Jan)  
Figure 7

*Homalocephalus heterurus* Jan, 1863:286.

*Pseudoxyrhopus heterurus* Günther, 1881:359. First use of combination.

**HOLOTYPE.**—Destroyed during the Second World War

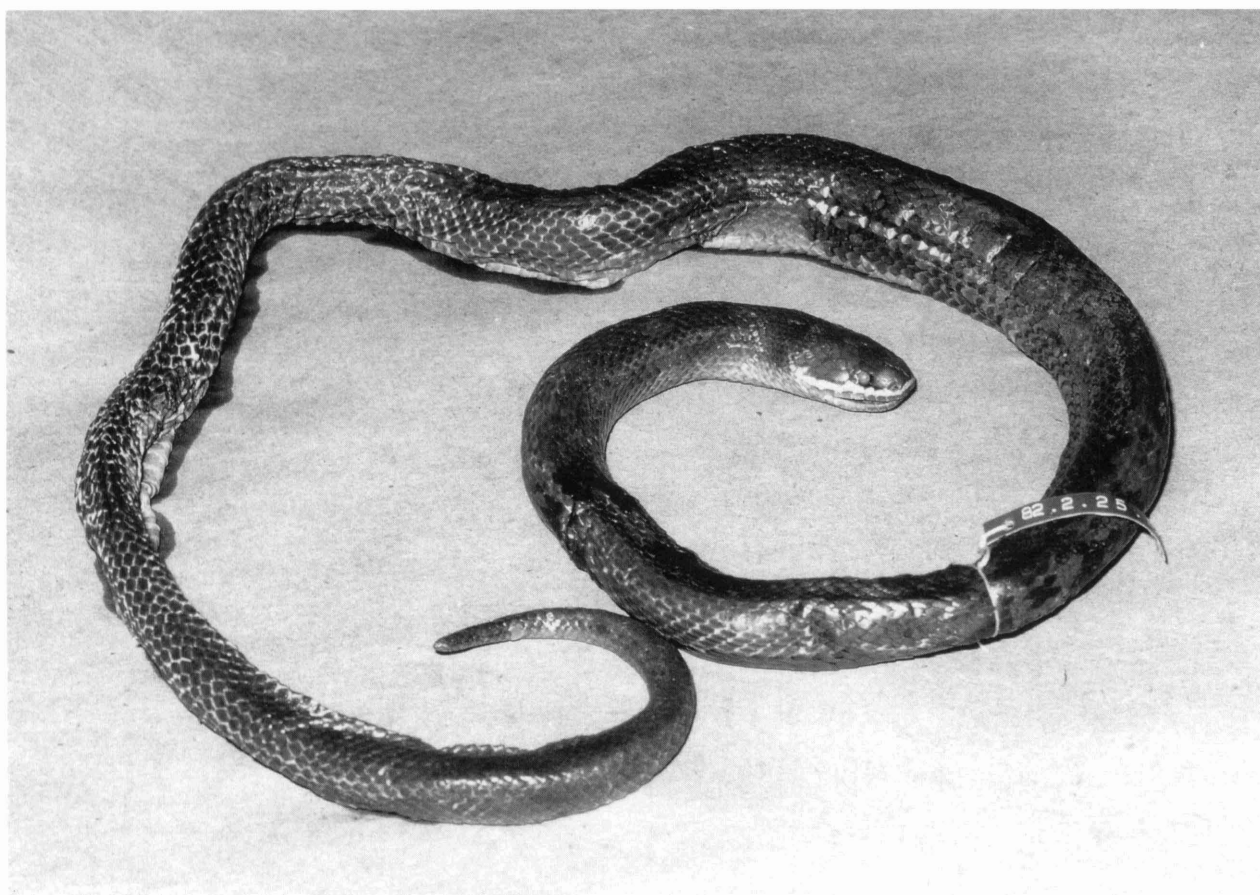


FIG. 6. *Pseudoxyrhopus ankafinaensis* holotype, BM 1882.2.25.65.

*vide* Dr. M. Podestà, *in litt.*, 30 September 1991; MSNM number unknown, sex and maturity not known, from "Madagascar," collected by unknown collector.

**MATERIAL EXAMINED.**—MNHN 583, sex and maturity unknown, collected by Coquerel in "Madagascar"; MNHN 1986.1372, sex and maturity unknown, collected 4 May 1967 by J. J. Petter at "Maroantsetra, Madagascar"; UMMZ 192018, adult female, collected 25 March 1990 by C.J. Raxworthy at Ambatovaky Special Reserve, 16°51'S, 49°25'E, 400 m altitude, Soanierana Ivongo Fivondronana, Toamasina (Tamatave) Province, Madagascar; UMMZ 195848, adult female, collected 12 March 1991 by C.J. Raxworthy at Manombo Special Reserve, 23°02'S, 47°44'E, 10 m altitude, Farafangana Fivondronana, Fianarantsoa Province, Madagascar; UMMZ 203645, adult female collected 4 December 1992 by C.J. Raxworthy at Manantenina River, Marojejy Reserve, 14°27'S, 49°47'E, 360 m altitude, Sambava Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar.

**DIAGNOSIS.**—A *Pseudoxyrhopus* with 21 dorsal scale rows at midbody; bluntly rounded snout; eight supralabials; anterior subcaudals undivided, posterior subcaudals divided; supralabials and rostral with white spots, which are sometimes partly fused to form a thin broken line; body coloration dark brown.

**DESCRIPTION OF UMMZ 192018.**—Ovaries fully devel-

oped with seven (right) and eight (left) small eggs in the oviduct, maximum egg size 4 x 3 mm. Snout-vent length 510 mm; tail length 95 mm; 21 rows of smooth dorsal scales at midbody; body round in cross section; 160 ventrals; 42 paired subcaudals, 27 anteriormost subcaudals in a single row, remainder in a double row; anal divided; eight supralabials, fourth and fifth contacting eye; nine infralabials, five in contact with anterior genials; anterior and posterior genials equal in length; rostral wider than high and visible from above; internasals shorter than prefrontals; frontal pentagonal, 1.1 times as long as wide, shorter than parietals, same length as distance between anterior margin of frontal and snout tip; loreal not quite as high as long; nasals divided; one preocular; two postoculars; temporals 1+2+3; bluntly rounded snout; eye small, diameter 0.22 times head depth at midorbit, pupil round; head slightly distinct from neck; 14+2 maxillary teeth, gradually increasing in size posteriorly, with a diastema before two posteriormost teeth, which are largest; 16 dentary teeth, anteriormost teeth increasing in size posteriorly to sixth, followed by ten posterior teeth that are smaller than anterior teeth.

Coloration in life uniform dark brown or brownish-purple dorsally on head, body, and tail (Fig. 7). A broken thin white line from snout to posterior supralabial, crossing supralabials, rostral, and nasals. Ventrally, chin spotted dark

brown, heaviest at anterior tip, fading to white on throat. Venter white, with a few tiny pale brown spots on anterior margin of each ventral scale. Undersurface of tail marked by a diffuse median dark brown line.

After three months in formalin and one year in alcohol, dorsal coloration dark brown. All other coloration unchanged.

**VARIATION.**—The fine illustration of the holotype (Jan and Sordelli, 1866: livr. 17, pl. 4, fig. 2i) shows the maxillary teeth arrangement as 13+2. The nasals of UMMZ 195848 are semidivided by an inferior suture. Other morphometric variation is given in Table 1.

**HABITAT AND DISTRIBUTION.**—The known time of capture and habitat description for each specimen are: UMMZ 192018, 2300 h, forest floor, primary rainforest; UMMZ 195848, 2330 h, forest floor, primary rainforest; UMMZ 203645, 1130 h, inside a rotten log, at least 30 m from the closest stream, bamboo dominated primary rainforest.

Three other snakes of this species were seen in the field: two adults on the forest floor at 2000 h and 2330 h, primary forest, 15°30'S, 49°46'E, 5–20 m altitude, Nosy Mangabe Island Special Reserve, Maroantsetra Fivondronana, Toamasina (Tamatave) Province, Madagascar, found 13 October 1985 by Q. Bloxam and identified by C.J. Raxworthy (see Raxworthy, 1988: fig. 5). Another specimen, which escaped from its bag after having been identified, was collected at 2000 h on the forest floor in primary rainforest, 16°51'S, 52°00'E, 600 m altitude, Ambatovaky Special Reserve, Soanierana Ivongo Fivondronana, Toamasina (Tamatave) Province, found 24 February 1990 by C.J. Raxworthy. All three of these snakes had undivided anterior subcaudal scales.

The new localities demonstrate that this species is widely distributed in the eastern rainforest belt between latitudes 16° and 23°S and ranges in altitudes from 0 to 600 m (Fig. 8). We strongly suspect this species is confined to lowland primary rainforest and is almost exclusively nocturnal and ground-dwelling.

**REMARKS.**—The holotype was reported to be destroyed during the Second World War, along with all of Jan's collection at the Museo Civico di Storia Naturale di Milano (Dr. M. Podestà, *in litt.*, 30 September 1991). We were unable to trace the catalogue number of the holotype. Jan (1863) reported only 35 subcaudal scales in the holotype, which is fewer than the number of subcaudals in the other nine specimens (45–59). This suggests that either the tail had been truncated or that Jan's count is erroneous. Sordelli's illustration of the holotype (Jan and Sordelli, 1866: livr. 17, pl. 4, fig. 2) does not show a damaged tail tip, and the total subcaudal count from the illustration is 52 scales. The anterior 15 subcaudals are shown undivided, while the description (Jan, 1863) gives this as 14. The illustration apparently was meant to show accurately the scalation of the holotype, which probably did have about 52 subcaudals rather than the 35 given in the description. Possibly this error was produced by a transposition from 53 to 35.

Guibé (1958) presented some scale counts for four *Pseudoxyrhopus heterurus* specimens without indicating their source. We think the specimen with 155 ventrals is Jan's holotype. The specimen with 150 ventrals and 53 subcaudals

is almost certainly MNHN 583. The other two specimens, with 142 ventrals and 45 and 47 subcaudals, are unknown to us. Both these specimens have similar ventral and subcaudal counts to *Pseudoxyrhopus sokosoko* n. sp., although Guibé reports they have undivided subcaudals.

*Pseudoxyrhopus imerinae* (Günther)

Figure 9

*Coronella microps* Boulenger, 1888:104. Preoccupied.

*Liophis imerinae* Günther, 1890:71.

*Pseudoxyrhopus imerinae* Boulenger, 1890:313. First use of combination.

**TYPE MATERIAL.**—BM 1887.12.22.34 and 1887.12.22.35 (1946.1.12.7 and 1946.1.12.8) (syntypes of *Coronella microps*), sex unknown, juveniles, from "Madagascar," collected by the Rev. Baron. BM 1889.8.28.22 (1946.1.7.80) (holotype of *Liophis imerinae*), sex and maturity unknown, "in the forest district east of Imerina, Madagascar," collected by the Rev. J. Wills.

**MATERIAL EXAMINED.**—BM 1887.12.22.34 and BM 1887.12.22.35 (syntypes); BM 1889.8.28.22 (holotype of *Liophis imerinae*); BM 1895.10.29.60, female, maturity unknown, collected by Rev. R. Baron from "Imerina," Madagascar; MNHN 1891.393, female, maturity unknown, collected by Sikora in "Madagascar"; MNHN 1950.152, sex and maturity unknown, collected by Waterlot in "Madagascar"; MNHN 1978.2921, sex and maturity unknown, collected 13 August 1966 by C. Blanc and G. Pasteur at "Ananokely, Ankaratra," 2200 m altitude, Madagascar; MNHN 1978.2922, sex and maturity unknown, collected December 1967 by C. Blanc at "Mont Ibity, 2200 m" altitude, Madagascar.

**DIAGNOSIS.**—A *Pseudoxyrhopus* with 19 rows of dorsal scales at midbody; eight supralabials; a slightly pointed snout that considerably overhangs tip of lower jaw; five dark longitudinal lines on body; a dark brown venter in adult.

**DESCRIPTION OF BM 1889.8.28.22.**—SVL 400 mm; tail 50 mm (tail tip missing); 19 rows of smooth dorsal scales at midbody; body round in cross section; 144 ventrals; 28 paired subcaudals (tail tip missing); anal divided; eight supralabials, fourth and fifth contacting eye; eight infralabials, five infralabials in contact with anterior genials; rostral wider than high and visible from above; internasals shorter than prefrontals; frontal pentagonal, 1.4 times as long as wide, shorter than parietals, longer than distance between anterior margin of frontal and snout tip; loreal almost as high as long; nasal semidivided by an inferior suture; one preocular (right) and two preoculars (left); two postoculars; temporals 1+2+3; somewhat pointed snout, which considerably overhangs lower jaw tip; eye small, diameter 0.25 head depth at midorbit, pupil round; head slightly distinct from neck.

Coloration in alcohol pale brown dorsally on head, body, and tail. Five dark, longitudinal lines present on body: a faintly marked, dark brown, vertebral line that starts at posterior margin of parietals, and two dark brown lines laterally on flanks, which start at neck and mark scale rows IV and VII (the same color pattern occurs in MNHN 1891.393; see Fig. 9). Vertebral line and more median two lines extend onto tail, but lateral two lines stop at tail base. Head marked dorsally with dark brown spots; a dark brown line passes





FIG. 7. *Pseudoxyrhopus heterurus*, UMMZ 192018.

Table 1. Morphometric variation in *Pseudoxyrhopus heterurus* and *P. sokosoko*. \* = holotype, F = female, A = adult, J = juvenile.

Character	<i>Pseudoxyrhopus heterurus</i>						<i>Pseudoxyrhopus sokosoko</i>			
	MSNM ? * <sup>a</sup>	MNHN 583	1986. 1372	UMMZ 192018	UMMZ 195848	UMMZ 203645	UMMZ 195846	UMMZ 195847*	UMMZ 203660	UMMZ 203661
sex	?	?	?	F	F	F	M	M	F	F
sexual maturity	?	?	?	A	A	A	J	A	A	A
SVL (mm)	420	445	420	510	347	420	153	285	320	295
tail length (mm)	105	111	110	95+	77	195	35	68	80	75
subcaudals	35 <sup>b</sup>	53	59	42+	52	56	46	45	46	51
subcaudals in single row	14 <sup>c</sup>	25	17	27	11	30	0	0	0	0
ventrals	155	150	151	160	159	161	145	142	144	142
infralabial number <sup>d</sup>	8/8	9/9	9/9	9/9	9/9	9/9	9/9	9/9	8/9	9/9

<sup>a</sup>Number unknown; type destroyed during Second World War. Data from Jan (1863).

<sup>b</sup>Jan & Sordelli (1866) illustrate 52.

<sup>c</sup>Jan & Sordelli (1866) illustrate 15.

<sup>d</sup>left/right

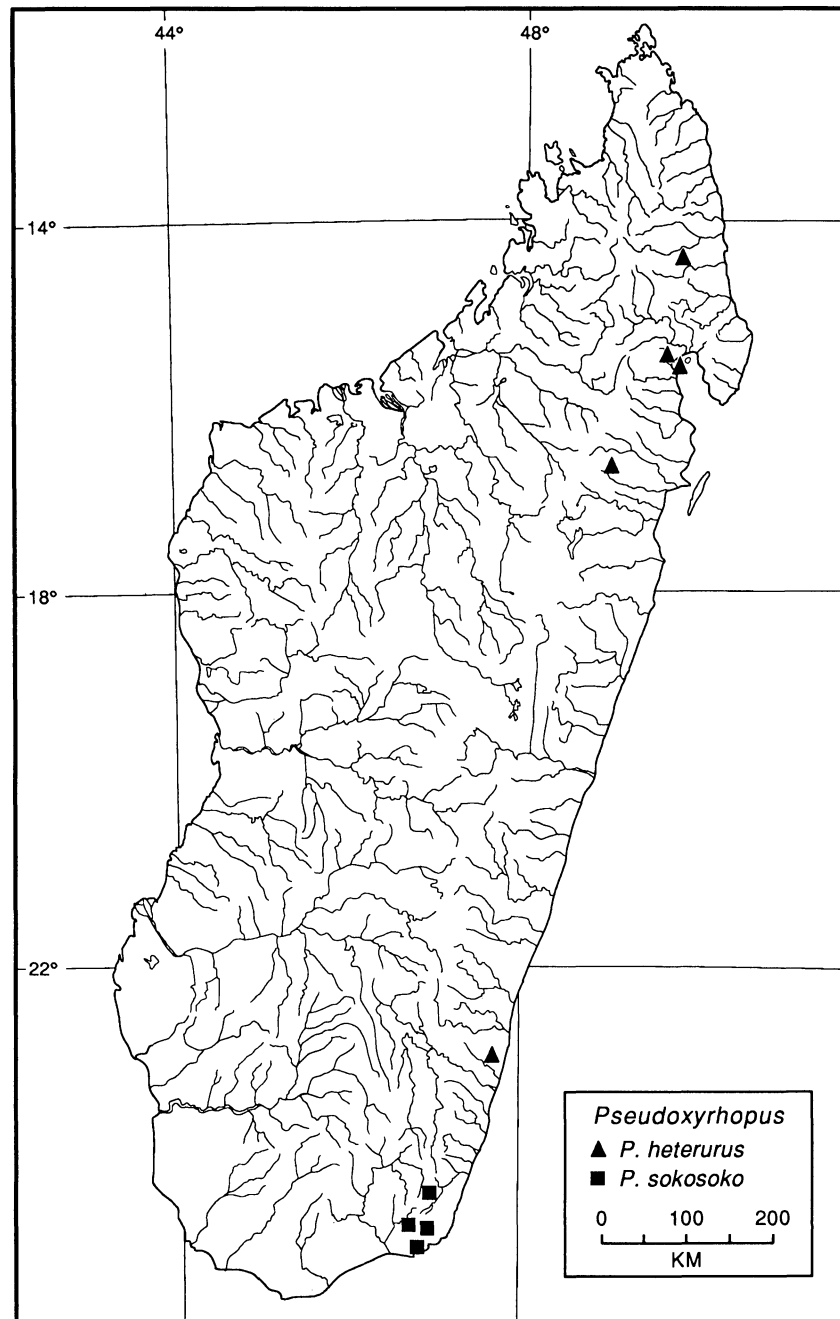


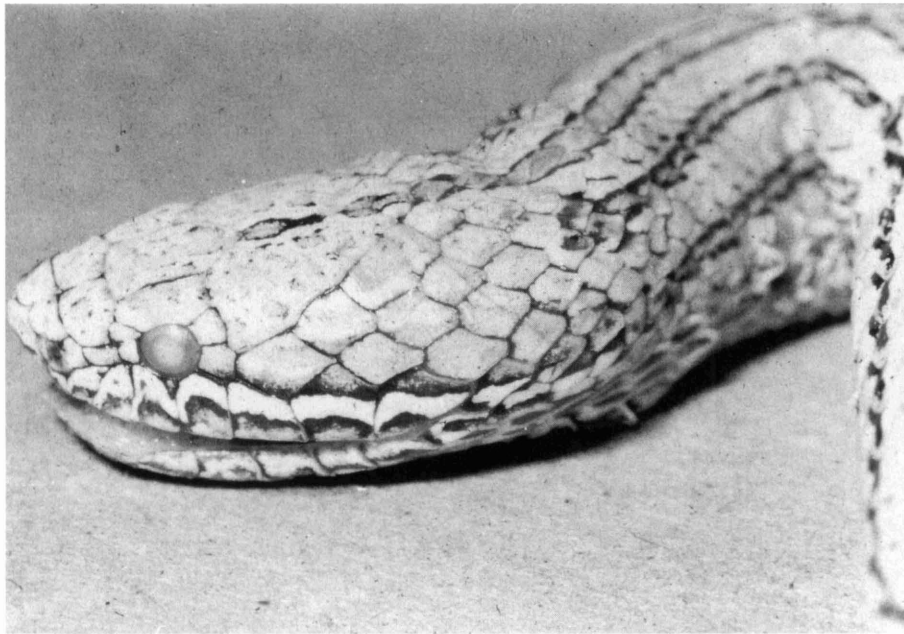
FIG. 8. Distribution of *Pseudoxyrhopus heterurus* and *Pseudoxyrhopus sokosoko*.

through eye, bordered below by a white line, itself edged dark brown below by partly fused spots. Chin brown with striking white spots. Undersurfaces of body and tail dark brown; ventral scales pale brown on posterior margins.

**VARIATION.**—The morphometric variation is given in Table 2. The coloration varies as follows. The vertebral line may itself be edged with darker brown at its lateral borders (BM 1895.10.29.60). There may be an additional two pairs of dark, thin, lateral lines ventrolaterally on scale rows I and II (MNHN 1978.2922). The venter and tail are pale brown in the juveniles (BM 1887.12.22.34 and BM 1887.12.22.35).

**HABITAT AND DISTRIBUTION.**—The only known localities for *Pseudoxyrhopus imerinae* are: the forest district east of Imerina (eastern rainforest between latitudes of 18° and 20°S), Imerina, Ankaratra Mountains in the High Plateau centered at 19°20'S, 47°15'E, and Mount Ibity in the High Plateau at 20°28'S, 47°01'E (Fig. 10). Snakes at both these latter sites were collected at 2200 m altitude. At Ankaratra there is still some relict primary montane forest, and possibly this is also the case at Ibity. However, it is not known whether the snakes were collected in this habitat.

*Pseudoxyrhopus imerinae* is probably restricted to the region

FIG. 9. *Pseudoxyrhopus imerinae*, MNHN 1891.393.Table 2. Morphometric variation in *Pseudoxyrhopus imerinae*. \* = syntype, F = female, A = adult, J = juvenile.

Character	BM 1887. 12.22.34*	BM 1887. 12.22.35*	BM 1889. 8.28.22	BM 1895. 10.29.60	MNHN 1891. 393	MNHN 1950. 152	MNHN 1978. 2921	MNHN 1978. 2922
sex	?	?	?	F	F	?	?	?
sexual maturity	J	J	?	?	?	?	?	?
SVL (mm)	137	130	400	360	362	350	366	340
tail length (mm)	28	31	50+	70	71	77	61	64
subcaudals	41	42	28+	43	41	43	41	41
ventrals	140	142	144	147	146	146	145	148
infralabials <sup>a</sup>	9/9	9/9	8/8	9/9	9/10	9/9	9/9	9/9
preoculars <sup>a</sup>	1/1	1/1	2/1	1/1	1/1	2/2	2/2	2/2
postoculars <sup>a</sup>	2/2	2/2	2/2	2/3	2/2	2/2	2/2	2/2

<sup>a</sup>left/right

of the central High Plateau and the adjacent eastern rainforest escarpment. Obviously, it can tolerate high altitudes of up to at least 2200 m. If it survives only in native forests, this species may have declined drastically in recent times, because much of the high plateau forest has been lost through clearing and burning.

REMARKS.—Boulenger (1890) illustrated the dentition of *Pseudoxyrhopus imerinae* with 14+2 maxillary teeth and 18 dentary teeth. The anteriormost dentary teeth increase in size to the sixth, followed by 12 posterior teeth, which are smaller than the anterior teeth.

The types of *Coronella microps* described by Boulenger were donated by the Rev. Baron in a collection with seven other Madagascan species. We have collected six of these other species only in primary rainforest, which makes us think Baron's specimens, including *Pseudoxyrhopus imerinae*, were taken in rainforest. One of the frog specimens (*Boophis*

*albilabris*) is given a more exact locality—"Eastern Imerina"—which also suggests Baron's collection was made in the eastern rainforest belt between latitudes of 18° and 20°S.

*Pseudoxyrhopus kely* new species  
Figures 11 and 12

HOLOTYPE.—UMMZ 192021, adult male, from Mandena, 24°58'S, 47°2'E, 20 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar, collected 4 September 1989 by C.J. Raxworthy.

PARATYPE.—UMMZ 192022, female (immature or not in breeding condition), from Ste. Luce Strand, 24°49'S, 47°09'E, 10 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar, collected 17 October 1989 by C.J. Raxworthy.

OTHER SPECIMENS.—None.

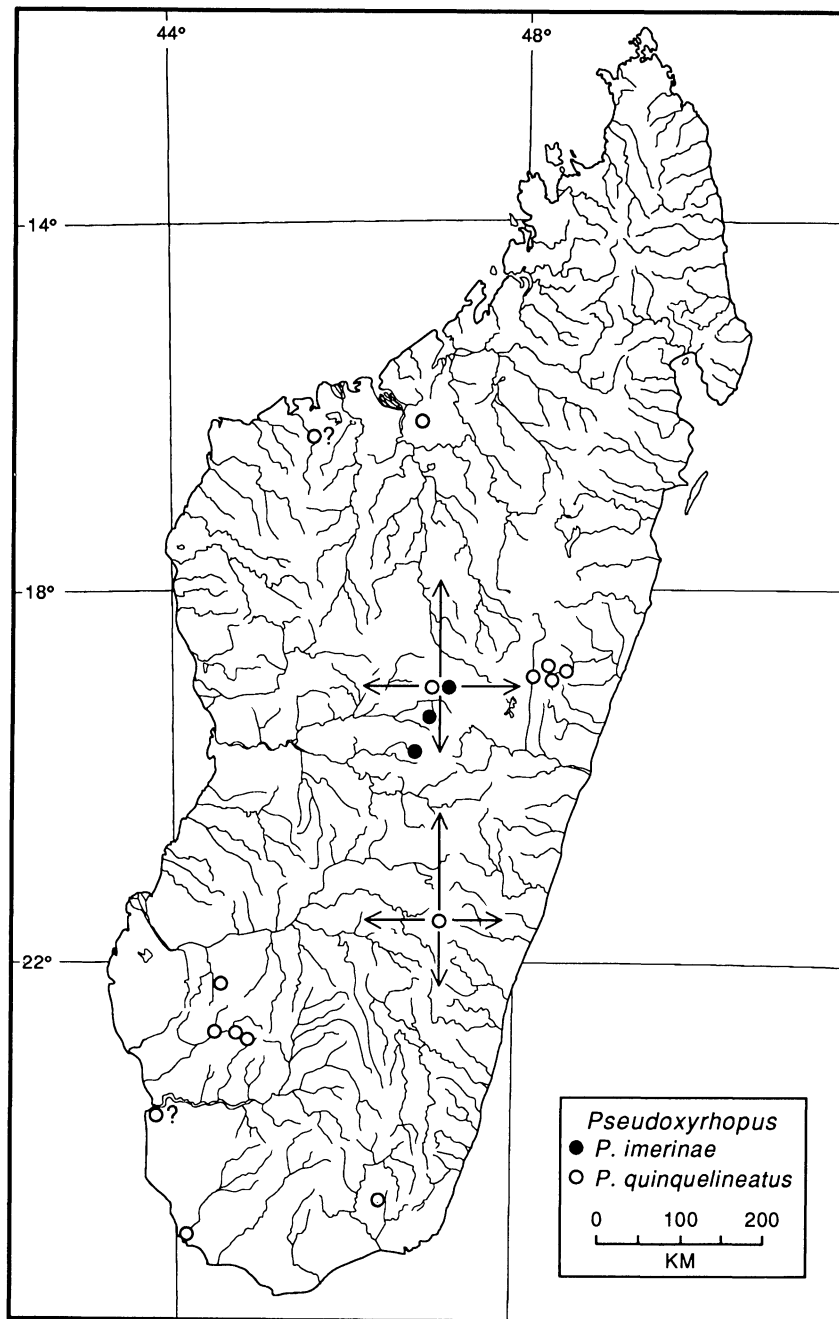


FIG. 10. Distribution of *Pseudoxyrhopus imerinae* and *Pseudoxyrhopus quinquelineatus*. Arrows indicate imprecise locality.

DIAGNOSIS.—A *Pseudoxyrhopus* with 19 dorsal scale rows at midbody, eight supralabials, bluntly rounded snout, pink venter, pale collar, and thin, dark longitudinal lines on body.

DESCRIPTION OF HOLOTYPE.—Specimen is well fixed and undamaged. Testes are large, and vasa deferentia contain spermatazoa (that were removed and viewed under a phase light microscope). SVL 180 mm; tail 37 mm; 19 rows of smooth dorsal scales at midbody; body round in cross section; 134 ventrals; 37 paired subcaudals; anal divided; eight supralabials, fourth and fifth contact eye; eight infralabials,

five in contact with anterior genials; anterior and posterior genials same length; rostral wider than high and visible from above; internasals shorter than prefrontals; frontal pentagonal, 1.1 times as long as wide, shorter than parietals, as long as distance between anterior margin of frontal and snout tip; loreal, almost as high as long; nasal partly divided by an inferior suture; one preocular, two postoculars; temporals 1+2+3; bluntly rounded snout; eye small, diameter 0.29 times head depth at midorbit, pupil round; head not distinct from neck; 8+1 maxillary teeth, posteriormost tooth much

larger and separated by a diastema from anterior teeth; 14 dentary teeth, six anteriormost increasing in size to sixth, followed by eight posterior teeth that are smaller than anterior teeth.

Body and tail color in life brown dorsally with darker brown vertebral line edged laterally by still darker thin dark brown line. Ventrolaterally on body, two more thin dark lines, the broadest on scale rows I-II, the narrowest above (very faint) on scale row IV. Longitudinal lines start at neck and terminate at tail tip, except faint vertebral line which fades at tail base. Head dark brown dorsally. Pale yellow transverse line behind head forming striking nuchal collar, which is barely broken dorsally by thin, dark brown vertebral line (Fig. 11). Nuchal collar terminates in the ventrolateral region and does not cross throat. Iris dark brown. Snout tip and supralabials white with dark brown blotches. Lower margins of supralabials heavily marked with dark brown blotches. Infralabials, chin, and throat dark brown, gradually broken up by white blotching posteriorly on throat. Ventral surfaces of body and tail bright pink, fading to white on throat. Venter unspotted except for a few very small, dark brown spots on anterior region of body.

After three months in formalin and two years in alcohol, dark brown pigments slightly lighter, pale yellow collar changed to white, and all trace of pink pigmentation on ventral surface of body lost, so that venter is now white. All other coloration unchanged.

**VARIATION.**—The paratype is a female. There are no eggs in the oviducts. The paratype differs from the holotype as follows: SVL 130 mm, tail length 27 mm, 139 ventrals, 38 subcaudals, nine infralabials, one postocular, nuchal collar not broken dorsally by a thin dark median line (Fig. 12).

**ETYMOLOGY.**—The name “kely” (pronounced “kaylee”) is the Malagasy word for small and refers to the small size of this species.

**JUSTIFICATION.**—Only one other *Pseudoxyrhopus* species, *P. imerinae*, has 19 dorsal scale rows, but it can be separated from *P. kely* by its rather pointed snout that overhangs the lower jaw tip, lack of a pale nuchal collar, dark brown venter, and six strong, dark, longitudinal lines (the most lateral two on scale rows IV and VII). Adult *Pseudoxyrhopus imerinae* grow to 400 mm SVL. The juvenile coloration of *Pseudoxyrhopus imerinae* is similar to the adult except the venter is lighter, with each scale darkened on the anterior margin. Other *Pseudoxyrhopus* species with 21 dorsal rows can be distinguished by the following characters: *P. ambreensis* has seven supralabials and is uniform brown above; *P. heterurus* is dark brown above, lacks a nuchal collar, the tail undersurface has a central median line, and the anterior subcaudals are frequently not divided; *P. quinquelineatus* typically has five, dark, longitudinal bands on the body and 45–60 subcaudals. The remaining three species of *Pseudoxyrhopus* all have 25 dorsal scales rows and more than 198 ventral scales.

**HABITAT AND DISTRIBUTION.**—UMMZ 192021 was caught in a pitfall trap with a drift fence, close to a low-lying moist area, in littoral forest; UMMZ 192022 was found in a fallen rotten log, 1200 h, in the littoral forest behind the Ste. Luce beach. This latter site was more than 100 m from the closest source of fresh water.

Both forests where *Pseudoxyrhopus kely* were collected oc-

cur on sand in the climatic transition zone between the arid Western and the humid Eastern Domains, with a mean annual rainfall of 1600–2000 mm (Ratsivalaka-Randriamanga, 1986). The littoral forests of this region cannot be classified as either lowland rainforest, euphorb (spiny) forest, or gallery forest and contain an unusual mixture of arid and humid-adapted herpetological species (Nussbaum and Raxworthy, pers. obs.).

Despite intense survey work made throughout the Tôlañaro region, no other specimens were found, and we therefore suspect *Pseudoxyrhopus kely* is restricted to littoral forests and may be endemic to the Tôlañaro region (Fig. 4). The two sites, Ste. Luce and Mandena, are just 20 km apart, and both are close to sea level (10–20 m altitude).

**REMARKS.**—Sexual maturity is attained at 180 mm SVL, which is comparable with the *Pararhadinaea* colubrids of Madagascar. *Pseudoxyrhopus kely* is by far the smallest *Pseudoxyrhopus* species. The next smallest species, *Pseudoxyrhopus ambreensis* and *P. heterurus*, are mature at a minimum SVL of 333 and 347 mm respectively. *Pseudoxyrhopus kely* is unusual in that it has just a single enlarged rear maxillary tooth, a feature shared only with *P. ambreensis* within the genus.

From the burrowing behavior of the snakes when caught, it appears that they live a largely fossorial life. The broad short head, bluntly rounded snout, and small eye all appear to be adaptations for burrowing. The stomach of UMMZ 192022 contained the remains of an adult *Amphiglossus melanopleura* (Scincidae) which we believe was consumed before capture. This diurnal skink, which is common at both collecting localities, was seen frequently among leaf litter on the forest floor.

*Pseudoxyrhopus microps* Günther

Figures 13 and 14

*Pseudoxyrhopus microps* Günther, 1881:359.

**HOLOTYPE.**—BM 1881.3.29.16 (BM 1946.1.7.76), mature male, from “Betsileo, Madagascar” collected by Mr. Waters.

**MATERIAL EXAMINED.**—BM 1881.3.29.16 (BM 1946.1.7.76) (holotype); MNHN 1978.44, female, maturity unknown, donated by Martens, collected from “Antalaha, Madagascar”; MNHN 1978.45 and MNHN 1978.46, sex and maturity unknown, collected on 20 November 1965 by Thiel at “Périnet, Madagascar”; UMMZ 192020, juvenile female, collected 26 November 1989 by R.A. Nussbaum at Marosohy Pass, 24°34'S, 46°49'E, 390 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar; UMMZ 195849, adult male, collected 13 November 1990 by C.J. Raxworthy at Manantantely, 24°59'S, 46°55'E, 250 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar; UMMZ 195850, juvenile female, collected 5 December 1990 by C.J. Raxworthy at Marovony, 24°06'S, 47°20'E, 70 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar; UMMZ 195851, adult male, collected 28 December 1990 by J.B. Ramanamanjato at Ampamakiesiny Pass, 14 km northwest of Ranomafana-Sud, 24°32'S, 47°51'E, 700 m altitude; Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar; UMMZ 195852, juvenile female, col-

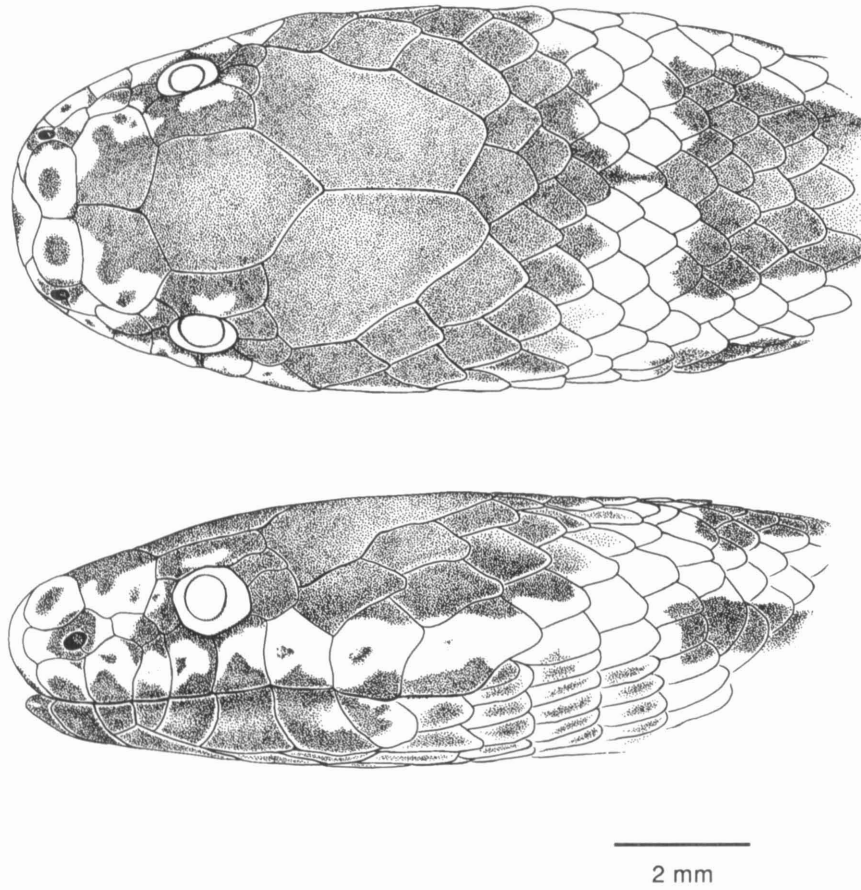


FIG. 11. Dorsal and lateral views of *Pseudoxyrhopus kely* holotype, UMMZ 192021.



FIG. 12. *Pseudoxyrhopus kely* paratype, UMMZ 192022.

lected 3 January 1991 by Jean-Baptiste Ramanamanjato at Manongotry Pass, 24°45'S, 46°52'E, 240 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar; UMMZ 195853, adult female, collected 4 January 1991 by A. Raselimanana at Manongotry Pass, 24°45'S, 46°52'E, 240 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar; UMMZ 200060, juvenile male, collected 8 January 1992 by A. Raselimanana and J.B. Ramanamanjato at Antomboka River Fitsahana, Montagne d'Ambre, 12°32'S, 49°10'E, 650 m altitude, Antsiranana (Diégo Suarez) Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar; UMMZ 200066, juvenile male, collected 5 January 1992 by A. Qualtrough at Antomboka River Fitsahana, Montagne d'Ambre, 12°32'S, 49°10'E, 600 m altitude, Antsiranana (Diégo Suarez) Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar; UMMZ 203646, adult male collected 20 November 1992 by A. Razafimanantsoa at Manantenina River, Marojejy Reserve, 14°26'S, 49°46'E, 700 m altitude, Sambava Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar; UMMZ 203647, juvenile female collected 12 January 1993 by A. Razafimanantsoa at Ankavanana River, Masoala, 15°19'S, 50°14'E, 90 m altitude, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar; CM 119068, adult female, collected 23 June 1989 by P. Freed at 7 km south of Andapa Village, 18°22'S, 49°07'E, 200–300 m altitude, Toamasina (Tamatave) Fivondronana, Toamasina Province, Madagascar.

**DIAGNOSIS.**—A *Pseudoxyrhopus* with 25 rows of dorsal scales at midbody, an elongated loreal scale twice as long as high, parietal scales longer than frontal scale, anal plate always divided, 208–232 ventral scales, 70–89 subcaudal scales (undamaged tail), and a dark brown body with or without 2–5 pale pink dorsolateral longitudinal lines.

**DESCRIPTION OF HOLOTYPE.**—SVL 1195 mm; tail length 160 mm (tail tip missing); 25 rows of smooth dorsal scales at midbody; body round in cross section; 222 ventrals; 46 subcaudals (tail tip missing) in a double row; anal divided; eight supralabials, fourth and fifth contacting eye; nine infralabials, four in contact with anterior genials; rostral wider than high, visible from above; internasals shorter than prefrontals; frontal pentagonal, 1.2 times as long as wide, shorter than parietals, equal in length to distance between anterior margin of frontal and snout tip; loreal elongated, twice as long as high; nasals semidivided by inferior suture; one preocular; two postoculars; temporals 1 + 2 + 3; bluntly rounded snout; eye small, eye diameter 0.21 times head depth at midorbit, pupil round; head slightly distinct from neck.

Coloration in alcohol dark brown dorsally on head, body, and tail, becoming paler on lower flanks of body. Head with faint paler brown blotches on temporal and parietal scales (Fig. 13). Supralabials paler brown with lighter markings on some borders. Chin, venter, and tail undersurface pale brown, with a few darker brown spots on anterior area of chin and a faint brown median line on tail.

**VARIATION.**—The nasal is completely divided in UMMZ 195850–1 and 195853. Other morphometric variation is given in Table 3. The teeth could not be seen in the holotype, but the following arrangement was found in UMMZ 195849 when the mouth was dissected on the right side: 16 + 2 maxil-

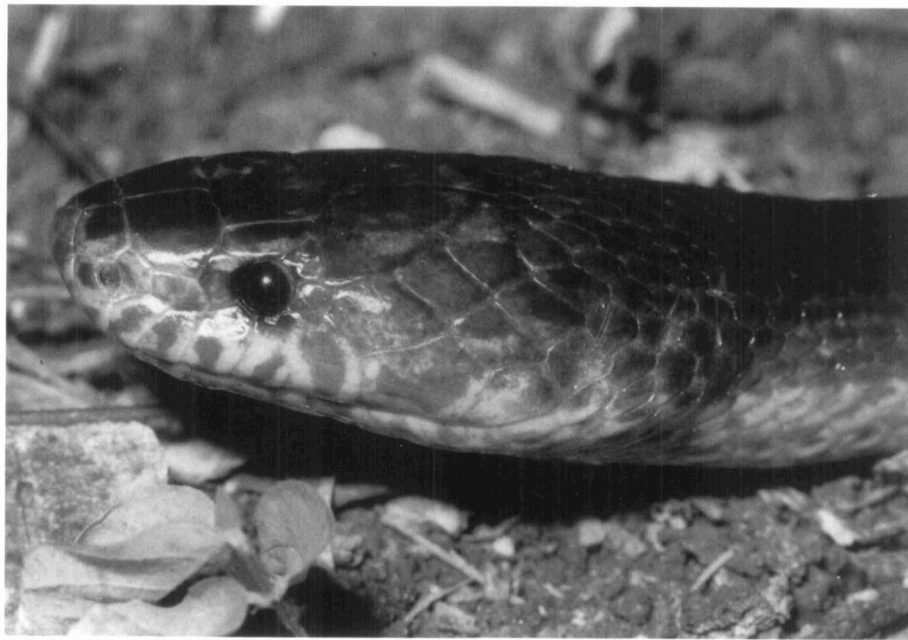
lary teeth, the two posteriormost teeth much larger and separated by a diastema from the anterior teeth; 18 dentary teeth, the anteriormost teeth increasing in size to the sixth, followed by the 12 posterior teeth, which are smaller than the anterior teeth. Boulenger (1890) illustrated the dentition of *Pseudoxyrhopus microps* with 16 + 2 maxillary teeth and 20 dentary teeth; the eight anterior dentary teeth are shown enlarged.

In life, juveniles up to 590 mm SVL have a dark brown body with a pair of pale pink, dorsolateral lines on scale rows VI and VIII, starting at the neck and terminating at the tail tip. On scale rows III and IV there may be another pale pink line bordered below with brown blotches. The head is strikingly marked by white blotches on a dark brown background; there is a pale brown nuchal collar; the supra- and infralabials are white, blotched with brown spots; above the eyes there is a thin white line; a median white broken line extends between the parietals and onto the frontal; and the lateral borders of the parietals are edged with white (Fig. 14). The chin is white with brown blotches that may continue onto the venter; and the tail undersurface is marked by a median line of brown spots. The juveniles UMMZ 200060 and UMMZ 200066 differ from other juveniles in that there are no white markings on the head except a jagged-edged white line on the supralabials. Specimen UMMZ 200066 also has a thin, pale pink, vertebral line one scale row in width, starting at the pale nuchal collar and terminating at the base of the tail.

The specimens UMMZ 195851 and 195849, 750 mm and 1,080 mm SVL respectively, show stages in the loss of the juvenile coloration, as the pale markings become progressively darker, more uniform brown. Specimen UMMZ 195851 has faint traces of longitudinal lines on the body which are absent in the largest specimen, UMMZ 195849. The head markings are still visible in the largest specimen, but the contrast between the dark and pale pigments is greatly reduced; the chin and throat are still marked by a few darker spots, but the venter is unspotted; and a median line of brown spots persists on the ventral surface of the tail. Specimen CM 119068, 715 mm SVL, is also very dark. The labials of the latter specimen are blotched pale brown, there is a faint trace of a pale nuchal collar, and a pale spot occurs on the frontal, but there is no trace of lines on the body.

**HABITAT AND DISTRIBUTION.**—The time of capture and habitat description for the UMMZ and CM specimens are: UMMZ 192020, dead on a path; UMMZ 195849, 2300 h, on forest floor by a small stream; UMMZ 195850, 2230 h, on a fallen log by a dried up stream; UMMZ 195851, 2100 h, on the forest floor 6 m from a stream; UMMZ 195852, 2205 h, crossing road; UMMZ 195853, 2300 h, crossing a road by a small stream; UMMZ 200060, 2000 h, 10 m from a river, on forest floor; UMMZ 200066, 2200 h, 1 m from a river, on the river bank; UMMZ 203646, 2100 h, 4 m from a river, on forest floor; UMMZ 203647, 2100 h, on a dead tree at 4 m height, on a small (2 by 4 m) sandy island in a 4 m wide river; CM 119068, 2220 h, on a road by a stream. All specimens except CM 119066 were collected in primary rainforest. CM 119068 was taken in secondary or disturbed rainforest.

All active snakes were found at night and usually close to streams. This species is nocturnal and probably feeds on

FIG. 13. *Pseudoxyrhopus microps*, UMMZ 195849.Table 3. Morphometric variation in *Pseudoxyrhopus microps*. \* = holotype, M = male, F = female, A = adult, J = juvenile.

Character	BM 1881.	MNHN 1978.	MNHN 1978.	MNHN 1978.	UMMZ 192020	UMMZ 195849	UMMZ 195850	UMMZ 195851	UMMZ 195852	UMMZ 195853	UMMZ 200060	UMMZ 200066	UMMZ 203646	UMMZ 203647	CM 119068
sex	M	F	?	?	F	M	F	M	F	F	M	M	M	F	F
sexual maturity	A	?	?	?	J	A	J	A	J	A	J	J	A	J	A
SVL (mm)	1195	805	800	780	500	1080	565	750	590	625	458	288	1120	440	715
tail length (mm)	160+	130+	137+	164	120	245+	132	163	150	143	117	71	120+	110	143+
subcaudals	46+	52+	55+	70	81	45+	81	76	89	82	81	84	40+	76	60+
ventral scales	222	220	208	218	231	219	232	232	227	232	214	208	221	212	221
supralabials <sup>a</sup>	8/8	8/8	8/8	8/8	?	8/8	9/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8
infralabials	9/9	9/9	9/9	9/9	9/9	9/9	9/9	9/8	9/9	9/8	9/9	9/9	10/10	9/9	9/9
postoculars <sup>a</sup>	3/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2	2/2
temporal formula <sup>a</sup>	1+2+3	1+2+3	1+2+4	1+2/3+4	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+4	1+2+3

<sup>a</sup>left/right<sup>b</sup>supralabials mutilated

frogs, an observation previously reported by Günther (1881), although the source of his information is unclear. We never found this species away from primary rainforest and conclude that it is probably restricted to this habitat.

For the BM and MNHN specimens, the following interpretations have been made about the localities: Betsileo refers to the southcentral region of Madagascar, on the High Plateau or possibly the western limit of the eastern escarpment; Antalaha is the name of a small port at 14°54'S, 50°15'E, in the northeast; Périnet refers to the town now called Andasibe at 18°56'S, 48°25'E or the Analamazaotra Reserve at 18°57'S, 48°26'E.

The known distribution of *P. microps* is large, from the extreme north at Montagne d'Ambre to the extreme south close to Tôlañaro (a latitudinal range of 12–25°S), although all of these localities fall within the humid rainforest domain (Fig. 15). The known altitudinal range is between 70 and 900 m. The Périnet specimen probably was collected at around

900 m, but the precise locality is unknown. No specimen has been recorded for certain on the High Plateau above 1000 m (the vague Betsileo record may refer to either the High Plateau or the eastern escarpment), and we suspect this species may be restricted to altitudes lower than 1000 m. Guibé (1958) listed "Ankarana" as a locality for this species, without providing the source of the information. We have not found a museum specimen with this locality, which probably is the limestone massif of Ankarana at 17°55'S, 49°06'E (although villages with the name Ankarana are also known in the eastern rainforest, e.g. at 23°05'S, 47°30'E). We are uncertain of the reliability and locality of this record.

REMARKS.—Our description of the color of this species differs from that of Günther (1881), who described the holotype as being uniform black above; possibly the holotype has faded. Guibé (1958) also described the coloration as uniform brownish-black above. It seems that the juvenile coloration was previously unknown. *Pseudoxyrhopus microps* mature





FIG. 14. *Pseudoxyrhopus microps* juvenile, UMMZ 195850.

at about 600 mm SVL, based on the much larger-sized gonads seen in specimens of this size and larger.

*Pseudoxyrhopus quinquelineatus* (Günther)  
Figure 16

*Liophis quinquelineatus* Günther, 1881:359.

*Pseudoxyrhopus quinquelineatus* Boulenger, 1890:313. First use of combination.

SYNTYPES.—BM 1881.3.29.13 and BM 1881.3.29.14 (BM 1946.1.12.33 and BM 1946.1.12.34), sex and maturity unknown, from “Betsileo,” Madagascar, collected by Mr. Waters.

MATERIAL EXAMINED.—BM 1881.3.29.13 and BM 1881.3.29.14 (BM 1946.1.12.33 and BM 1946.1.12.34) (syntypes); BM 1893.9.6.2, female, maturity unknown, collected by L. Greening from “Madagascar”; BM 1930.7.1.236, female, maturity unknown, collected by E.J. White at “Am-poza, 15 miles E of Ankazoabo, SW Madagascar”; BM 1930.7.1.237, female, maturity unknown, collected by E.J. White “about 40 miles S. of Ankazoabo, S.W. Madagascar”; MNHN 1978.49, male, maturity unknown, collected 15 December 1963 by C. Domergue at “Moramanga, Madagascar”; MNHN 1978.50, sex and maturity unknown, collected 25 January 1964 by C. Domergue at “100 km, Route Tamatave, Madagascar”; MNHN 1978.51-2, males, maturity unknown, collected 6 December 1964 and 20 January 1965 by C. Domergue at “Ampijoroa, Madagascar”; MNHN 1978.53, male, maturity unknown, collected 16 March 1965 by C. Domergue at “piste Soalara, PK 80, Madagascar”; MNHN 1978.54, sex and maturity unknown, collected 17 November 1965 by C. Domergue from “Périnet, Madagascar”; MNHN 1978.2923, adult male, collected February 1971 by J. Kely from “Anodaisoro, Antananarivo, Madagascar”; MNHN 1978.2924, sex and maturity unknown, collected June 1972

by A. Peyrieras from “forêt d’Herea (Sakaraha), 580 m, Madagascar”; MNHN 1989.2846, male, maturity unknown, collected 24 February 1961 by G. Razafy at “forêt d’Euphorbes, Andeoka, Mahafaly Plateau, Madagascar”; MNHN 1989.2847, maturity and sex unknown, collected 23 June 1962 by C. Domergue at “10 km Ouest de Moramanga, Route de Tamatave, Madagascar”; UMMZ 203648, adult male, collected 17 April 1993 by J.B. Ramanamanjato at Zombitsy, 22°50’S, 44°42’E, 800 m altitude, Sakaraha Fivondronana, Toliara (Tuléar) Province, Madagascar; UMMZ 203662, adult male, collected 14 June 1993 by R.A. Nussbaum at Amboanemba, 24°39’S, 46°29’E, 280 m altitude, Amboasary Fivondronana, Toliara (Tuléar) Province, Madagascar.

DIAGNOSIS.—A *Pseudoxyrhopus* with 21 rows of dorsal scales at midbody, eight supralabials, a somewhat pointed snout which projects considerably forward of lower jaw tip, and five dark dorsal longitudinal lines on the body.

DESCRIPTION OF SYNTYPE BM 1881.3.29.14.—SVL 350 mm; tail 77 mm; 21 rows of smooth dorsal scales at midbody; body round in cross section; 142 ventrals; 45 subcaudals in a double row; anal divided; eight supralabials, the fourth and fifth contacting eye; nine infralabials; three infralabials in contact with anterior genials; rostral wider than high, easily visible from above; internasals shorter than prefrontals; frontal pentagonal, 1.3 times longer than wide, shorter than parietals, equal in length to distance between anterior margin of frontal and snout tip; loreal almost as high as long; nasal semidivided by inferior suture; one preocular; two postoculars; temporals 1 + 2 + 3; somewhat pointed snout which overhangs tip of lower jaw; eye small, diameter 0.25 times head depth at midorbit, pupil round; head slightly distinct from neck.

Coloration in alcohol pale brown dorsally on head, body,

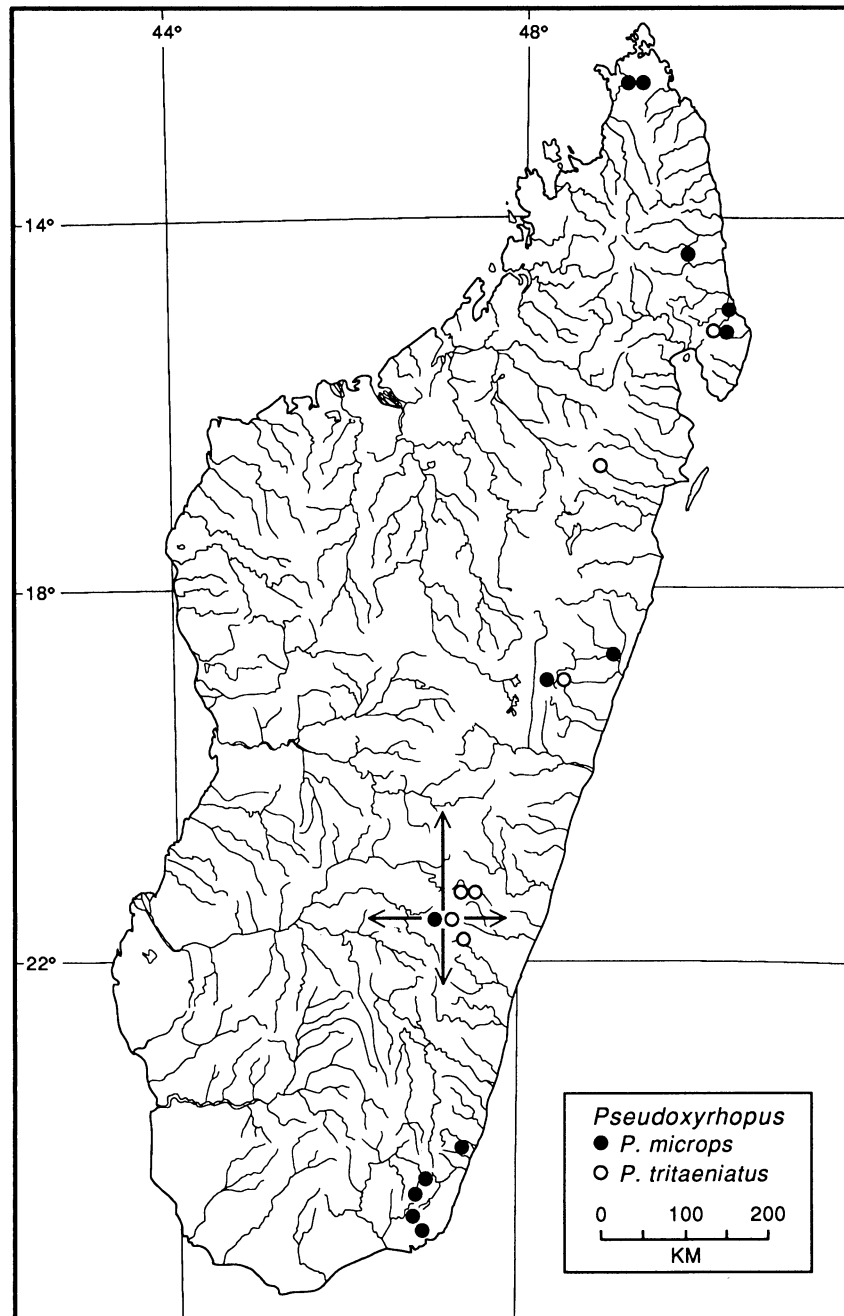


FIG. 15. Distribution of *Pseudoxyrhopus micros* and *Pseudoxyrhopus tritaeniatus*. Arrows indicate imprecise locality.

and tail with five thin longitudinal dark brown lines on dorsal surface of body (the same color pattern occurs in MNHN 1978.51; see Fig. 16). Two lateral pairs start at neck on scale rows IV-V and VIII, terminating at tail base. Middle vertebral line slightly darker and broader, starting at posterior border of parietals and terminating at tail tip. Supralabials and snout tip pale brown, with each labial and rostral marked by single dark brown spot. Pale brown supralabial line edged above by darker brown coloration of upper parts of head; border between pale and dark brown just above dorsal mar-

gin of supralabials, continuing across snout between internasals and prefrontals. Chin, throat, venter and tail pale yellow; chin marked with some small brown spots, densest at chin tip.

VARIATION.—Morphometric variation is presented in Table 4. There may be a median dark brown line on the tail undersurface (BM 1881.3.29.13), which may extend forward to form a broken line on the venter (MNHN 1978.51). The longitudinal dark dorsal lines may be very faint (MNHN 1978.53) or even absent (MNHN 1989.2846, UMMZ

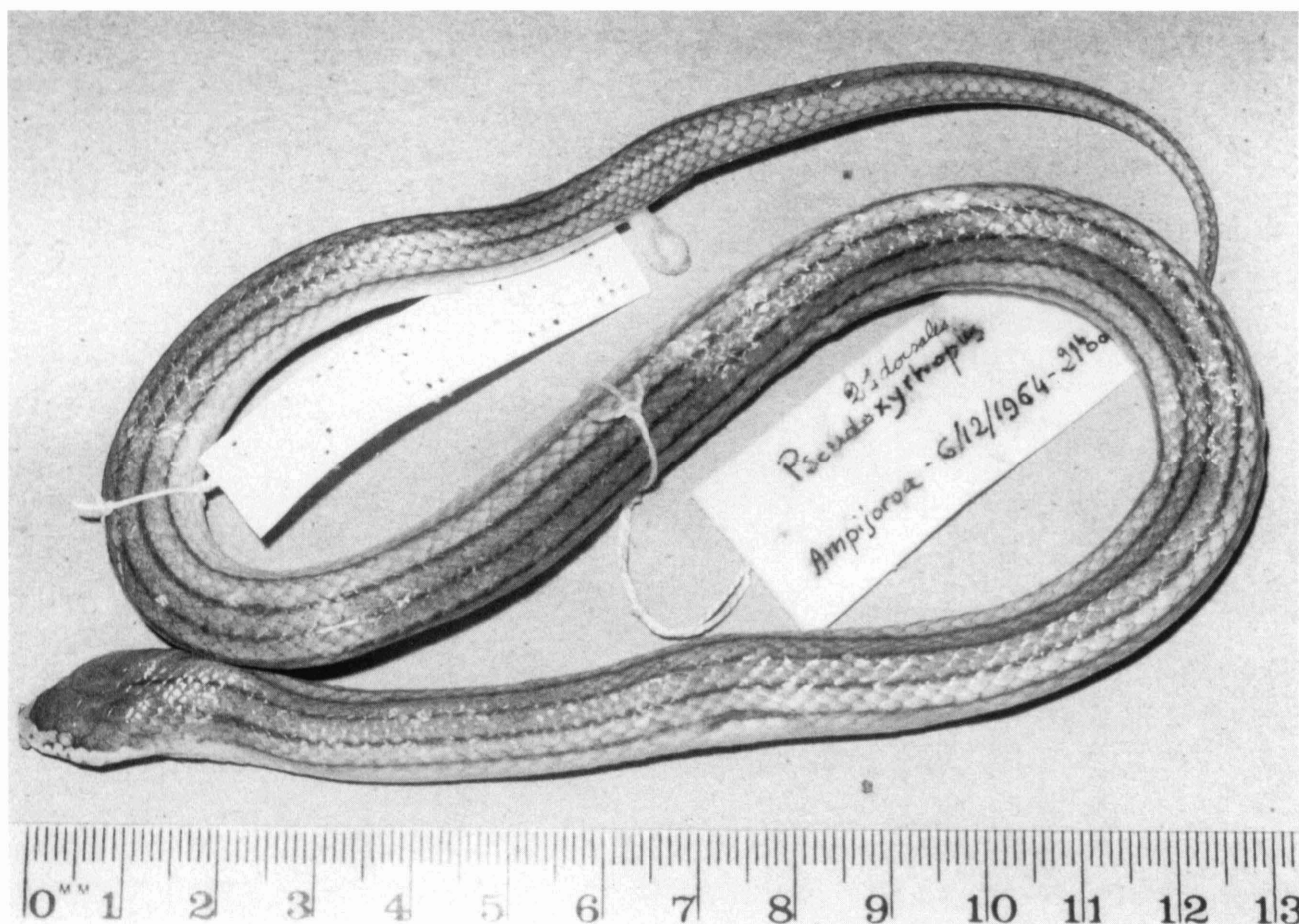


FIG. 16. *Pseudoxyrhopus quinquelineatus*, MNHN 1978.51.

203648). The juvenile (MNHN 1978.2924) has a distinctly dark brown head, which fades posterior to parietals to the light brown coloration of the body.

**DISTRIBUTION AND HABITAT.**—The time of capture and habitat description (where known) of each specimen are: MNHN 1989.2846, 0600 h, in euphorb (spiny) forest; MNHN 1989.2847, 1730 h; UMMZ 203648, 1100 h, inside a rotten tree stump, primary dry deciduous forest; UMMZ 203662, 1030 h, under a log on sand, disturbed euphorb (spiny) forest on the flood plain of a small stream.

The localities of the material examined are in some cases imprecise, but the following interpretations have been made: Betsileo refers to the south-central region of the Island on the High Plateau, or possibly the western limit of the eastern escarpment; Ampoza, 15 miles east of Ankazoabo is at 22°20'S, 44°20'E; 40 miles south of Ankazoabo is at 22°56'S, 44°31'E; we have been unable to find Herea, but Sakaraha is at 22°55'S, 44°32'E; Moramanga is at 18°57'S, 48°08'E; 100 km, Route Tamatave, probably refers to the 100 km marker stone on the Toamasina (Tamatave) road from Antananarivo, which would be at 18°54'S, 48°08'E; Ampijoroa is at 16°15'S, 46°48'E; Piste Soalara, PK 80, may refer to the village Soalara, south of Toliara at 23°36'S, 43°44'E, but more likely it is a misspelling of Soalala, with Pk 80 referring

to the 80 km road marker on the road from Ambolomoty to Soalala, which would be at 16°10'S, 46°00'E; Périnet refers to the town now called Andasibe at 18°56'S, 48°25'E, or to the Analamazaotra Special Reserve at 18°57'S, 48°26'E; 10 km west of Moramanga is at 18°57'S, 48°17'E; we have been unable to find Anodaisoro, but Antananarivo, which is also mentioned in the locality, is centered at 18°56'S, 47°32'E; Andeoka, Mahafaly Plateau, probably refers to the town of Androka on the Mahafaly Plateau at 25°02'S, 44°04'E.

This species is found in both the humid Eastern and the arid Western Domains (Fig. 10). The forests at Amboanemba, Ampijoroa, Ankazoabo, Mahafaly, and Zombitsy are western dry deciduous and euphorb (spiny) forests, compared to Andasibe and Moramanga which are in eastern rainforest. Finally, the Antananarivo and possibly Betsileo localities demonstrate a distribution which includes the High Plateau. The known altitudinal range is close to sea level (less than 100 m) to about 1300 m. We do not know whether these snakes were collected in primary forest or in secondary habitats, except for MNHN 1989.2846 and UMMZ 203662, which were collected in euphorb (spiny) forest, the dominant primary forest in the south, and UMMZ 203648, collected in primary deciduous dry forest, typical of the west. The distribution of this species is potentially quite large, covering

Table 4. Morphometric variation in *Pseudoxyrhopus quinquelineatus*. \* = syntype, M = male, F = female, A = adult, J = juvenile.

Character	BM 1881.3	BM 1881.3	BM 1893.	BM 1930.	BM 1930.	MNHN 1978.	MNHN 1978.	MNHN 1978.	MNHN 1978.	MNHN 1978.	MNHN 1978.	MNHN 1978.	MNHN 1978.	MNHN 1989.	MNHN 1989.	UMMZ 203648	UMMZ 203662
sex	?	?	F	F	F	M	?	M	M	M	?	M	?	M	?	M	M
sexual maturity	?	?	?	?	?	?	?	?	?	?	?	A	?	?	?	A	A
SVL (mm)	400	350	450	195	290	366	415	355	342	383	475	460	177	370	164	265	255
tail length (mm)	85	77	105	46	62	100	109+	90	86	98	108	107	39	90	46	70	73
subcaudals	46	45	52	49	48	59	54+	52	55	55	52	51	51	51	65	55	48
ventrals	140	142	152	149	148	141	142	142	144	140	148	143	155	143	144	142	139
supralabials <sup>a</sup>	8/7	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8	8/8
postoculars <sup>a</sup>	1+2+2/3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+4/3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3

<sup>a</sup>left/right

the west, southwest, High Plateau, and at least the central section of the rainforest belt.

REMARKS.—Boulenger (1890) illustrated the dentition of *Pseudoxyrhopus quinquelineatus* with 14+2 maxillary teeth and 18 dentary teeth. The anterior dentary teeth increase in size to the sixth, followed by 12 posterior teeth, which are smaller than the anterior teeth.

An additional specimen of this species (not seen) is in the Smithsonian collection (USNM 149903). It was collected 7 May 1963 at Périnet (Andasibe).

The activity pattern of this species is unknown. The two UMMZ specimens were found during the day in refuges and the capture times of the two MNHN are at dawn and dusk. The slightly pointed overhanging snout indicates fossorial behavior. *Pseudoxyrhopus quinquelineatus* shares this and other scalation and coloration characters with *P. imeriniae*.

*Pseudoxyrhopus sokosoko* new species  
Figures 17 and 18

HOLOTYPE.—UMMZ 195847, adult male, from Am-pamakiesiny Pass 14 km northwest of Ranomafana-Sud, 24°32'S, 47°51'E, 800 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar, collected 27 December 1990 by J.B. Ramanamanjato.

PARATYPES.—UMMZ 195846, juvenile male, from Manantely, 24°59'S, 46°56'E, 75 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar, collected 7 November 1990 by R.A. Nussbaum; UMMZ 203660, adult female, from Ambatorongorongo, 25°05'S, 46°47'E, 380 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar, collected 16 February 1993 by R.A. Nussbaum; UMMZ 203661, adult female, from Andondo River, 24°48'S, 46°44'E, 150 m altitude, Tôlañaro (Fort Dauphin) Fivondronana, Toliara (Tuléar) Province, Madagascar, collected 25 May 1993 by R.A. Nussbaum.

OTHER SPECIMENS.—None.

DIAGNOSIS.—A *Pseudoxyrhopus* with 21 dorsal scale rows at midbody, bluntly rounded snout, eight supralabials, subcaudals divided, white line on supralabials and rostral, and dark brown dorsal coloration on body.

DESCRIPTION OF HOLOTYPE.—Specimen is well fixed and undamaged. Testes are large. Snout-vent length 285 mm; tail length 68 mm; 21 rows of smooth dorsal scales at midbody; body round in cross section; 142 ventrals; 45 subcaudals, all in a double row; anal divided; eight supralabials,

fourth and fifth contacting eye; nine infralabials, five in contact with anterior genials; anterior and posterior genials equal in length; rostral wider than high and visible from above; internasals shorter than prefrontals; frontal pentagonal, as long as wide, shorter than parietals, longer than distance between anterior margin of frontal and snout tip; loreal not quite as high as long; nasals divided; one preocular; two postoculars; temporals 1+2+3; bluntly rounded snout; eye small, diameter 0.27 times head depth at midorbit, pupil round; head slightly distinct from neck; 14+2 maxillary teeth, gradually increasing in size posteriorly, with a diastema before two posteriormost teeth, which are largest; 15 dentary teeth, anterior teeth increasing in size posteriorly to sixth, followed by nine posterior teeth that are smaller than anterior teeth.

Coloration in life uniform dark brown on head, body, and tail (Fig. 17). Posterior half of body with faint thin pink line on scale row IV-V; line terminates above cloaca. Thin white line from snout to posterior supralabial, crossing supralabials, rostral, and nasals. Ventrally, chin spotted dark brown, heaviest at anterior tip, and fading to white on throat. Venter pale brown, with tiny pale brown spots on anterior margins of each ventral scale, densest on median line. Undersurface of tail marked by partly fused spots that form a median pale brown line.

After three months in formalin and one year in alcohol pale pink line on body changed to pale brown. All other coloration unchanged.

VARIATION.—Specimen UMMZ 203661 has a pale pink venter and tail undersurface. Specimen UMMZ 195846 has a pale body line that starts on the anterior half of the body (at the 20th ventral) and continues to the tail tip, the dorsal rows I-III of the body are pale white (Fig. 18), and the venter is marked with tiny faint spots that form a median line. Specimen UMMZ 195846 is a juvenile, and the markings described for this specimen may be the typical juvenile condition. Other morphometric variation is given in Table 1.

ETYMOLOGY.—The Malagasy word "sokosoko" means approaches or goes secretly or stealthily, and refers to the secretive and nocturnal habits of this species.

JUSTIFICATION.—Three other species, *Pseudoxyrhopus am-breensis*, *P. quinquelineatus* and *P. heterurus*, have 21 dorsal scale rows. *Pseudoxyrhopus ambreensis* has seven supralabials, a pale nuchal collar and a red spot on the snout tip; *P. sokosoko* has eight supralabials and lacks a pale nuchal collar and red spot on the snout tip. *Pseudoxyrhopus quinquelineatus* has a slightly pointed snout tip, a rostral that strongly over-



FIG. 17. *Pseudoxyrhopus sokosoko* holotype, UMMZ 195847.

hangs the mental and, typically, thin dark longitudinal lines on the body; *P. sokosoko* has a rounded snout, a rostral that does not strongly overlap the mental and lacks thin dark longitudinal lines on the body. *Pseudoxyrhopus heterurus* has undivided anterior subcaudals, 150–161 ventrals, 52–59 subcaudals, and is mature at SVL 347–510 mm; *P. sokosoko* has divided anterior subcaudals, 142–145 ventrals, 45–51 subcaudals, and is mature at 285–320 mm.

**HABITAT AND DISTRIBUTION.**—The time of capture and habitat description for each specimen are: UMMZ 195846, 1030 h, under wood chips; UMMZ 195847, 2200 h, on rocks by a stream; UMMZ 203660, 1445 h, in humus under a rotten log; UMMZ 203661, 1335 h, inside a rotten log. All specimens were taken in primary rainforest, which in the case of UMMZ 195846 and UMMZ 203660 was partly degraded by human exploitation.

This species is known from rainforest in the Anosy and Vohimena Mountains in extreme southeastern Madagascar (Fig. 8), and ranges in altitude from 75 to 800 m. We strongly suspect this species is confined to primary rainforest and is nocturnal and ground-dwelling.

**REMARKS.**—*Pseudoxyrhopus sokosoko*, known from the extreme southeast, is probably the sister species to *P. heterurus*, known from the east and northeast. *Pseudoxyrhopus sokosoko*

has fewer ventrals and subcaudals and is smaller than *P. heterurus*. *Pseudoxyrhopus sokosoko* also lacks undivided anterior subcaudals, a character unique to *P. heterurus* within *Pseudoxyrhopus*. *Pseudoxyrhopus sokosoko* and *P. heterurus* are allopatric, with the closest sites, Ampamakiesiny (*P. sokosoko*) and Manombo (*P. heterurus*), separated by 195 km.

*Pseudoxyrhopus tritaeniatus* Mocquard  
Figures 19 and 20

*Pseudoxyrhopus tritaeniatus* Mocquard, 1894:4.

*Pseudoxyrhopus dubius* Mocquard, 1904:305. New synonym.

**TYPE MATERIAL.**—MNHN 1891.24 (holotype of *Pseudoxyrhopus tritaeniatus*), sex and maturity unknown, from “Provient de Betsileo, Madagascar,” collected by Catat. MNHN 1898.7 (holotype of *Pseudoxyrhopus dubius*), male, maturity unknown, from “Madagascar,” collected by Rousson.

**MATERIAL EXAMINED.**—MNHN 1891.24 (holotype of *Pseudoxyrhopus tritaeniatus*); MNHN 1898.7 (holotype of *Pseudoxyrhopus dubius*); MNHN 1930.365, male, maturity unknown, collected between 1926 and 1930 by R. Decary from “Massif de l’Ikongo, Madagascar”; MNHN 1978.43, sex and maturity unknown, collected 22 April 1964 by Chabaud and Golvan at “Périnet, Madagascar”; MNHN 1978.47, male,



FIG. 18. *Pseudoxyrhopus sokosoko* paratype, UMMZ 195846.

maturity unknown, collected between 1958 and 1959 by Paulian at "Périnet, Madagascar"; MNHN 1978.48, immature, sex unknown, collected December 1962 by unknown collector at "Périnet, Madagascar"; UMMZ 192019, adult female, collected 27 February 1990 by C.J. Raxworthy at Ambatovaky Special Reserve, 16°51'S, 52°00'E, 600 m altitude, Soanierana Ivongo Fivondronana, Toamasina (Tamatave) Province, Madagascar; UMMZ 195854, adult male, collected 28 January 1991 by C.J. Raxworthy at Vatoharanana, National Park of Ranomafana, 21°17'S, 47°26'E, 950 m altitude, Ifanadiana Fivondronana, Fianarantsoa Province, Madagascar; UMMZ 200059, adult male, collected 25 July 1989, by P. Daniels in Talatakely, National Park of Ranomafana, 21°17'S, 47°26'E, 1000 m altitude, Ifanadiana Fivondronana, Fianarantsoa Province, Madagascar; UMMZ 203649, adult

male, collected 14 January 1993 by A. Razafimanantsoa at Ankavanana River, Masoala, 15°19'S, 50°14'E, 90 m altitude, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar.

DIAGNOSIS.—A *Pseudoxyrhopus* with 25 rows of dorsal scales at midbody, a loreal scale usually almost as high as long, parietal scales longer than frontal scale, anal plate divided or entire, 199–217 ventral scales, and a red body with three to five dark brown dorsal longitudinal lines.

DESCRIPTION OF HOLOTYPE.—SVL 540 mm; tail length 102 mm; 25 rows of smooth dorsal scales at midbody; body round in cross section; 199 ventrals; 58 paired subcaudals; anal divided; eight supralabials, fourth and fifth contacting eye; eight infralabials, four in contact with anterior genials; rostral wider than high and visible from above; internasals

shorter than prefrontals; frontal almost pentagonal, with an anterior border that is not quite straight; frontal as long as wide, shorter than parietals, equal in length to distance between anterior margin of frontal and snout tip; a small scale located between prefrontals and frontal; loreal almost as high as long; one preocular; two postoculars; temporals 1 + 2 + 4 (left), 1 + 3 + 4 (right); bluntly rounded snout; eye small, diameter 0.26 times head depth at midorbit, pupil round; head slightly distinct from neck.

In alcohol body and tail white dorsally with three longitudinal dark brown lines that start at neck and terminate on tail. Middle vertebral band, on scale rows IX-XVII, much thicker than lateral bands on scale rows IV-VI. Head dark brown dorsally. Supralabials and rostral white, ventrally bordered with dark brown jagged line. White nuchal collar formed by break between dark brown coloration of head and longitudinal lines of body (Fig. 19). Chin heavily marked by brown blotches. A broken, faint median line of small brown spots on venter, most dense at posterior part of body. Some ventral scales with small brown spots on posterior borders. Throat, venter, and tail undersurfaces white. Tail undersurface has thin brown median line.

**VARIATION.**—The small scale located between the prefrontals and frontals in the holotype is absent in other examined material. Specimens UMMZ 195854 and UMMZ 203649 have an unusually elongated loreal scale, which is twice as long as high. Other morphometric variation is presented in Table 5. *Pseudoxyrhopus tritaeniatus* is the only *Pseudoxyrhopus* species that exhibits variation in the condition of the anal plate, which may be divided, semidivided, or entire.

The teeth could not be seen in the holotype. The teeth of UMMZ 195854 were viewed by dissection of the right side of the mouth: 16 + 2 maxillary teeth, the two posterior teeth larger and separated by a diastema from the anterior teeth; 18 dentary teeth, the six anterior ones increasing in size to the sixth, followed by 12 posterior teeth that are smaller than the anterior teeth.

The body and tail color in life is dorsally red, typically with four dark brown longitudinal lines, the thinnest on scale rows IV-VI, and the others on rows IX-XII. There may be rarely a fifth thin broken vertebral line (MNHN 1930.365, UMMZ 203649). The median line and/or pair of lines may end before the dark brown marking on the head to give the appearance of a red collar (MNHN 1891.24, UMMZ 192019), or the thicker median lines may fuse with the dark brown on the head (UMMZ 195854) (Fig. 20). The supralabials may be marked by just a few small brown blotches (MNHN 1898.7). The venter and tail undersurfaces may be spotted (UMMZ 192019) or unspotted (UMMZ 195854). All trace of red pigment is lost in the Paris specimens, but some pink pigment can still be seen on the UMMZ specimens.

**HABITAT AND DISTRIBUTION.**—The time of capture and description of the collecting sites are as follows for the UMMZ specimens, all of which were taken in primary rainforest: UMMZ 192019, 2040 h on forest floor, 20 m from a stream; UMMZ 195854, 2000 h on forest floor, 40 m from a small stream; UMMZ 200059, 1900 h, on forest floor, on a ridge top about 100 m from the closest stream; UMMZ 203649, 2030 h, on a tree root, 0.8 m from the closest stream.

The localities of the MNHN specimens are interpreted as follows: Betsileo refers to the south-central region of Madagascar, on either the High Plateau or possibly the western limit of the eastern escarpment; Massif de l'Ikongo probably refers to the mountain range west of Ikongo town, which is centered at 21°54'S, 47°28'E; Périnet refers to the town now called Andasibe at 18°56'S, 48°25'E, or to the Analamazaotra, Special Reserve at 18°57'S, 48°26'E.

The three UMMZ specimens were collected in primary rainforest. We suspect this species is restricted to rainforest along the eastern escarpment (although the Betsileo record may represent a locality from the High Plateau). *Pseudoxyrhopus tritaeniatus* has an eastern distribution which extends between latitudes of 15° (Ankavanana) and 22°S (Ivongo) (Fig. 15), and includes a known elevational range of 70 to 1000 m.

**REMARKS.**—Guibé (1958) listed Ambatomainty as a locality for this species based on MNHN 1950.153, a skin, which we were unable to find in 1992 in the Museum collection. Guibé thought the Ambatomainty locality (which means "Black Rock" in Malagasy) referred to a large town in the west, but in fact 38 villages in Madagascar have this name (Dept. of Interior, 1955), including sites in the east. As all the other known *Pseudoxyrhopus tritaeniatus* localities are in the humid Eastern Domain, we consider it unlikely that this species is found in western Madagascar.

#### *Heteroliodon* Boettger

*Heteroliodon* Boettger, 1913:313. Type species *Heteroliodon torquatus* Boettger, 1913, by monotypy.

**DIAGNOSIS.**—Colubrids without grooves on teeth; two posteriormost teeth of maxilla separated by a small diastema from anterior teeth; one or both posterior maxillary teeth slightly enlarged compared to anterior teeth; anterior dentary teeth same size as posterior dentary teeth, middle (fifth and sixth) dentary teeth considerably enlarged; loreal scale present; large eye, diameter 0.35 times head depth at midorbit.

**DESCRIPTION.**—Teeth without grooves; twelve maxillary teeth, the two posteriormost teeth may be slightly enlarged compared to the anterior teeth, and are separated from the anterior teeth by a very small diastema; 14 dentary teeth, middle (fifth and sixth) dentary teeth considerably enlarged compared to anterior and posterior teeth; hypapophyses developed throughout vertebral column; head hardly distinct from neck; eye large, diameter 0.35 times head depth at midorbit, pupil round; nasal divided or semi-divided; rostral scale much wider than high, clearly visible in dorsal view, and extending considerably anterior to tip of lower jaw; body cylindrical; dorsal scales smooth, without pits, in 17 rows at midbody; subcaudals in a double row; anal plate divided.

**CONTENT.**—One species: *Heteroliodon occipitalis* (Boulenger). For justification of synonymy, see section on the status of *Pseudoxyrhopus occipitalis*, above.

**DISTRIBUTION.**—South and southwest Madagascar.

**REMARKS.**—Boettger (1913) thought *Heteroliodon* closely related to *Leioheterodon* Duméril and Bibron 1854. He stated that all generic characters agreed between the two genera except the following: in *Heteroliodon* the nasals are semidi-

FIG. 19. *Pseudoxyrhopus tritaeniatus* holotype, MNHN 1891.24.Table 5. Morphometric variation in *Pseudoxyrhopus tritaeniatus*. \* = holotype, M = male, F = female, A = adult, J = juvenile, D = divided, SD = semidivided, U = undivided.

Character	MNHN 1891.24*	MNHN 1898.7	MNHN 1930.365	MNHN 1978.43	MNHN 1978.47	MNHN 1978.48	UMMZ 192019	UMMZ 195854	UMMZ 200059	UMMZ 203649
sex	?	M	M	?	M	?	F	M	M	M
sexual maturity	?	?	?	?	?	J	A	A	A	A
SVL (mm)	540	730	437	840	680	292	765	850	670	785
tail length (mm)	102	110+	98	155+	90+	69	165	110+	135	160+
anal plate	D	SD	U	D	D	D	D	U	SD	U
subcaudals	58	44+	65	57+	40+	73	76	46+	66	57+
ventrals	199	203	213	206	208	211	216	207	204	217
infralabials	8/8	9/9	9/9	9/9	9/9	9/9	9/9	9/9	9/9	9/9
temporal formula <sup>a</sup>	1+2/3+4	1+2+3	1+2+4	1+2+4	1+2+3	1+2+3	1+2+3	1+2+3	1+2+3	1+3/2+3

<sup>a</sup>left/right

vided; the rostral has a sharper angle between the dorsal and ventral surfaces and does not project backwards between the internasals; the eye is moderate in size; and there are 17 rows of dorsal scales. He also stated that the tooth arrangement had not been examined.

Guibé (1958) gave the following description of the genus: maxillary teeth 10–15, the last two larger and separated from the preceding teeth by an interval; dentary teeth subequal in size; head distinct from the neck; eye large, pupil round; rostral flattened above and below, with a slightly distinct median line, the edge overhanging the mouth; dorsal scales in 17 rows; anal divided; subcaudals double; hypapophyses present on the vertebrae. When Guibé published this new description, the genus was still represented only by the *H. torquatus* holotype. It is not clear whether Guibé examined the specimen himself or if he took the new information from another source unknown to us.

Examination of the teeth of the holotype of *Pseudoxyrhopus occipitalis* BM 1946.1.12.28 and UMMZ 197143 shows that the posterior maxillary teeth are enlarged, but only very slightly, and the diastema is not very obvious. The "subequal" dentary teeth are in fact very unequal in size, with the two middle teeth considerably enlarged.

*Heteroliodon occipitalis* (Boulenger) **new combination**  
Figures 21 and 22

*Pseudoxyrhopus occipitalis* Boulenger, 1896:613.

*Heteroliodon torquatus* Boettger 1913:313. New synonym.

TYPE MATERIAL.—BM 1946.1.12.28 (holotype of *Pseudoxyrhopus occipitalis*); sex and maturity unknown, from "Southwest Madagascar"; collected by Mr. Last. SMF 7271a (holotype of *Heteroliodon torquatus*, not seen), sex and maturity unknown, from "Andranohinaly, im Hinterland von Tu-





FIG. 20. *Pseudoxyrhopus tritaeniatus*, UMMZ 195854.

lear, SW Madagascar," collected during February 1904 by A. Voeltzkow.

**MATERIAL EXAMINED.**—BM 1946.1.12.28, holotype of *Pseudoxyrhopus occipitalis*; BM 1930.7.1.238, male, maturity unknown, collected by E.J. White at "Itampolové, S.W. coast, 60 miles N of Tuléar, Madagascar"; MNHN A.62, maturity and sex unknown, collected August 1964 by C. Blanc at "Sous une écorce en forêt cotière, Ambararata, Sud de Morondava, Madagascar"; MNHN 1978.33, maturity and sex unknown, collected 26 July 1965 by G. Razafy at "PK 40, RN9, Madagascar"; UMMZ 197143, adult male collected 18 October 1990 by R.A. Nussbaum, J.B. Ramanamanjato, A. Raselimanana, and C.J. Raxworthy one km northwest of Beraketa, 24°54'S, 46°24'E, 50 m altitude, Amboasary Fivondronana, Toliara (Tuléar) Province, Madagascar; UMMZ 203658 and 203659, juvenile male and adult male collected 13 and 14 June 1993 by R.A. Nussbaum at Amboanemba, 24°39'S, 46°29'E, 280 m altitude, Amboasary Fivondronana, Toliara (Tuléar) Province, Madagascar.

**DIAGNOSIS.**—Characters of the genus.

**DESCRIPTION OF HOLOTYPE.**—SVL 240 mm; tail length 70 mm; 17 rows of smooth dorsal scales at midbody; body round in cross section; 174 ventrals; 62 paired subcaudals; anal divided; seven supralabials, third and fourth contact eye; seven infralabials, four infralabials in contact with anterior genials; anterior genials 1.5 times as long as posterior genials; rostral wider than high and visible from above; internasals shorter than prefrontals; frontal hexagonal, 1.5 times as long as wide, shorter than parietals, longer than distance between anterior margin of frontal and snout tip; loreal, 1.5 times as long as high; nasal semidivided by inferior suture (left) and divided (right); one preocular; two postoculars; temporals 1 + 2 + 3; snout bluntly rounded when viewed dor-

sally, but somewhat pointed and strongly projecting forwards over lower jaw when viewed laterally; lower jaw narrower than upper jaw; eye large, diameter 0.35 head depth at midorbit, pupil round; head distinct from neck; 12 maxillary teeth, two posteriormost teeth (11th and 12th) separated by small diastema from anterior teeth; 11th maxillary tooth slightly larger (left) or same size (right) as anterior teeth, 12th tooth missing on both sides but socket visible; 14 dentary teeth, middle (fifth and sixth) teeth considerably larger than anterior and posterior teeth.

In alcohol coloration of head, body, and tail brown. Neck marked by white transverse nuchal collar on posterior margin of parietals and first three transverse scale rows (Fig. 21), ventrolaterally uniting with white coloration of throat. Supralabials and rostral white, forming a white line that unites posteriorly with white nuchal collar. Pale brown vertebral line three scale rows wide along middle section of body, with diffuse lateral border; vertebral line starts at neck (at sixth transverse scale row posterior to parietal scales) and terminates at extreme tail tip. Body white ventrolaterally. Chin, throat, venter, and tail undersurfaces white and unspotted. Iris black.

**VARIATION.**—Specimen UMMZ 197143 has a rostral with a short, incomplete median groove on the ventral surface and a mental with a faint, incomplete median groove. A median groove on the rostral was also reported by Guibé (1958) for SMF 7271a. Other morphometric variation for the eight known specimens is summarized in Table 6. The tooth arrangement of UMMZ 197143 differs from the holotype only in that the 11th maxillary tooth is lost and the 12th is slightly enlarged compared to the anterior teeth. No variation was found in coloration (Fig. 22).

**HABITAT AND DISTRIBUTION.**—Specimen UMMZ 197143

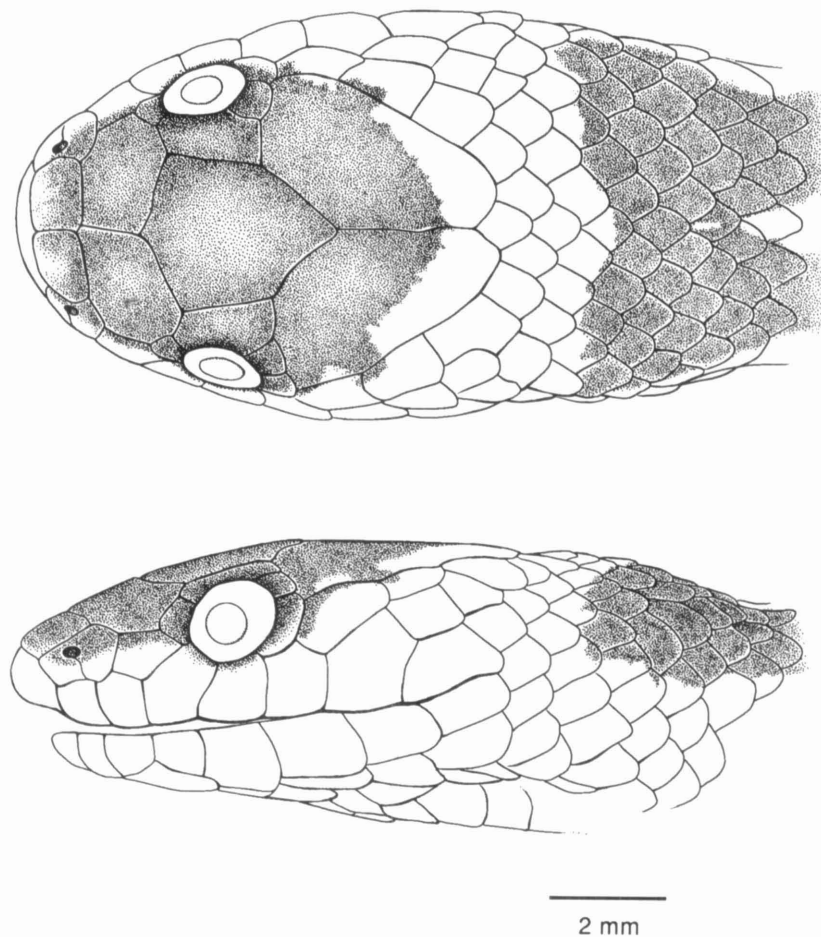


FIG. 21. Dorsal and lateral views of *Heteroliodon occipitalis*, holotype BM 1946.1.12.28.

was captured in a pitfall trap in arid euphorb (spiny) forest dominated by succulents of the endemic family Didiereaceae, in an area which is regularly grazed by domestic goats and is selectively logged for charcoal production by the local communities; UMMZ 203658 was found at 1140 h, 0.5 m above ground in a crack in a granitic boulder and UMMZ 203659 at 1050 h inside a dry rotten log, both adjacent to a dry stream bed in disturbed euphorb (spiny) forest. The localities of the other specimens are interpreted as follows: Andranohinaly, Toliara (Tuléar) region, 23°17'S, 43°59'E; Itampolové, southwest coast, 60 miles north of Toliara (Tuléar) is almost certainly Tampolove, on the coast 130 km north of Toliara, at 22°14'S, 43°16'E; Ambararata, south of Morondava, is at 20°38'S, 44°05'E. The localities of all eight specimens are in the dry southern and southwestern regions of Madagascar where the primary forest is euphorb (spiny) or deciduous (Fig. 23). This species is probably restricted to this region.

REMARKS.—Specimens UMMZ 197143 and 203659 are adults. The testes are large and swollen. There is a surprisingly small degree of variation in the SVL of the seven largest snakes (238–265 mm), and we suspect that all these specimens are adults. Specimen UMMZ 203658, with a SVL of 150 mm, is a juvenile. Brygoo (1983) considered the type of

*Heteroliodon torquatus* to be a juvenile, probably because of its small size. *Heteroliodon occipitalis* is one of the smallest colubrid snakes in Madagascar.

Guibé (1958) described the thin pale band of the body of *Heteroliodon torquatus* as being lateral (not vertebral as described by Boettger, 1913 and shown in his Plate 28) and the nasal as divided (not semi-divided as described by Boettger). The coloration error may have been made during the translation of the original text.

The pointed overhanging snout and upper jaw may be adaptations for burrowing in dead wood and Didiereaceae stems. However, the large eye is certainly not typical of burrowing snakes in Madagascar. It is not known whether this species is nocturnal, diurnal, or crepuscular; and its food habits are unknown.

#### *Pararhadinaea* Boettger

*Pararhadinaea* Boettger, 1898:33. Type species *Pararhadinaea melanogaster* Boettger, 1898, by monotypy.

*Rhabdotophis* Werner, 1909:58. Type species *Rhabdotophis subcaudalis* Werner, 1909, by monotypy.

DIAGNOSIS.—Colubrids without grooves in teeth; posteriormost one or two teeth of maxilla enlarged compared to

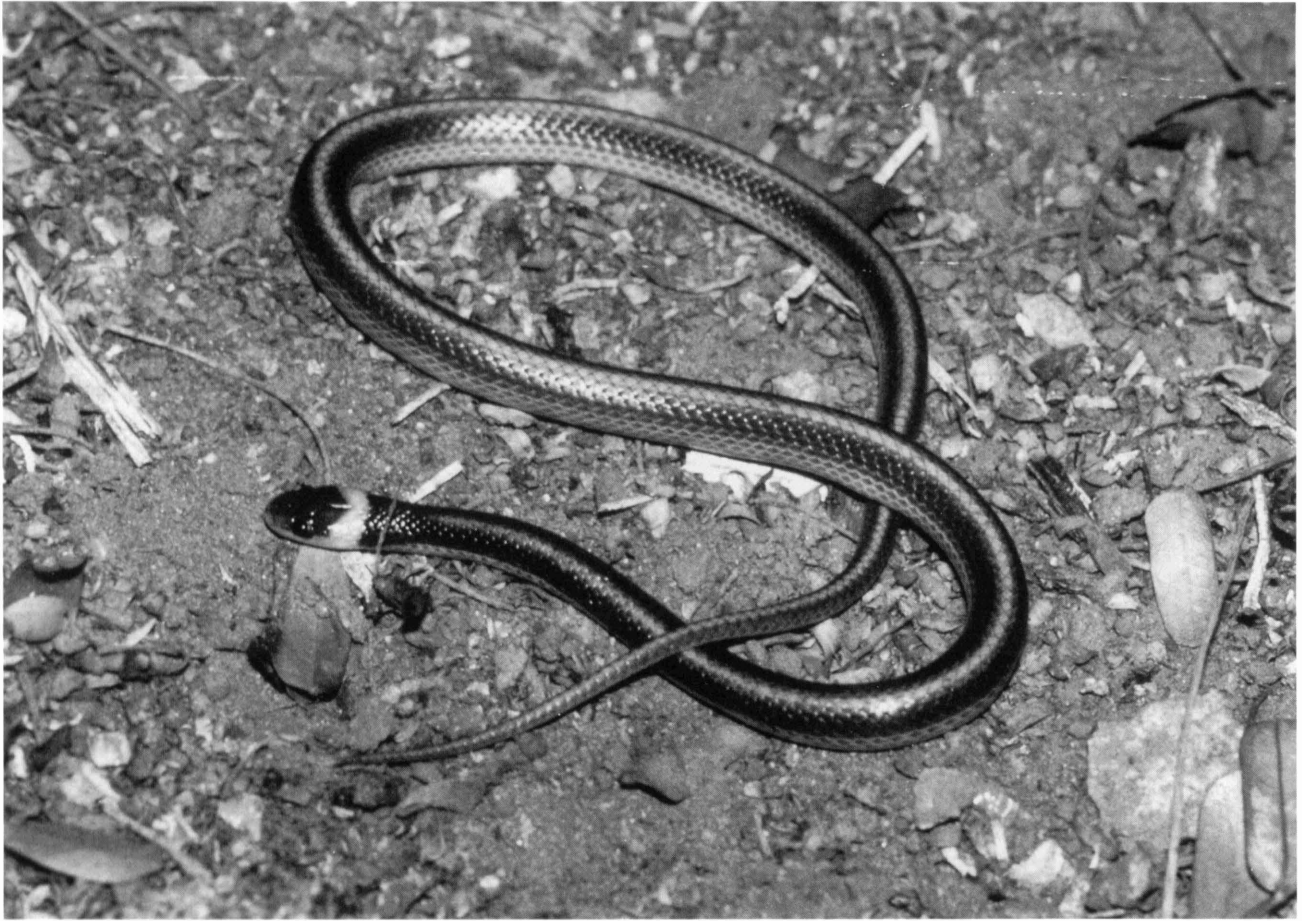


FIG. 22. *Heteroliodon occipitalis*, UMMZ 197143.

Table 6. Morphometric variation in *Heteroliodon occipitalis*. \* = holotype, M = male, F = female, A = adult, J = juvenile.

Character	BM 1946.1. 12.28*	BM 1930.7. 1.238	MNHN A.62	MNHN 1978.33	UMMZ 197143	UMMZ 203658	UMMZ 203659	SMF 7271a <sup>a</sup>
sex	?	M	?	?	M	M	M	?
sexual maturity	?	?	?	?	A	J	A	?
SVL (mm)	240	238	253	248	250	150	265	244
tail length (mm)	70	69	67	71	71	38	47+	77
subcaudals	62	61	62	66	69	62	38+	65
ventrals	174	161	180	178	178	175	162	170
postoculars <sup>b</sup>	2/2	2/2	2/2	1/1	2/2	2/1	2/3	2/2
temporal formula <sup>b</sup>	1+2+3	1+2+3	1+2+3	1+2+2/3	1+2+3	1+2+3	1+2+3	1+2+?

<sup>a</sup>Data from Boettger (1913); specimen not seen.

<sup>b</sup>left/right

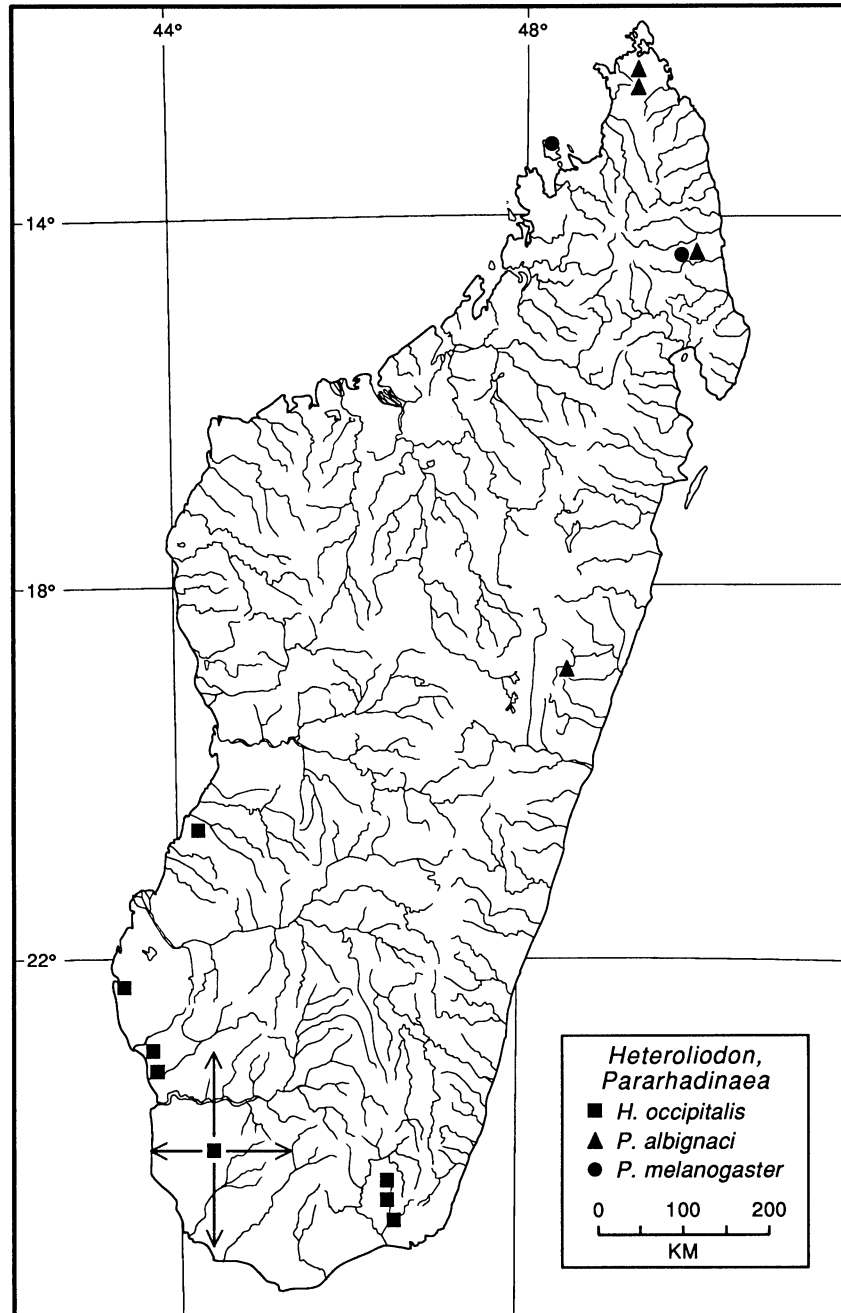


FIG. 23. Distribution of *Heteroliodon occipitalis*, *Pararhadinaea albignaci* and *Pararhadinaea melanogaster*. Arrows indicate imprecise locality.

anterior teeth; anterior dentary teeth same size as posterior dentary teeth, middle one or two dentary teeth considerably enlarged; loreal absent; eye small, diameter less than 0.3 times head depth at midorbit.

**DESCRIPTION.**—Teeth without grooves; 6–17 maxillary teeth, the posteriormost one or two teeth enlarged compared to the anterior teeth, and may be separated from the anterior teeth by a diastema; 5–11 dentary teeth, the middle one or two teeth considerably enlarged compared to anterior and posterior teeth; hypapophyses developed throughout verte-

bral column; head not distinct from neck; eye small, diameter less than 0.30 times head depth at midorbit, pupil round; nasal entire or divided; rostral scale much wider than high, clearly visible from dorsal view; body cylindrical; dorsal scales smooth, without pits, in 17 rows at midbody; subcaudals in a double row; anal plate divided.

**CONTENT.**—Two species: *Pararhadinaea melanogaster* Boettger, and *P. albignaci* Domergue.

**DISTRIBUTION.**—North and east Madagascar.

*Pararhadinaea albignaci* Domergue

Figure 24

*Pararhadinaea albignaci* Domergue, 1984:153.

HOLOTYPE.—MNHN 1982.1221 (not seen), male, maturity unknown, from "Forêt tropicale d'Analamazaotra (Périnet), altitude 900 m," Madagascar, collected 5 January 1970 by J. Thiel.

MATERIAL EXAMINED.—UMMZ 200064, adult female with five eggs in oviducts (largest 1.0 x 0.5 mm), collected 27 December 1991 by J.B. Ramanamanjato, A. Raselimanana, and C.J. Raxworthy at Antomboka River Fitsahana, Montagne d'Ambre, 12°32'S, 49°10'E, 650 m altitude, Antsiranana (Diégo Suarez) Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar; UMMZ 200065, adult male with large testes, collected 18 January 1992 by J.B. Ramanamanjato, A. Raselimanana, and C.J. Raxworthy at Antomboka River Fitsahana, Montagne d'Ambre, 12°32'S, 49°10'E, 650 m altitude, Antsiranana (Diégo Suarez) Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar; UMMZ 203642, adult female with eight eggs in right oviduct and six eggs in left oviduct (largest 1.0 x 0.5 mm), collected 4 December 1992 by R.A. Nussbaum at Manantenina River, Marojejy Reserve, 14°27'S, 49°47'E, 350 m altitude, Sambava Fivondronana, Antsiranana (Diégo Suarez) Province, Madagascar.

DIAGNOSIS.—A *Pararhadinaea* with a single undivided nasal, a small triangular-shaped preocular, one postocular, and three dark longitudinal lines on the body.

DESCRIPTION OF UMMZ 200064.—SVL 240 mm; tail length 8 mm (tail tip lost); 17 rows of smooth dorsal scales at midbody; body round in cross section; 190 ventrals; 10 paired subcaudals; anal divided; seven supralabials, third and fourth contact eye; eight infralabials, four infralabials in contact with anterior genials; anterior genials equal in length to posterior genials; rostral wider than high and visible from dorsal view; internasals shorter than prefrontals; frontal hexagonal, 1.3 times as long as wide, shorter than parietals, longer than distance between anterior margin of frontal and snout tip; loreal absent; single nasal; preocular small and triangular in shape; one postocular; temporals 1+2+3; snout bluntly rounded when viewed dorsally; eye very small, diameter 0.20 head depth at midorbit, pupil round; head not distinct from neck; 6+2 maxillary teeth, posteriormost two teeth separated by diastema from anterior teeth and enlarged; 12 dentary teeth, middle (fifth and sixth) teeth considerably larger than anterior and posterior teeth.

In life coloration of head, body, and tail dark brown. Neck with white transverse nuchal collar on posterior margin of parietals and first four transverse scale rows, collar fusing ventrolaterally with white line that borders ventrals. On body a pale pink longitudinal line on scale rows IV-VI; line starts three transverse scale rows behind nuchal collar and terminates at tail tip. Dark brown dorsal and white ventral coloration separated along body by sharp border at scale row II. Chin brown, with each scale bordered with pale brown. Venter white, with transversely enlarged brown spots on most ventrals; spots widest on anterior half of body. The tail undersurface is white with a median line of brown spots.

In alcohol, only change has been loss of pale pink pigment of longitudinal line on body, which has become white.

VARIATION.—Specimens UMMZ 200065 and UMMZ 203642 showed the following variation: SVL 253 and 370 mm; tail length 38 and 45 mm; 180 and 196 ventrals; 37 and 36 paired subcaudals; frontal 1.4 and 1.2 times as long as wide; eye diameter 0.19 and 0.15 head depth at midorbit. The holotype, MNHN 1982.1221, shows the following variation (data from Domergue, 1984): body slightly flattened dorsoventrally; SVL 210 mm; tail length 27 mm; 185 ventrals; 30 subcaudals; 5+1 maxillary teeth, with a large diastema; 5 dentary teeth, the middle enlarged. Domergue (1984) thought it probable that some teeth were lost because the holotype was found dead on a road. This may also explain the dorsoventral flattening reported for the holotype.

In alcohol UMMZ 200065 has small, pale brown spots on the rostral, internasals, prefrontals, second supralabial, temporals and parietals. The white longitudinal line fades and is broken on the posterior region of the tail. The transversely enlarged, brown spots frequently completely cover the ventral scales on the anterior half of the body.

In alcohol UMMZ 203642 (Fig. 24) has a pale yellow nuchal collar, and the head has a pale yellow line that starts on the rostral, extends onto the supralabials, and fuses with the nuchal collar on the lateral region of the neck. The left and right supralabial lines do not meet on the rostral. The longitudinal line on dorsal rows IV-VI is pale pink. The ventrals are dark brown except at their white lateral borders. The ventral surface of the tail is heavily spotted with dark brown.

HABITAT AND DISTRIBUTION.—Specimens UMMZ 200064 and UMMZ 200065 were caught in pitfall traps next to drift fences in primary rainforest; UMMZ 203642 was caught at 1600 h, in soil and humus at 20 cm depth under a large log, in disturbed primary rainforest with considerable admixture of bamboo. The holotype, MNHN 1982.1221, was found in the morning, dead on a surfaced road after heavy rains, between Andasibe (Périnet) and the Analamazaotra Forestry Station, at 18°56'S, 48°25'E. This road now borders degraded primary rainforest at 900 m altitude.

*Pararhadinaea albignaci* is limited to the north and east regions of Madagascar, between latitudes of 12° and 19°S. The three localities are in areas of primary rainforest, between 300 m and 900 m altitude (Fig. 23).

*Pararhadinaea melanogaster* Boettger*Pararhadinaea melanogaster* Boettger, 1898:33.*Rhabdotophis subcaudalis* Werner, 1909:58.

TYPE MATERIAL.—SMF.7313.1a (holotype of *Pararhadinaea melanogaster*, not seen), female, maturity unknown, from "Insel Nossibé," Madagascar, collected in 1897 by A. Voeltzkow. SMNS specimen, number unknown (holotype of *Rhabdotophis subcaudalis*, not seen), male, maturity unknown, from "Madagaskar." collected by H. Rolle.

MATERIAL EXAMINED.—None.

DIAGNOSIS.—A *Pararhadinaea* with a divided nasal, a rectangular-shaped preocular, two postoculars, and five dark longitudinal lines on the body.

DESCRIPTION OF MNHN 1982.1220.—Holotype of *Pararhadinaea melanogaster marojejyensis*; data from Domergue (1984): SVL 151 mm; tail length 34 mm; 17 rows of smooth dorsal scales at midbody; 147 ventrals; 42 paired subcaudals;

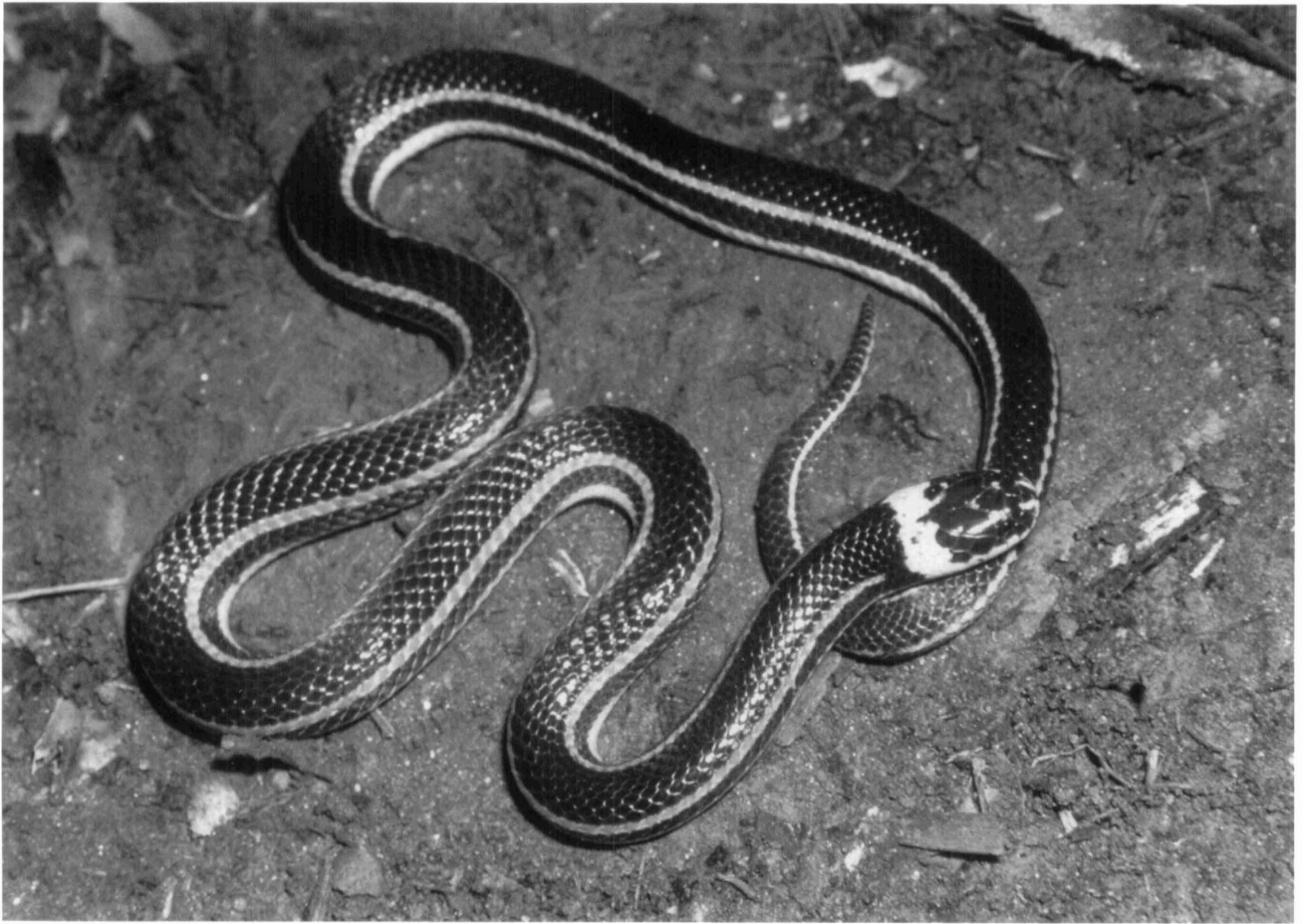


FIG. 24. *Pararhadinaea albignaci*, UMMZ 203642.

anal divided; seven supralabials, third and fourth contact eye; eight (left) and nine (right) infralabials, four infralabials in contact with anterior genials; anterior genials longer than posterior genials; rostral wider than high and visible from above; internasals shorter than prefrontals; frontal hexagonal, 1.5 times as long as wide, shorter than parietals, longer than distance between anterior margin of frontal and snout tip; loreal absent; nasal divided; one preocular; two postoculars; temporals 1+2+3; bluntly rounded snout; eye small, diameter 0.29 head depth at midorbit, pupil round; head not distinct from neck.

In alcohol, coloration of head, body, and tail yellowish-brown. Head dorsally dark brown on the parietals, frontal, supraoculars and prefrontals. Supralabials pale brown. A dark brown line starts at nostril and terminates at third row of temporals, where it fuses with two lateral dark longitudinal lines on scale rows II-IV and V-VI of neck. Body with five dark brown longitudinal lines, two pairs of lateral lines on scale rows II-IV and V-VI and a vertebral line on scale rows VIII-IX; all lines start at neck and terminate at extreme tail tip. At tail base two dark lateral bands fuse into single line. Chin and throat white with black spot on each scale, venter black with white lateral stripe, and tail undersurface white with large black spots on posterior subcaudals.

**VARIATION.**—The holotypes of *Pararhadinaea melanogaster* and *Rhabdotophis subcaudalis* show the following variation: SVL 202 mm and 182 mm; tail length 39 mm and 30 mm; ventrals 163 and 167; subcaudals 41 and 37 (Domergue, 1984).

Boettger (1898) described the teeth of the holotype of *Pararhadinaea melanogaster* as follows: 17 equally spaced maxillary teeth, increasing gradually in size posteriorly, the posteriormost tooth considerably enlarged; 11 dentary teeth, the sixth considerably enlarged. Werner (1909) reported about 10–12 maxillary teeth for the holotype of *Rhabdotophis subcaudalis*. Guibé (1958) gave a range of 15–18 maxillary teeth without indicating the source of his information.

**HABITAT AND DISTRIBUTION.**—The known localities are SMF.7313.1a, Nosy Be Island at 13°20'S, 48°20'E and MNHN 1982.1220, Marojejy Reserve at 14°27'S, 49°45'E (Fig. 23). The holotype of *Rhabdotophis subcaudalis* was collected from an unknown locality in Madagascar. Both the known sites have a primary climax vegetation of rainforest, with elevations between 0–430 m for Nosy Be and 200–1800 m for Marojejy. This species appears to be restricted to northern Madagascar.

**REMARKS.**—*Rhabdotophis subcaudalis* was placed in the genus *Pseudoxyrhopus* by Boulenger (1915) and subsequently

recognized as a junior synonym of *Pararhadinaea melanogaster* by Guibé (1958). Domergue (1984) described the subspecies *Pararhadinaea melanogaster marojejensis* based on the lower number of ventrals (147) of the Marojej specimen compared to the other two known specimens (163–7). Boettger (1898) reported that a second smaller specimen of *Pararhadinaea melanogaster* was deposited at the Lübeck Museum (Germany).

KEY TO *HETEROLIODON*, *PARARHADINAEA*, AND  
*PSEUDOXYRHOPUS* SPECIES

- 1a. 17 dorsal scales at midbody ..... 2  
1b. 19–25 dorsal scales at midbody ..... 4
- 2a. Eye large, larger than 0.3 times head depth at midorbit. Rostral strongly overhangs mental. Loreal present. .... *Heteroliodon occipitalis*  
2b. Eye small, smaller than 0.3 times head depth at midorbit. Rostral hardly overhangs mental. Loreal absent ..... 3
- 3a. Three dark longitudinal lines on body. Preocular triangular and small. One postocular  
..... *Pararhadinaea albignaci*  
3b. Five dark longitudinal lines on body. Preocular rectangular and not small. Two postoculars  
..... *Pararhadinaea melanogaster*
- 4a. Dorsal scales at midbody in 19 rows ..... 5  
4b. Dorsal scales at midbody in 21–25 rows ..... 6
- 5a. Snout tip somewhat pointed. Rostral strongly overhangs mental. Nuchal collar absent, venter dark brown ..... *Pseudoxyrhopus imeriniae*  
5b. Snout tip bluntly rounded. Rostral does not strongly overhang mental. Pale nuchal collar present, venter pink (in life) or white (in preservative)  
..... *Pseudoxyrhopus kely*
- 6a. Dorsal scales at midbody in 21 rows ..... 7  
6b. Dorsal scales at midbody in 25 rows ..... 10
- 7a. Seven supralabials. Pale nuchal collar present. Red spot on the snout tip (in life)  
..... *Pseudoxyrhopus ambreensis*  
7b. Eight supralabials. Nuchal collar absent. No red spot on snout tip (in life) ..... 8
- 8a. Snout tip somewhat pointed. Rostral strongly overhangs mental. Dorsum pale brown, typically with five dark longitudinal lines  
..... *Pseudoxyrhopus quinquelineatus*  
8b. Snout tip blunt and rounded. Rostral does not strongly overhang mental. Dorsum dark brown, sometimes with two pale pink longitudinal lines ..... 9
- 9a. Anterior subcaudals undivided, more than 149 ventrals ..... *Pseudoxyrhopus heterurus*  
9b. Anterior subcaudals divided, less than 146 ventrals ..... *Pseudoxyrhopus sokosoko*
- 10a. Parietals equal in length to frontal  
..... *Pseudoxyrhopus ankafinaensis*  
10b. Parietals longer than frontal ..... 11
- 11a. Dorsum brown with or without thin pink (in life) or white (in preservative) longitudinal lines. Loreal always twice as long as high, 70–89 subcaudals, anal always divided ..... *Pseudoxyrhopus microps*  
11b. Dorsum red (or white in preservative) with dark brown longitudinal lines. Loreal typically almost as high as long, 58–76 subcaudals, anal single, semi-divided, or divided ..... *Pseudoxyrhopus tritaeniatus*

BEHAVIOR

The seven *Pseudoxyrhopus* species studied in the field appear to have similar habits. *Pseudoxyrhopus kely*, *P. ambreensis* and *P. quinquelineatus* are unlike the other three species in that they have an obvious tendency to burrow, digging their snouts into the substrate and vibrating the head and anterior region of the body. They are probably largely fossorial. These three species were found great distances from streams. *Pseudoxyrhopus kely* is known to feed on small *Amphiglossus* skinks, and leaf-litter lizards may be an important prey item for these species. That the juvenile *Pseudoxyrhopus sokosoko* was found in wood chips during the day indicates that this species, and probably all *Pseudoxyrhopus*, burrow to some degree. *Pseudoxyrhopus heterurus*, *P. microps* and *P. tritaeniatus* are all nocturnal and largely ground-dwelling snakes, frequently encountered close to small streams in rainforest. At night these river banks are normally populated by stream-dwelling *Mantidactylus* frogs that may be preyed upon by *Pseudoxyrhopus*.

Very little is known about the behavior of *Heteroliodon* and *Pararhadinaea*. *Pararhadinaea albignaci* was found 20 cm below ground, suggesting this snake is at least partly fossorial. *Heteroliodon occipitalis* and *Pararhadinaea albignaci* were both caught in pitfall traps and *Pararhadinaea melanogaster* was found dead on a road, demonstrating that these species are surface active. Because we have never seen these snakes active on the surface during the day, it seems probable that all three species are nocturnal.

The scarcity of *Pseudoxyrhopus*, *Heteroliodon* and *Pararhadinaea* specimens in museum collections probably does not reflect rarity in nature, but rather their secretive habits. Most species are probably nocturnal and some may be partly fossorial. Nocturnal snakes in general are not well represented in collections from Madagascar.

*Pseudoxyrhopus tritaeniatus*, *P. microps* and *P. ambreensis* frequently have truncated tails. The incidence of tail tip loss among these species was 50%, 43%, and 50% respectively, which is far higher than all the other species (with the exception of *P. ankafinaensis* which is represented only by the holotype with a truncated tail). Tail tip damage is probably due to attack from nocturnal mammalian predators such as tenrecs (Insectivora, Tenrecidae) and mongooses (Car-

nivora, Viverridae). It is not clear why these three species seem to suffer more tail injuries than the other species.

### MORPHOLOGICAL VARIATION

Significant variation is rare in all the *Pseudoxyrhopus* species, with the exception of *P. tritaeniatus*, which has an anal plate either divided, semidivided or entire. It is noteworthy that no individual variation was found in the number of dorsal scale rows for *Pseudoxyrhopus*, *Pararhadinaea* or *Heteroliodon*. The coloration of each species is also extremely stable, although in two species, *Pseudoxyrhopus sokosoko* and *P. microps*, juvenile coloration is very different from the adult. Longitudinal stripes are known to occur at some stage of development in all *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* species with the exception of *Pseudoxyrhopus heterurus*. Although the juvenile coloration of this species is unknown, it is probably striped. Dorsal coloration is either brown or brownish-purple with the striking exception of *Pseudoxyrhopus tritaeniatus*, which is bright red. This bright red color may be aposematic, although all *Pseudoxyrhopus* are thought to be non-venomous. There are no obvious venomous species of snakes in Madagascar which *Pseudoxyrhopus tritaeniatus* might be mimicking, but there are bright red, noxious millipedes in the rainforest that could serve as models.

We found very little geographic variation among the specimens we examined. *Pseudoxyrhopus microps* shows remarkably little variation considering that it occurs throughout the full latitudinal range of the island. The juvenile *Pseudoxyrhopus microps* from Montagne d'Ambre are unusual in that they lack some of the white markings on the head present in juveniles from the southeast.

The relationship between the ventral and subcaudal scale counts for all undamaged specimens of *Pseudoxyrhopus* is shown in Figure 25. Most species form a relatively distinct cluster, showing little overlap with other species (except for *Pseudoxyrhopus sokosoko*, *P. ambreensis*, and *P. quinquelineatus*), demonstrating that ventral and subcaudal scale counts can be used to help identify most *Pseudoxyrhopus* species. Two obvious phenetic groups appear in Figure 25, one group with fewer than 170 ventrals, and the other group with more than 190 ventrals.

### PHYLOGENETIC RELATIONSHIPS

The relationships of the Madagascan snake genera have not yet been studied, although they are all currently considered to be boodontine colubrids in the Lycodontinae-Boodontinae group (Cadle, 1987). However, the Lycodontinae-Boodontinae group may not be monophyletic. *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* may represent either an ancient Madagascan lineage (similar to the situation found in the Madagascan boids and iguanids) or a more modern African or Asian invasion. The relationships within and between *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* have not been determined.

Some characteristics of *Pseudoxyrhopus*, *Pararhadinaea* and

*Heteroliodon* are listed in Table 7. These three genera have very similar dentition and share the following characters: teeth without grooves, maxillary teeth with a diastema, posteriormost maxillary teeth enlarged, and median dentary teeth enlarged. No other Malagasy colubrid genus has enlarged median dentary teeth. *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* also share a very similar body form (thick neck that is hardly narrower than the head, and a rounded head profile) and have similar habits (all species are probably nocturnal and ground dwelling).

The other Malagasy colubrid genera are dissimilar to *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* in dentition, body form and habits. The genera that lack grooved teeth, *Dromicodryas*, *Leioheterodon*, *Liopholidophis*, *Liophidium* and *Micropisthodon*, are diurnal and largely surface active (except *Micropisthodon* for which the habits are unknown), with narrow necks and generally angular head profiles. The genera with grooved teeth, *Alluaudina*, *Brygophis*, *Geodipsas*, *Ithycyphus*, *Langaha*, *Lycodryas*, *Madagascarophis* and *Mimophis*, also have slender necks, angular head profiles, and are either arboreal (nocturnal and diurnal) or surface active (diurnal), with the exception of *Madagascarophis* and *Geodipsas*, which are nocturnal and partly surface active.

Because of the phenetic similarity of *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* in dentition, body form and habits, we suspect they represent a monophyletic group. Because of the significant morphological and behavioral differences of *Pseudoxyrhopus*, *Pararhadinaea*, *Heteroliodon* compared to the other Malagasy genera, we suspect the sister-group to *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* will prove to be a non-Malagasy genus. However we have not yet identified non-Malagasy genera that appear to closely resemble these Malagasy colubrids.

The character states that separate *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* are: *Pseudoxyrhopus*—anterior dentary teeth larger than posterior teeth; *Pararhadinaea*—no loreal scale; and *Heteroliodon*—eye diameter greater than 0.3 times head depth at midorbit. Based on these characters, we continue for the moment to recognize all three genera, but it is impossible without additional data to determine the relationships of the three genera to each other. The polarity of these character states has not yet been determined because the outgroups remain unknown.

Variation within *Pseudoxyrhopus* is summarized in Table 8. Four phenetic groups can be recognized based on shared characters of unknown polarity. *Pseudoxyrhopus kely* and *P. ambreensis* have fewer than 12 posterior dentary teeth and a single enlarged maxillary tooth. *Pseudoxyrhopus heterurus* and *P. sokosoko* have fewer than 12 posterior dentary teeth and two enlarged maxillary teeth. The remaining species have 12 or more posterior dentary teeth: *Pseudoxyrhopus imerinae* and *P. quinquelineatus* have a strongly overhanging rostral, which is otherwise absent in *Pseudoxyrhopus*; *P. ankafinaensis*, *P. microps* and *P. tritaeniatus* share much higher scale counts (dorsals, ventrals, and subcaudals) than all the other species. Based on this evidence we suspect the following *Pseudoxyrhopus* species are sister taxa: *P. ambreensis* and *P. kely*, *P. heterurus* and *P. sokosoko*, *P. imerinae* and *P. quadrilineatus*, and (as an unresolved group of three) *P. tritaeniatus*, *P. microps* and *P. ankafinaensis*.



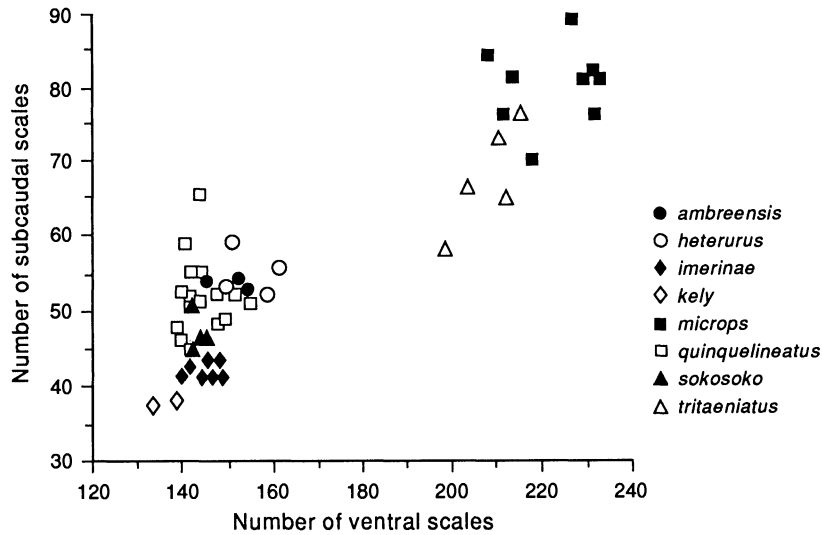


FIG. 25. *Pseudoxyrhopus* ventral-subcaudal scale number relationship. Subcaudal counts are for undamaged tails only.

Table 7. Characters of *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon*.

Character	<i>Pseudoxyrhopus</i>	<i>Pararhadinaea</i>	<i>Heteroliodon</i>
teeth without grooves	+	+	+
maxillary teeth with diastema	+	+	+
posteriormost maxillary teeth enlarged	+	+	+
median dentary teeth enlarged	+	+	+
anterior dentary teeth larger than posterior	+	-	-
loreal scale present	+	-	+
eye diameter < 0.3 times head depth at midorbit	+	+	-

Table 8. Character variation within *Pseudoxyrhopus*. Abbreviations: *ambre.* = *ambreensis*; *heterur.* = *heterurus*; *soko.* = *sokosoko*; *imerin.* = *imerinae*; *quinquel.* = *quinquelineatus*; *ankaf.* = *ankafinaensis*; *tritaen.* = *tritaeniatus*.

Character	<i>Pseudoxyrhopus</i>								
	<i>ambre.</i>	<i>kely</i>	<i>heterur.</i>	<i>soko.</i>	<i>imerin.</i>	<i>quinquel.</i>	<i>ankaf.</i>	<i>microps</i>	<i>tritaen.</i>
less than 12 posterior dentary teeth	+	+	+	+	-	-	-	-	-
single enlarged maxillary tooth	+	+	-	-	-	-	-	-	-
rostral strongly overhangs mental	-	-	-	-	+	+	-	-	-
more than 21 dorsal rows	-	-	-	-	-	-	+	+	+
more than 190 ventrals	-	-	-	-	-	-	+	+	+
more than 70 subcaudals	-	-	-	-	-	-	+ <sup>a</sup>	+	+

<sup>a</sup>Estimated from mutilated tail of holotype (see synopsis).

## BIOGEOGRAPHY

*Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* seem to be incapable of oceanic dispersal because no species is known from other Indian Ocean islands or mainland Africa. The majority of *Pseudoxyrhopus* species occur in the humid rainforest of the Eastern Climatic Domain: *Pseudoxyrhopus ambreensis*, *P. heterurus*, *P. sokosoko*, *P. imeriniae*, *P. microps*, *P. tritaeniatus* and *P. ankafinaensis*. Two of these species, *Pseudoxyrhopus imeriniae* and *P. ankafinaensis*, are restricted to high altitude regions of the High Plateau above 1300 m altitude. Of the other species, *Pseudoxyrhopus kely* is known from littoral forests in a climatic transitional zone between the Eastern and Western Domains and *P. quinquelineatus* from both dry and humid forests of each Domain. Both species of *Pararhadinaea* are restricted to rainforest in the north and east in the Eastern Climatic Domain. *Heteroliodon* is known only from the arid south and southwest of the Western Climatic Domain, and is probably restricted to deciduous and euphorb (spiny) forests.

The groups of presumed closely related species occur in both allopatry and sympatry. *Pararhadinaea albignaci* and *P. melanogaster* are sympatric in northern Madagascar, occurring in rainforest of similar elevation. *Pseudoxyrhopus quinquelineatus* and *P. imeriniae* are allopatric with distinct altitudinal differences in distribution. *Pseudoxyrhopus kely* and *P. ambreensis* are allopatric with restricted ranges in relict forests of the southeast and north respectively. *Pseudoxyrhopus heterurus* and *P. sokosoko* are allopatric, with *P. sokosoko* restricted to the extreme southeast and *P. heterurus* to the east and northeast. Considering the larger *Pseudoxyrhopus*, *P. ankafinaensis* appears to be a high altitude specialist and is probably allopatric with both *P. microps* and *P. tritaeniatus*, which are distributed in lower elevation rainforest of the east. Speciation in the majority of cases appears to be associated with allopatry, either by elevation or isolation in different geographic regions or relict forests.

## CONSERVATION

*Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* are present in all the major primary forests that occur in Madagascar. All the *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon* seen by us in the field were in primary forests with minimal degradation. It appears that all these species are adapted to specific forest types and are unable to exploit new secondary habitats that have become available as a result of deforestation.

Five species were found in protected areas: *Pseudoxyrhopus heterurus* at Nosy Mangabe Special Reserve, Ambatovaky Special Reserve, Manombo Special Reserve, and Marojejy Strict Reserve; *P. tritaeniatus* at Ambatovaky Special Reserve, Ranomafana National Park, and the planned Masoala National Park; *P. quinquelineatus* at the planned Zombitsy National Park; *P. ambreensis* at Montagne d'Ambre National Park; and *P. microps* at Montagne d'Ambre National Park, Marojejy Strict Reserve, and the planned Masoala National Park. *Pseudoxyrhopus microps* almost certainly occurs in Parcel One of the Andohahela Strict Reserve, because Marosohy and Manon-

gotry are within one kilometer of the Reserve's boundary. Analamazaotra Special Reserve probably protects populations of *Pseudoxyrhopus microps*, *P. tritaeniatus* and *P. quinquelineatus*, although it is not known if the Périnet locality actually refers to the interior of the Special Reserve, which was established only in 1970. *Pararhadinaea albignaci* occurs at Montagne d'Ambre National Park, Marojejy Strict Reserve, and probably Analamazaotra Special Reserve. *Pararhadinaea melanogaster* occurs at Marojejy Strict Reserve and probably Lokobe Strict Reserve on Nosy Be Island.

Five species are not known to be currently protected within reserves: *Heteroliodon occipitalis*, *Pseudoxyrhopus ankafinaensis*, *P. imeriniae*, *P. kely* and *P. sokosoko*. *Heteroliodon occipitalis* and *Pseudoxyrhopus sokosoko* probably occur in the Andohahela Strict Reserve, because Beraketa is just 15 km west of Parcel Two and both Ampamakiesiny and the Andondo River are within ten kilometers of Parcel One of the Andohahela Strict Reserve. *Pseudoxyrhopus imeriniae* appears to be restricted to high altitude forest on the High Plateau, and because of severe forest fragmentation may be restricted to small isolated populations. Protecting remaining natural habitats at Ankaratra and Ibity Mountain would be beneficial to this species and to other reptiles such as *Calumma brevicornis hilleni*, *Millotissaurus mirabilis*, *Lygodactylus arnoulti* and *Lygodactylus blanci*, all of which are restricted to these sites.

*Pseudoxyrhopus kely* is known so far only from the littoral forests at Ste. Luce and Mandena close to Tôlañaro (Fort Dauphin). This species may be endemic to this region. Protection of representative littoral forest within a new reserve would be desirable to maintain populations of this small snake.

*Pseudoxyrhopus ankafinaensis* is currently known from a single specimen collected in 1880 at Ankafina Mountain. The scale of deforestation that has taken place on the High Plateau and the isolated nature of this fragment of High Plateau rainforest (which must have contracted significantly in area over the last 100 years), suggest *P. ankafinaensis* has become reduced to small populations or may even have gone extinct.

## LITERATURE CITED

- Angel, F. 1934. Sur la validité spécifique de deux espèces de couleuvres de Madagascar. Arch. Mus. Hist. Nat. (Paris) 12(6):465-467.
- Blanc, C.P. 1972. Les Reptiles de Madagascar et des îles voisines. Monograph. biol. 21:501-614.
- Boettger, O. 1898. Katalog der Reptilien-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main. II (Schlangen). Druck von Gebrüder Knauer, Frankfurt am Main. 160 pp.
- Boettger, O. 1913. Reptilien und Amphibien von Madagascar, den Inseln und dem Festland Ostafrikas. (Sammlung Voeltzkow 1889-1895 und 1903-1905.) In Reise in Ostafrika von Prof. A. Voeltzkow 3(4):269-375. E. Schweizerbart, Stuttgart.
- Brygoo, E.R. 1983. Les Ophidiens de Madagascar. Mem. Inst. Butantan (1982) 46:19-58.
- Boulenger, G.A. 1888. Descriptions of new reptiles and batrachians from Madagascar. Ann. Mag. Nat. Hist., Ser. 6, 1:101-107.
- . 1890. On the ophidian genus *Pseudoxyrhopus* Gthr. Ann. Mag. Nat. Hist., Ser. 6, 6:311-314.

- . 1893. Catalogue of the Snakes in the British Museum (Natural History). Vol. 1. British Museum (Natural History), London. 448 pp.
- . 1896. Catalogue of the Snakes in the British Museum (Natural History). Vol. 3. British Museum (Natural History), London. 727 pp.
- . 1915. A list of snakes of Madagascar, Comoro, Mascarenes and Seychelles. Proc. Zool. Soc. Lond. 1915:369–382.
- Cadle, J.E. 1987. Geographic distribution: problems in phylogeny and Zoogeography. In R.A. Seigel, J.T. Collins and S.S. Novak (eds.), Snakes: Ecology and Evolutionary Biology: 77–105. Macmillan Publishing Co., New York.
- Department of the Interior. 1955. Gazetteer 2. Madagascar, Réunion and the Comoro Islands. Office of Geography (Department of the Interior), Washington, D.C. 498 pp.
- Domergue, C.A. 1969. Clé simplifiée pour la détermination sur le terrain des serpents communs de Madagascar. Bull. Acad. Malgache (1967) 45(2):13–26.
- . 1984. Notes sur les serpents de la région malgache. IV. Le genre *Pararhadinaea* Boettger, 1898. Descriptions d'une espèce et d'une sous-espèce nouvelles. Bull. Mus. natl. Hist. nat. (Paris.), 4th Ser., 6A(1):149–157.
- Foiben Taosarintanain I Madagasikara. 1986. Adranofanjava, U 31. 1:100,000, 2nd Ed. Foiben Taosarintanain I Madagasikara, Antananarivo.
- Guibé, J. 1958. Les Serpentes de Madagascar. Mém. Inst. scient. Madagascar, Ser. A, 12:189–260.
- Günther, A. 1881. Ninth contribution to the knowledge of the fauna of Madagascar. Ann. Mag. Nat. Hist., Ser. 5, 7:357–360.
- . 1890. Tenth contribution to the knowledge of the fauna of Madagascar. Ann. Mag. Nat. Hist., Ser. 6, 5:69–72.
- Hoge, A.R. 1958. Die systematische stellung von *Xenodon punctatus* Peters 1880 und *Philodryas taeniatus* Hensel 1868. Mitt. zool. Mus. Berlin 34:49–56.
- Institute Géographique National. 1973. Alakamisy Ambohimaha, O 53N. 1:50,000, 1st Ed. Institute Géographique National, Paris. Centre à Madagascar, Tananarive.
- IUCN/UNEP/WWF. 1987. Madagascar, an Environmental Profile. M.D. Jenkins (ed.). IUCN, Cambridge. 374 pp.
- Jan, G. 1863. Enumerazione sistematica degli ofidi appartenenti al gruppo Coronellidae. Arch. Zool. Anat. Fis. 2(2):213–330.
- and F. Sordelli. 1866. Iconographie Générale des Ophiidiens. Tome Premier (Livrais. 1 à 17). Georges Jan and Ferdinand Sordelli, Milan. 100 pls.
- MacPhee, R.D.E. 1987. The shrew tenrecs of Madagascar: systematic revision and Holocene distribution of *Microgale* (Tenrecidae, Insectivora). Amer. Mus. Novit. (2889):1–45.
- Mocquard, F. 1894. Diagnoses de quelques Reptiles nouveaux de Madagascar. C.R. Somm. Séances Soc. Philom. Paris 1(9):3–5.
- . 1904. Description de quelques Reptiles et d'un Batracien nouveaux de la collection du Muséum. Bull. Mus. Hist. nat. (Paris) 10(6):301–309.
- . 1909. Synopsis des familles, genres et espèces des Reptiles écailloux et des Batraciens de Madagascar. Nouv. Arch. Mus. Hist. nat., Paris, Sér. 5, 1:1–110.
- Peters, W. 1880. Über neue oder weniger bekannte Amphibien des Berliner Zoologischen Museums. Monatsber. Dtsch. Akad. Wiss. Berlin 1880:217–224.
- Ratsivalaka-Randriamanga, S. 1986. Le climat de Fort Dauphin et son impact sur l'homme et la végétation. Thèse de Doctorat de IIIème Cycle de Géographie. Université de Tananarive, Antananarivo. 186 pp.
- Raxworthy, C.J. 1988. Reptiles, rainforest and conservation in Madagascar. Biol. Conserv. 43:181–211.
- Smith, H.M., K.L. Williams, V. Wallach, and D. Chiszar. 1992. *Pseudoxyrhopus* Günther, 1881 (Reptilia, Serpentes): proposed conservation. Bull. Zool. Nomen. 49:284–286.
- Welch, K.R.G. 1982. Herpetology of Africa: A Checklist and Bibliography of the Orders Amphisbaenia, Sauria and Serpents. Robert E. Kreiger, Malabar. 293 pp.
- Werner, F. 1909. Beschreibung neuer Reptilien aus dem Kgl. Naturalienkabinett in Stuttgart. Jahresh. Ver. Naturk. Württemberg 65:55–63.
- Williams, K.L. and V. Wallach. 1989. Snakes of the World. Volume I. Synopsis of Snake Generic Names. Robert E. Krieger, Malabar. 234 pp.

Accepted for publication January 29, 1993.



















