THE SNAKE GENUS *SIBYNOMORPHUS* (COLUBRIDAE: DIPSADINAE: DIPSADINI) IN PERU AND ECUADOR, WITH COMMENTS ON THE SYSTEMATICS OF DIPSADINI

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CONTENTS

ABSTRACT. *Sibynomorphus*, an assemblage of about a dozen species of South American gastropod-eating colubrids, has a peculiar distribution. Six species occur in northern Peru and southwestern Ecuador. The others are distributed south of the Amazon basin in Brazil, Bolivia, Paraguay, Uruguay, and Argentina. Species of *Sibynomorphus* known from Ecuador and Peru are reviewed. *Sibynomorphus oligozonatus* and *S. petersi* are reported from Peru for the first time. Study of existing collections considerably amplifies understanding of the geographic ranges and character variation within *S. oligozonatus, S. oneilli, S. petersi,* and *S. williamsi*. *Sibynomorphus vagrans* is known only from its type locality (Bellavista, Cajamarca Department, Peru), and *S. vagus* (type locality unknown) is known only from near the single historically reported locality for the species (Huancabamba, Piura Department, Peru). *Sibynomorphus oligozonatus* (four specimens known) is distributed in southwestern Ecuador (Azuay and Loja Provinces) and northern Peru (Piura Department). *Sibynomorphus oneilli* is distributed in the Cordillera Oriental and Cordillera Occidental of northern Peru from southern Ancash Department to southern Cajamarca and Amazonas Departments. Available specimens of *S. petersi* extend the known range from Azuay and Loja Provinces in southwestern Ecuador, along the western Andean slopes to southern Ancash Department, Peru (Pacific versant); a single specimen is also known from the upper Río Chotano in central Cajamarca Department, thus documenting that this species occurs on the Amazonian versant. *Sibynomorphus williamsi* is known from central Peru in Lima and Ancash Departments from near sea level to at least 2,900 m in the Andes (and perhaps as high as 3,600 m)—an elevational range unmatched in any other species of the genus. Two species (*S. vagrans* and *S. vagus*) are restricted to the Amazonian versant, two are restricted to the Pacific versant (*S. oligozonatus* and *S. williamsi*), and two are found on both versants (*S. oneilli* and *S. petersi*). A key to the species of *Sibynomorphus* in Peru and Ecuador is provided.

Hemipenes are described for *Sibynomorphus oligozonatus, S. petersi, S. vagrans, S. vagus,* and *S. williamsi*. Their organs are similar to hemipenes of other Dipsadini in having a well-defined capitulum ornamented with papillate calyces, several rows of large spines encircling the organ proximal to the capitulum, an exceptionally large basal nude pocket, and the di-

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vision of the sulcus spermaticus within the capitulum. In *Sibynomorphus* and in some other Dipsadini the branches of the sulcus spermaticus are centrolineal, but their tips pass somewhat to the lateral surface of the hemipenial lobe(s). The exceptional size of the nude pocket might be a synapomorphy of Dipsadini but further comparative studies are needed, especially because the pocket has probably been overlooked in many species.

The natural history of all northern species of *Sibynomorphus* is summarized, but very little is known. Most localities are in relatively dry to arid habitats, such as dry deciduous forests or thorn forests, on the western Andean slopes or inter-Andean valleys. A few localities for *S. petersi* in northern Peru are in areas of mesic to humid forests, although specimens are from forest edge or ecotones in this area. *Sibynomorphus williamsi* is characteristic of the lomas formations on the central Peruvian coast, but it also occurs on the Andean slopes at higher elevations.

Sibynomorphus shares with three other genera of Neotropical Dipsadinae (*Dipsas, Sibon, Tropidodipsas*) a behavioral propensity and associated morphological characteristics for consuming gastropods. In accordance with some previous authors, I suggest that the name Dipsadini be applied inclusively to this clade of four genera of Neotropical molluscivorous colubrids, notwithstanding previous arguments for excluding *Tropidodipsas.* Several external characters indicate that *Sibynomorphus* is most closely related to *Dipsas* within Dipsadini. Nonetheless, the monophyly of *Sibynomorphus* has not been demonstrated and the possibility remains that *Dipsas* is paraphyletic with respect to *Sibynomorphus,* which itself is conceivably polyphyletic. The peculiar distribution of *Sibynomorphus* is somewhat similar to other components of the herpetofauna of southern Ecuador and northern Peru (Andes, Pacific versant, and coast). However, *Sibynomorphus* as presently understood lacks some geographic components (e.g., Amazonia, Guayana) associated with these other taxa.

Some investigations have suggested that *Sibynomorphus* be synonymized with *Dipsas,* but analytical issues such as taxon and character sampling are problematic with previous studies. None of the northern species of *Sibynomorphus* have been included in broader comparative studies. I advocate a broader survey of nominal taxa of Dipsadini before making further changes in the generic nomenclature in this group. Some outstanding questions concerning the systematics and natural history of *Sibynomorphus* are outlined. Especially needed are more detailed studies of microhabitat occurrence and behavior of all species and field studies to further delineate their distributions. The significance of exceptional color pattern variation that occurs within *S. oneilli, S. petersi,* and *S. vagus* needs to be explored, perhaps in conjunction with their role as potential mimics of sympatric species of *Bothrops* (Viperidae). Similarly, the extensive variation in scutellation that occurs generally in many Dipsadini needs functional, mechanistic, and evolutionary explanation.

RESUMEN. *Sibynomorphus,* un grupo de aproximadamente una docena de especies de colubridos sudamericanos que comen gasterópodos, tiene una distribución extraña. Seis especies occuren en el norte del Perú y el Ecuador sudoccidental y los demás son distribuidas al sur de la cuenca Amazónica en Brazil, Bolivia, Paraguay, Uruguay, y Argentina. Se revisan las especies de *Sibynomorphus* de Ecuador y Perú. Se reportan para la primera vez *S. oligozonatus* y *S. petersi* del Perú. El estudio de colecciones que existe aumenta considerablemente el conocimiento de los rangos geográficos y la variación de carácteres de *S. oligozonatus, S. oneilli, S. petersi,* y *S. williamsi.* Todavía se conoce *S. vagrans* solamente de su localidad típica (Bellavista, Departamento de Cajamarca, Perú), y se conoce *S. vagus* (localidad típica desconocida) solamente cercana a la única localidad histórica para la especie (Huancabamba, Departamento de Piura, Perú). *Sibynomorphus oligozonatus* (conocido de cuatro especímenes) se distribuido en el suroeste de Ecuador (provincias Azuay y Loja) y el norte de Perú (departamento de Piura). *Sibynomorphus oneilli* se distribuido en la Cordillera Oriental y la Cordillera Occidental del norte del Perú desde el sur del departamento de Ancash hasta el sur de los departamentos Cajamarca y Amazonas. Los especímenes disponibles de *S. petersi* se extiende el rango conocido desde las provincias Azuay y Loja en el suroeste de Ecuador, a lo largo de las vertientes andinas occidentales hasta el sur del departamento de Ancash, Perú (vertiente Pacífico); un espécimen único se conoce también del alto Río Chotano en el centro del departamento de Cajamarca, que documenta que esta especie también se encuentra en la vertiente Amazónica. *Sibynomorphus williamsi* se conoce del Perú central en los departamentos Lima y Ancash desde cerca del nivel del mar hasta a menos 2,900 m en los Andes (y quizás tan alto como 3,600 m)—un rango elevational incomparable en algún otra especie del género. Dos especies (*S. vagrans* y *S. vagus*) son restringidas a la vertiente Amazónica, dos especies son restringidas a la vertiente Pacífica (*S. oligozonatus* y *S. williamsi*), y dos especies se encuentran en las dos vertientes (*S. oneilli* y *S. petersi*). Se presenta un clave para las especies de *Sibynomorphus* en Perú y Ecuador.

Se describe los hemipenes de *Sibynomorphus oligozonatus, S. petersi, S. vagrans, S. vagus,* y *S. williamsi.* Sus órganos son similar a los hemipenes de otros Dipsadini al tener un capítulo bien definido y ornamentada con cálices que llevan papilas, una serie de espinas grandes que rodean el órgano proximal al capítulo, un excepcionalmente grande bolsillo desnudo basal, y un surco espermático que divide dentro del capítulo. En *Sibynomorphus* y algunas otras especies de Dipsadini las ramas del surco espermático son centrolineal pero sus puntas pasan un tanto al lado lateral del lóbulo(s) del hemipene. El tamaño excepcional del bolsillo desnudo puede ser una sinapomorfía de Dipsadini pero se necesitan más estudios comparativos, especialmente dado que el bolsillo se ha pasado por alto en muchas especies.

Se resumen la historia natural de todas especies septentrionales de *Sibynomorphus* pero se conoce muy poca de estas especies. La mayoría de las localidades son en hábitats relativamente secos o áridos, tal como bosques caducifolios o bosques espinales, sobre las vertientes occidentales andinas o en valles interandinos. Unas pocas localidades para *S. petersi* en el norte del Perú son en áreas de bosques húmedos o muy húmedos, aunque los ejemplares son del borde de los bosques o los ecotonos en esta región. *Sibynomorphus williamsi* es caracteristico de las lomas en la costa central del Perú pero también se ocurre en las vertientes andinos a elevaciones más altas.

Sibynomorphus comparte con tres otros géneros neotropicales de Dipsadinae (*Dipsas, Sibon,* y *Tropidodipsas*) una propensión conductual y características morfológicas asociadas para consumir gasterópodos. De acuerdo con algunos autores anteriores, sugero que el nombre Dipsadini sea aplicado inclusivamente a este clado de cuatro géneros de colubridos neotropicales moluscivoros, no obstante razones anteriores para excluir *Tropidodipsas.* Varias características externales indican que *Sibynomorphus* es relacionado más cercano a *Dipsas* entre los Dipsadini. Sin embargo, la monofilia de *Sibynomorphus* no se ha sido demostrado y queda la posibilidad que *Dipsas* es parafilético respecto a *Sibynomorphus,* que sí mismo puede ser polifilético. La distribución extraña de *Sibynomorphus* es algo similar a otros componentes de la herpetofauna del sur de Ecuador y el norte del Perú (Andes, vertientes Pacíficas, y la costa). Sin embargo, la distribución de *Sibynomorphus,* en cuanto al entendimiento actual, carece de algunos componentes geográficos (p.e., Amazonia, Guayana) asociados con estos otros taxones.

A pesar de algunos estudios que sugeren que *Sibynomorphus* pase al sinonimia de *Dipsas,* algunos asuntos analíticos, inclusive cuestiones de muestreo de caracteres y taxones, son problemáticos con estudios anteriores. Ninguno de las especies septentrionales de *Sibynomorphus* han sido incluidos en estudios comparativos amplios. Recomendo un estudio más amplio de especies nominales de Dipsadini antes que iniciar más cambios en la nomenclatura genérica de este grupo. Se explica algunas cuestiones pendientes acerca de la sistemática y la historia natural de *Sibynomorphus.* Especialmente se necesitan estudios más detallados de los microhábitas y comportamiento de todas especies y estudios de campo para refinar sus distribuciones geográficas. Se necesita explorar la importancia de la variación excepcional de patrones de coloración en *S. oneilli, S. petersi,* y *S. vagus,* tal vez conjunto con su rol como mímicos potenciales de especies simpátricas de *Bothrops* (Viperidae). Igualmente, la variación extensa en escamación que ocurre generalmente en Dipsadini necesita explicación en términos funcionales, mecanicistos, y evolutivos.

INTRODUCTION

Recent investigations clarified the systematics and distributions of several species of snakes of the genus *Dipsas* (Colubridae: Dipsadinae: Dipsadini[2]) in Panama and northern South America (Cadle, 2005; Cadle and Myers, 2003; Fernandes et al., 2002). Nonetheless, despite Peters' comprehensive review of Dipsadini (Peters, 1960), much additional work is needed on the systematics of this group. This is nowhere more apparent than in the endemic South American genus *Sibynomorphus,* which comprises about a dozen currently recognized species (Franco et al., 2002, 2003; Hoge et al., "1978/1979" [1981]; Peters and Orejas-Miranda, 1970; Scrocchi et al., 1993).

Sibynomorphus has a peculiar distribution. Six or seven species are distributed south of the Amazon in Argentina, Brazil, Paraguay, Uruguay, and Bolivia.[3] The other six species are found along the coast of central Peru; the western Andean foothills of northern Peru and southwestern Ecuador; or the Andes and inter-Andean valleys of the Río Marañón, the Río Santa, and their tributaries in northern Peru (Amazonian and Pacific versants, respectively). Thus, the range of the genus is disjunct

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[2] Dipsadini is here used for snakes of the genera *Dipsas, Sibon, Tropidodipsas,* and *Sibynomorphus,* essentially equivalent to the Dipsadinae of Peters (1960) with the addition of *Tropidodipsas.* See later herein: Sibynomorphus *and the Dipsadini: Directions for Further Research.*

[3] These include *Sibynomorphus inaequifasciatus, S. lavillai, S. mikanii, S. neuwiedii, S. turgidus,* and *S. ventrimaculatus* (Hoge et al., "1978/1979" [1981]; Peters, 1960; Scrocchi et al., 1993). Additionally, *S. garmani* (Cope), previously considered a synonym of *S. mikanii,* was apparently resurrected in an unpublished thesis that I have not seen (Franco, 1994); the name appears in two online abstracts (Franco et al., 2002, 2003). *Sibynomorphus inaequifasciatus* Duméril, Bibron, and Duméril, is known only from the original description. The holotype, said to be "doubtfully from Brazil but certainly from South America," has not been located (Peters, 1960: 146–148).

and the northern and southern species occupy distinct physiographic and climatic zones. Scrocchi et al. (1993) briefly reviewed the species of *Sibynomorphus* from southern South America, but species from Peru and Ecuador remain poorly known and have not received comprehensive review because most were described subsequent to Peters' (1960) work on the group. The lack of a modern review has led to inaccurate identifications of museum material and misunderstandings concerning their distributions.

As recently as the 1960s, when the systematics of *Sibynomorphus* was last reviewed (Peters, 1960; Peters and Orejas-Miranda, 1970), the genus was unreported from Ecuador, and only *S. vagus* (Jan, 1863) and *S. vagrans* (Dunn, 1923) were known from Peru (but see later comments on the name *Leptognathus atypicus* Cope).[4] Jan (1863) had described *Leptognathus vagus* from a specimen said to be from "Hong Kong." This name has been applied to a species from near the town of Huancabamba in northern Peru (Piura Department), known primarily from a series in the Museum of Comparative Zoology collected by G. K. Noble (Dunn, 1923) and a later series from near the same locality (Rossman and Kizirian, 1993). Dunn (1923) described *Pseudopareas vagrans* from specimens collected by Noble in the inter-Andean valley of the upper Río Marañón of northern Peru (Bellavista, Cajamarca Department), and the type series comprises the only known specimens. Both of these earliest described northern species of *Sibynomorphus* are from inter-Andean valleys on the Amazonian versant of the Andes at the western limits of the Amazon basin.

Since 1970, two additional species of *Sibynomorphus* from Peru and two from southern Ecuador have been described: *Sibynomorphus williamsi* Carrillo de Espinoza (1974) from coastal Lima Department, Peru (type locality: Jicamarca); *S. oneilli* Rossman and Thomas (1979) from Amazonas Department, Peru (type locality: between Balsas and Abra Chanchillo); *S. oligozonatus* Orcés and Almendáriz (1989) from Azuay Province, Ecuador (type locality: Zhila); and *S. petersi* Orcés and Almendáriz (1989) from Azuay and Loja Provinces, Ecuador (type locality: Zhila, Azuay Province). Few specimens have been reported for most of the northern species of *Sibynormorphus. Sibynomorphus oligozonatus* and *S. oneilli* were described only on the basis of their holotypes and until now *S. oligozonatus* has been known only from the type. Rossman and Kizirian (1993) reported two additional specimens of *S. oneilli* from Cajamarca Department, Peru, and additional specimens of *S. vagus* from near the previously known locality. *Sibynomorphus petersi* has been known only from three specimens reported in the original description. Of the species of *Sibynomorphus* described since 1970, three (*S. williamsi, S. oligozonatus,* and *S. petersi*) have heretofore been known only from the Pacific versant, and *S. oneilli* only from the Amazonian versant.

Even considering the recently described species, it is clear that the species limits and distributions of *Sibynomorphus* in Ecuador and Peru are incompletely understood. As part of biological surveys in northern Peru (Cadle, 1989, 1991, 1998, 2005; Cadle and Chuna, 1995; Cadle and McDiarmid, 1990; Cadle and Myers, 2003), I obtained a few specimens of *Sibynomorphus,* prompting me to review the species known from Peru and Ecuador. The results of that review form the basis of this report.

Although the accumulated material improves our understanding of variation and the distributions of some taxa, some outstanding problems remain. Nonetheless, a comprehensive review of these species is needed to facilitate future systematic work

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[4] Peters (1960: 57–58) synonymized *Sibynomorphus macedoi* Prado and Hoge (1947; type locality: Pucallpa, Ucayali Department, Peru) with *Dipsas catesbyi,* a conclusion I accept without having seen the type.

on this group. In this report, I document the occurrence of *S. oligozonatus* and *S. petersi* in Peru and the presence of *S. petersi* and *S. oneilli* on both Amazonian and Pacific versants, and I amplify knowledge of variation in all species. Scrocchi et al. (1993) provided a brief review of the southern South American species and literature subsequent to Peters (1960, 1965).

METHODS

General Methodology and Scale Terminology. This review is based on study of most specimens of *Sibynomorphus* from Ecuador and Peru in collections, including holotypes of all species except *S. petersi* and *S. vagus.* My own field experience with the genus is limited to a few specimens from northern Peru, here referred to *S. petersi.*

Systematic methods and characters used herein follow previous studies (e.g., Cadle, 1996, 2005; Cadle and Myers, 2003). I used the Dowling (1951) method for ventral counts (beginning the count with the first plate bordered on each side by the first dorsal row), but for most specimens, I also recorded preventral scales (unpaired plates anterior to the ventrals that are wider than long) for reasons detailed by Myers (1974: 37; 2003: 6–8). Scale terminology follows Peters (1960), but amplification of the scoring of some scales is useful.

Scales on the ventral surface of the head are highly variable in *Sibynomorphus* and other dipsadines. One or two pairs of infralabials are in contact posterior to the mental scale. Posterior to these contacting infralabials, I counted as *chin shields* those scales along the midline (no distinct mental groove in *Sibynomorphus*) that were about equal in length and width considering each scale individually. These scales are squarish or polygonal and occur in pairs with the occasional exception of a posterior shield that is unpaired (resulting in a chin shield count of 3.5 pairs, for example). Another one to three pairs of *gular* scales were often present posterior to the chin shields; gular scales are distinguished from the chin shields because each gular scale is wider than long. Gular scales were not scored for this study. The gular scales are followed by the unpaired preventrals (when present).

For the *Dipsas oreas* group (*D. oreas, D. elegans,* and *D. ellipsifera*) Cadle (2005: 71–73, fig. 1) described patterns of covariation between the shape of the loreal scale and whether the preocular was fused with the prefrontal or not. These scales are more uniform in species of *Sibynomorphus,* and a few specimens were intermediate between some of the six “loreal pattern” states defined by Cadle (2005). As in *Dipsas,* the loreal in *Sibynomorphus* was either squarish or polygonal, or much longer than tall, and the preocular was fused or not with the prefrontal. In addition, some specimens of *Sibynomorphus* have other patterns, such as multiple preoculars, which were not observed in the *D. oreas* group; these patterns are discussed in the species accounts.

Because of great variability in scutellation and color patterns in *Sibynomorphus,* I present detailed discussion of individual specimens where pertinent to facilitate future work on *Sibynomorphus.* For testing sexual dimorphism in ventral and subcaudal counts and color pattern characteristics, I used Student’s *t* test on the sample means after testing for homogeneity of variances (Sokal and Rohlf, 1981). When variances were unequal (only in the case of color pattern characters for *Sibynomorphus petersi*), I used an approximation to the *t* test for two samples described by Sokal and Rohlf (1981: 408–412). Sexual dimorphism was also evident in relative tail lengths. However, because relative tail lengths are ratios (tail length/total length), the assumptions of the *t* test are unlikely to be met without tranforming the data, a process not undertaken here. However, the frequency distributions of relative tail lengths between the sexes of species of *Sibynomorphus* considered herein overlapped minimally or not at all.

Snout–vent lengths (SVLs) and total

lengths were measured with a meter stick or a plastic ruler to the nearest millimeter. For a few comparisons, I used head dimensions, which were measured with dial vernier calipers to the nearest 0.05 millimeter. Head lengths were measured in two ways: (1) obliquely from the tip of the snout to the posterior tip of the mandible (HL–mandible) and (2) from the tip of the snout to the posterior end of the interparietal suture (HL–parietal). Eye diameter (ED) was measured with dial vernier calipers under a dissecting microscope as the greatest horizontal dimension of the eye. Figure 3 was drawn with a camera lucida mounted in a dissecting microscope.

Hemipenial Techniques and Descriptions. Everted hemipenes of *Sibynomorphus petersi* and *S. williamsi* described herein are from field-everted organs. Hemipenes of *S. oligozonatus, S. vagrans,* and *S. vagus* were manually everted from the inverted organs of museum specimens according to methods detailed by Myers and Cadle (2003). Hemipenial terminology follows Myers (1974: 30–33), Myers and Campbell (1981), and Zaher (1999). Some remarks about the terminology of general orientation is useful because of some differences in the way inverted and everted organs are described. The position of inverted hemipenes is fixed relative to the snake's body and they can be described by standard anatomical terminology (e.g., dorsal/ventral, medial/lateral, proximal/distal) for orientation with reference to the snake's body. In addition, the number of subcaudal scales subtending portions of the inverted hemipenis is commonly used as a relative measure of proportions for inverted hemipenes.

On the other hand, everted hemipenes are frequently described once they have been separated from the snake's body and subjected to further preparation—eversion in the case of manual eversions, inflation, injection with colored jelly, etc. (Myers and Cadle, 2003). In descriptions of everted organs, structures on the hemipenis itself provide the best markers for orientation. The sulcus spermaticus provides a convenient landmark and the terms *sulcate* (side with the sulcus) and *asulcate* (side opposite the sulcus) were defined by Myers and Trueb (1967) to denote these surfaces of the hemipenial body. In *Sibynomorphus* and many other snakes the hemipenial body bears a nude pocket approximately midway between the sulcate and asulcate surfaces, a position referred to as *lateral* (e.g., Cadle, 2005; Cadle and Myers, 2003; and herein).[5] In this context, *lateral* is used with respect to the orientation provided by the sulcate/asulcate sides of the hemipenial body only, and not with respect to the snake's body. A laterally positioned nude pocket thus has a sulcate lip or edge (toward the sulcate side) and an asulcate lip or edge (toward the asulcate side). Terms such as proximal (toward the base of the organ) and distal (toward the apex) are still useful in describing everted hemipenes because their meaning is the same with respect to both inverted or everted organs.

Localities and Geographical Data. Reference to the "Río Zaña Study Site" in the account for *Sibynomorphus petersi* refers to a locality in western Cajamarca Department that is better known herpetologically than other localities in northern Peru; see Cadle (2005: 70–71) for discussion and additional references. Elevations for my col-

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[5] Current use of the terms *sulcate, asulcate,* and *lateral* differs from definitions in Dowling and Savage's (1960) classic work. Dowling and Savage used the terms *sulcate* and *asulcate* to refer to the two primary tissue layers of the hemipenis: the *sulcate layer* referred to the entire external surface of the everted organ, which bears the sulcus spermaticus on one side; the *asulcate layer* referred to the internal tissue layer of the everted organ (Dowling and Savage, 1960: 19 and pl. I). Dowling and Savage (1960: 21) used the term *lateral* to refer to what is now called the asulcate surface of the organ and *medial* for what is now referred to as the sulcate surface. Myers and Trueb (1967) redefined *sulcate* and *asulcate* to their current usage because those terms seem most useful and least confusing as descriptors for the gross topology of hemipenes (the usual mode of study), rather than as names of tissue layers that are best studied in histological section.

lecting localities were determined in the field with a Thommen© altimeter calibrated in meters, sometimes in conjunction with topographic maps. Coordinates and elevations for other localities, unless otherwise stated, were derived from Paynter (1993); Stephens and Traylor (1983); Peruvian departmental maps published by the Instituto Geográfico Militar (IGM; now the Instituto Geográfico Nacional), Lima; or online versions of the gazetteers of the U.S. Board on Geographic Names at the GEOnet© Names Server: http://earth-info.nga.mil/gns/html/index.html. Stiglich (1922) is indispensable in locating obscure Peruvian localities, such as small haciendas, and I have also found occasional use for the Global Gazetteer (version 2.1, 26 January 2006) at www.fallingrain.com/world. Bracketed data in the list of specimens examined are inferences not supplied with the original collections data. Museum abbreviations used in the text are identified at the beginning of the *Specimens Examined and Locality Records.*

Geographical discussions follow Simpson (1975) for the names of the principal chains of the Andes in northern Peru. There is little cause for confusion except that some references and atlases (e.g., Hopkins, 1997) more finely divide the nomenclature of some of the ranges. In particular, I follow Simpson (1975) in using the name "Cordillera Oriental" for all of the Andean ranges lying east of the inter-Andean portion of the Río Marañon. Other authors use that term for the relatively low ridges east of the Río Huallaga and designate the higher mountains between the Río Marañon and Río Huallaga as "Cordillera Central" (see Fig. 7 and Simpson, 1975: 276). As used herein, the Cordillera Blanca, Cordillera Negra, and Cordillera de Huancabamba are parts of the Cordillera Occidental.

Key to Species of *Sibynomorphus* in Ecuador and Peru

Because of the variability of color patterns and scale characters within *Sibynomorphus,* individual specimens must be identified by a combination of characters and with careful attention to sexual differences. The six northern species of *Sibynomorphus* are rare or absent in most collections, and accurately identified comparative material is generally unavailable. As a consequence, misidentification of museum specimens is frequent. The most common misidentifications of northern *Sibynomorphus* in collections that I surveyed involved *S. petersi, S. vagus,* and *S. oneilli* (which is not saying much because *S. oligozonatus* has been known only from the holotype and *S. vagrans* only from the type series; *S. williamsi* is seemingly absent from non-Peruvian collections). Ecuadorian specimens of *S. petersi* were commonly misidentified as *Dipsas variegata* (following Peters, 1960) or, in older collections, as *Dipsas oreas* (see Cadle, 2005; Cadle and Myers, 2003, for discussion), whereas Peruvian specimens of *S. petersi* and *S. oneilli* were commonly misidentified as the better known *S. vagus.*

A previous key to all species of *Sibynomorphus* (Scrocchi et al., 1993) was adequate on the basis of variation within species known at the time. However, *S. oligozonatus* and *S. oneilli* were known only from their holotypes, and this report documents additional variation within all species that was not available to Scrocchi et al. (1993). For example, in their key, color pattern characteristics (with or without definitive bands, number of dorsal bands) were critical to differentiating some species (*S. petersi, S. oneilli, S. vagus*), but on the basis of the new material examined for this report, I infer extremely variable color patterns within these species (e.g., "definitive bands" present in some individuals of *S. petersi* and *S. vagus* and individuals without bands in *S. oneilli*). Indeed, the variation of color patterns and scutellation within most of the northern species of *Sibynomorphus* and overlap of meristic characters between species made the construction of a workable key difficult. I have not studied species of *Sibynomorphus* that occur south of the Amazon basin in any detail, but the following key should permit identification of species known from Peru and Ecuador. Considering present understanding of variation within these species and their geographic distributions, not to mention the possibility of new species occurring in this area, the key should be used in conjunction with detailed descriptions and comparisons of specimens when possible.

A few comments concerning the presence or absence of a separate preocular used in the first couplet of the key should be made. The key considers only the "normal" conditions of the preocular(s) in *Sibynomorphus*—that is, cases in which a single preocular superior to the loreal is present (Cadle 2005; Peters, 1960: 26; Figs. 11, 15, 23 herein), cases in which this preocular is fused with the prefrontal scale and a separate preocular is absent (see Fig. 3), or cases in which more than one preocular is present, in which case the loreal is separated from the eye by the inferior preocular(s). Less commonly, an irregular preocular can be formed by, for example, a suture across the posterior corner of the loreal. In the key, these irregular conditions would not be considered in determining presence or absence of a preocular.

That said, I should enter a caveat: the presence or absence of a separate preocular seems to be highly variable intraspecifically within some species of *Dipsas* (e.g., Cadle, 2005; Cadle and Myers, 2003). Although *Sibynomorphus* seems less variable in this character than *Dipsas,* some of the species in the key are represented by few specimens, and this character could prove more variable once sample sizes are larger. For this reason, use of the key in conjunction with the detailed discussions and illustrations in the species accounts will provide more accurate identifications.

To facilitate the identification of a specimen in hand, Table 1 provides summaries of systematic characters for all six species of *Sibynomorphus* occurring in Ecuador or Peru. The summary distributions in the key are documented herein.

KEY

1. Supralabials 6 or 7, with 3–4 or 4–5 touching the eye. No separate preocular (preocular fused with prefrontal). Venter usually only lightly spotted with dark pigment, if at all, or dusky and without discrete spots. Discrete crossbands on body present at least anteriorly, and anteriorly at least twice the width of the pale interspaces 2

   Supralabials 8 or more, with 4–5 touching the eye (rarely fewer than 8). One or more preoculars usually present (some individuals of *S. oneilli* lack separate preoculars). Venter usually heavily pigmented, often with half-moon–shaped or squarish spots. Distinct dorsal crossbands present or not, wider than interspaces or not 3

2. Distinct bold crossbands present only on anterior half of body, broken into series of paler vertebral and lateral blotches posteriorly; dorsal blotches on posterior body distinctly narrower than pale interspaces. Head only slightly broader than neck. Known variation in ventrals: 177 (one female), 145 (two males), and 163 (one male) .... *Sibynomorphus oligozonatus* Orcés and Almendáriz

   (Andes of Azuay and Loja Provinces, southwestern Ecuador, Pacific versant; one specimen without specific locality from Piura Department, Peru)

   Distinct bold crossbands present the whole length of the body (often broken into middorsal and offset lateral blotches posteriorly, but these maintain their boldness); dorsal blotches on posterior body equivalent to, or (usually) slightly wider than, pale interspaces. Head distinctly broader than neck. Known variation in ventrals: 181–188 (females), 173–182 (males) .... *Sibynomorphus williamsi* Carrillo de Espinoza

   (coastal lomas formations and Andean foothills and slopes in Lima and Ancash Departments, Peru)

3. Anterior body with 5–10 discrete crossbands that are much broader than the pale interspaces (bands encompass 5–9 dorsal rows middorsally, 3–6 rows laterally, excluding the nape band, which is always wider than any other bands; interspaces encompass 0.5–2 scale rows middorsally). Top of head very ornately patterned, including a relatively broad irregular dark band across the posterior edge of the prefrontals (sometimes interrupted at one or more points). Ventrals 149–155 in males,

154–159 in females. Subcaudals 80–87 in males, 72–79 in females .... *Sibynomorphus vagrans* Dunn (known only from the vicinity of Bellavista, Cajamarca Department, in the inter-Andean valley of the upper Río Marañón of northern Peru; Amazonian versant).

Discrete crossbands on anterior body present or not; if present anteriorly, bands are only slightly wider than, or equivalent to, the pale interspaces (usually narrower than interspaces). Top of head ornately patterned or not, but without a discrete band across the posterior edge of the prefrontals 4

4\. Ventrals <155 (known range 144–152) in males, <160 (known range 151–158) in females. Subcaudals ≤65 in males, ≤60 in females. Maximum known size: 368 mm SVL (males), 326 mm SVL (females) .... *Sibynomorphus vagus* (Jan) (known only from the vicinity of Huancabamba, Piura Department, Peru; Amazonian versant)

Ventrals >150 in males, >160 in females. Subcaudals >60 in males, >55 in females. Maximum size to ≥470 mm SVL in males, ≥595 mm SVL in females 5

5\. A discrete dark spot or irregular marking, usually outlined with a narrow pale edge, on each prefrontal; head generally with many dark markings. Dorsum usually with narrow, often zigzag, crossbands (bands may be reduced to an indistinct series of irregular vertebral and lateral spots). Infralabials usually 10–12 (rarely 9). Ventrals: males, 164–183; females, 173–188. Subcaudals: males, 75–87; females, 65–77 .... *Sibynomorphus petersi* Orcés and Almendáriz (Azuay and Loja Provinces, southwestern Ecuador, south along the western slope of the Cordillera Occidental to southern Ancash Department, Peru; Río Chotano valley, Amazonian versant, in Cajamarca Department, Peru)

No discrete dark spots outlined with a pale edge on prefrontals; top of head unpatterned or with a few dark markings, primarily on parietals and frontal. Discrete narrow blackish crossbands usually present the length of the body; anterior bands about equal to interspaces; posterior bands much narrower than interspaces (crossbands may be broken up on posterior body and some individuals lack bands, having instead an obscure network or reticulations). Infralabials 8 or 9. Ventrals: males, 152–168; females, 163–177. Subcaudals: males, 62–77; females, 56–64 .... *Sibynomorphus oneilli* Rossman and Thomas (Cordillera Oriental and Cordillera Occidental from southern Ancash to southern Cajamarca and Amazonas Departments, Peru, in the Río Marañón and Río Santa drainages)

***Sibynomorphus oligozonatus* Orcés and Almendáriz**

Figures 1–6

Dipsas mikanii oreas, part: Parker, 1938: 444 (a female from the "Catamayo valley 30 km west of Loja," here inferred to be BMNH 1935.11.3.108, which Parker thought possibly represented a "distinct species" from the rest of the series) (misidentification). The rest of this series discussed by Parker is identified here as *S. petersi.*

Sibynomorphus oligozonatus Orcés and Almendáriz (1989). Type locality: "Zhila (2,250 m) 79°17′26″W, 03°39′45″S [see footnote 19], parroquia Oña, cantón Girón, Provincia Azuay [Ecuador]." Holotype, EPN 3612 (Fig. 1). Almendáriz and Orcés (2004).

Notes on the Holotype of *Sibynomorphus oligozonatus*

With a few minor exceptions, my data for the holotype of *Sibynomorphus oligozonatus* (EPN 3612) are virtually identical to those reported in the original description (Orcés and Almendáriz, 1989) (see Table 2). The difference in ventral counts is probably due to different methods of counting (i.e., whether the preventrals were included in the ventral count or not—see *Methods*). My notes for the holotype indicate that the "tail tip is damaged and may include one or two additional subcaudals."

The holotype (Fig. 1) has broad dark brown crossbands on the anterior half of the body, alternating side to side. Posteriorly, these crossbands break up into narrow zigzag lateral bars alternating with an irregular series of middorsal blotches. The dorsal ground color (interspaces) is whitish anteriorly, medium brown posteriorly. The venter is immaculate white posterior to the head, with fine dark speckling displaced laterally and increasing posteriorly.

The only substantive difference between my assessment of the holotype and that in the original description concerns the maturity of the specimen. Orcés and

TABLE 1. SUMMARY OF STANDARD TAXONOMIC DATA FOR THE SIX SPECIES OF *SIBYNOMORPHUS* THAT OCCUR IN ECUADOR OR PERU. FOR HEAD SCALES, EACH SIDE OF THE HEAD OF EACH SPECIMEN WAS SCORED AS AN INDEPENDENT OBSERVATION BECAUSE OF FREQUENT ASYMMETRY. N = NUMBER OF SPECIMENS OR OBSERVATIONS. SVL = SNOUT-VENT LENGTH. MEANS ARE ±1 SD. FOR *S. OLIGOZONATUS*, ONLY CHARACTER RANGES ARE GIVEN BECAUSE OF SMALL SAMPLE SIZES (3 MALES, 1 FEMALE). ADDITIONAL DATA SUMMARIES BY SPECIMEN OR GEOGRAPHY ARE GIVEN IN THE ACCOUNTS FOR *S. OLIGOZONATUS*, *S. ONEILLI*, AND *S. PETERSI*.

	Sibynomorphus sp.					
	oligozonatus	*oneilli*	*petersi*	*vagrans*	*vagus*	*williamsi*
Total length (SVL) (mm)						
Largest male	462 (348)	623 (470)	763 (609)[1]	543 (387)	483 (368)	563 (435)
Largest female	550 (428)	790 (624)	771 (595)	557 (425)	408 (326)	718 (561)
Tail length/total length						
Male	0.24–0.26	0.22–0.26 0.24 ± 0.014 (N = 9)	0.22–0.28 0.25 ± 0.02 (N = 8)	0.25–0.29 0.27 ± 0.01 (N = 13)	0.23–0.24 0.24 ± 0.005 (N = 4)	0.21–0.24 0.23 ± 0.01 (N = 5)
Female	0.22	0.20–0.22 0.21 ± 0.008 (N = 5)	0.20–0.24 0.22 ± 0.01 (N = 11)	0.23–0.26 0.24 ± 0.01 (N = 6)	0.20–0.21 0.20 ± 0.005 (N = 4)	0.19–0.22 0.20 ± 0.01 (N = 12)
Maxillary teeth	12 (N = 2) 13 (N = 1) 15 (N = 1)	13 (N = 5) 14 (N = 2) 15 (N = 4) 16 (N = 2)	14 (N = 3) 15 (N = 4) 16 (N = 2) 17 (N = 1)	15 (N = 2) 16 (N = 5) 17 (N = 2)	14 (N = 1) 15 (N = 2) 16 (N = 2)	12 (N = 2) 13 (N = 3) 14 (N = 1)
Dorsal scales	15–15–15	15–15–15 (N = 16) 15–15–13 (N = 1)	15–15–15	15–15–15	15–15–15	15–15–15
Ventrals						
Male	145 (N = 2), 163 (N = 1)	152–168 161.1 ± 5.22 (N = 10)	164–183 173.5 ± 5.39 (N = 11)	149–155 151.4 ± 1.66 (N = 13)	144–152 148.6 ± 3.44 (N = 5)	173–182 177.0 ± 3.61 (N = 5)
Female	177	163–173 167.0 ± 3.51 (N = 7)	173–188 178.5 ± 4.33 (N = 13)	154–159 157.0 ± 1.79 (N = 6)	151–158 154.0 ± 2.92 (N = 5)	181–188 184.0 ± 2.36 (N = 10)
Subcaudals						
Male	66–68	62–77 67.7 ± 5.07 (N = 9)	75–87 81.0 ± 3.66 (N = 8)	80–87[2] 83.4 ± 2.43 (N = 13)	60–65 62.8 ± 2.22 (N = 4)	67–73 69.0 ± 2.55 (N = 5)
Female	68	57–64 61.0 ± 2.65 (N = 5)	65–77 73.0 ± 3.69 (N = 12)	72–79 73.8 ± 2.64 (N = 6)	56–60 57.2 ± 1.89 (N = 4)	56–66 61.6 ± 3.28 (N = 9)

Table 1. Continued.

	Sibynomorphus sp.					
	oligozonatus	*oneilli*	*petersi*	*vagrans*	*vagus*	*williamsi*
Anal scale	Single	Single	Single	Single	Single	Single
Preoculars	0 (N = 8)	0 (N = 11) 1 (N = 17) 2 (N = 2) 3 (N = 2)	1 (N = 35) 2 (N = 6) 3 (N = 3)	1 (N = 26) 2 (N = 12)	1 (N = 20)	0 (N = 32)
Postoculars	2 (N = 6) 3 (N = 2)	2 (N = 29) 3 (N = 1)	2 (N = 46) 3 (N = 1)	2 (N = 35) 3 (N = 3)	1 (N = 1) 2 (N = 19)	2 (N = 24) 3 (N = 4)
Primary temporals	2 (N = 8)	1 (N = 5) 2 (N = 31)	1 (N = 6) 2 (N = 39)	1 (N = 8) 2 (N = 25) 3 (N = 5)	1 (N = 19) 2 (N = 1)	2 (N = 23) 3 (N = 6)
Secondary temporals	3 (N = 7) 4 (N = 1)	1 (N = 1) 2 (N = 3) 3 (N = 21) 4 (N = 5)	2 (N = 6) 3 (N = 38) 4 (N = 2)	2 (N = 15) 3 (N = 23)	2 (N = 18) 3 (N = 2)	2 (N = 1) 3 (N = 21) 4 (N = 7)
Tertiary temporals	3 (N = 4)[3]	2 (N = 2) 3 (N = 9) 4 (N = 15)	2 (N = 2)[3] 3 (N = 4) 4 (N = 2)	3 (N = 33) 4 (N = 5)	0 (N = 1) 1 (N = 1) 2 (N = 13) 3 (N = 5)	3 (N = 13) 4 (N = 15) 5 (N = 1)
Supralabials (touching eye)	6 (3–4) N = 4 7 (3–4) N = 1 7 (4–5) N = 2	6 (3–4) N = 2 7 (3–4) N = 8 8 (3–5) N = 4 8 (4–5) N = 17 8 (4–6) N = 1 9 (4–6) N = 1 10 (4–6) N = 1	7 (3–4) N = 2 7 (4–5) N = 2 8 (4–5) N = 35 9 (4–5) N = 2	8 (3–5) (N = 1) 8 (4–5) (N = 33) 9 (4–5) (N = 1) 9 (4–6) (N = 1) 10 (4–6) (N = 2)	7 (3–4) N = 3 7 (4–5) N = 4 8 (3–4) N = 2 8 (4–5) N = 11	6 (3–4) (N = 29) 7 (3–4) (N = 1)
Infralabials	9 (N = 1) 10 (N = 5)	8 (N = 1) 9 (N = 3) 10 (N = 9) 11 (N = 16) 12 (N = 3) 13 (N = 1)	9 (N = 5) 10 (N = 22) 11 (N = 10) 12 (N = 4)	9 (N = 1) 10 (N = 4) 11 (N = 19) 12 (N = 12) 13 (N = 2)	8 N = 2 9 N = 8 10 N = 9 11 N = 1	8 (N = 1) 9 (N = 4) 10 (N = 20) 11 (N = 3)

TABLE 1. CONTINUED

	Sibynomorphus sp.					
	oligozonatus	*oneilli*	*petersi*	*vagrans*	*vagus*	*williamsi*
Number of dorsal bands or blotches on body	(Generally only anterior body with well-defined bands)	38–63 when present; sometimes absent or fragmented	Male: 29–35 31.2 ± 1.69 (*N* = 10) Female: 31–59 38.0 ± 8.01 (*N* = 12) (bands sometimes absent)	(Only anterior body with well-defined bands)	(Often irregular flecks or reticulations; bands, when present, are discrete only anteriorly)	35–48 41.5 ± 3.74 (*N* = 15)

[1] The largest male is the holotype (Orcés and Almendáriz, 1989), which was not examined in this study. The largest male examined by me was 657+ mm total length, 520 mm SVL. On the basis of measurements in the original description, the holotype has a shorter tail (20% of total length) than males I examined.

[2] Peters (1960) reported a lower bound of 74 subcaudals for male *S. vagrans*, which could be a count obtained from one of the paratypes not examined for this study (see text footnote 25).

[3] Extensively fragmented or fused tertiary temporals, making scoring somewhat arbitrary.

Almendáriz (1989) reported that the holotype of *Sibynomorphus oligozonatus* was an adult male. However, several characteristics indicate that it is more likely a subadult (the hemipenis of the holotype is described subsequently in this account). Cadle (1996: 43–44), following a suggestion of Charles W. Myers, reviewed observations indicating that the extent of mineralization of hemipenial spines could be used to infer the sexual maturity of colubrids. Immature male snakes have nonmineralized hemipenial spines and spinules, whereas in adults, these ornaments are mineralized, a characteristic that can be assessed with a fine needle (some experience and comparisons of juveniles and adults is helpful);[6] the mineralization of spines in adult hemipenes compared with juveniles was also noted by Cope (1895: 189). A specific pattern of progressive mineralization of individual spines (tip to base) and on the hemipenis overall (proximal to distal) is apparent.

The proximal edge of the capitulum of the hemipenis of the holotype of *S. oligozonatus* is fringed with nonmineralized or poorly mineralized spinules (rather than mineralized spines). In addition, spines on the hemipenial body proximal to the capitulum are mineralized only at their tips. These characteristics suggest that the specimen is not fully mature, and the holotype is also relatively small (SVL 265 mm, total length 351 mm) compared with the other referred males, AMNH 110587 (SVL 330 mm, total length 446 mm) and MUSM 2196 (SVL 348 mm, total length 462 mm). These characters are only suggestive that the holotype is not fully adult and more definitive internal examination

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[6] If sufficient material, including juveniles to adults, is available, a useful technique for visualizing hemipenial spine mineralization is a simple adaptation of methods for clearing and alizarin staining to demonstrate mineralized tissue such as bone (e.g., Dingerkus and Uhler, 1977). Cadle (1996) used this approach to examine the ontogeny of spine mineralization in *Geodipsas*.

Table 2. Scale counts, measurements, and other data for specimens of *Sibynomorphus oligozonatus*. Bilateral counts are separated by a solidus (left/right). SVL = snout-vent length. Bracketed data for the holotype are from the original description (Orcés and Almendáriz, 1989) and are given only in cases of discrepancy from my own data (see text).

	EPN 3612 Holotype Subadult (?) male	AMNH 110587 Adult male	BMNH 1935.11.3.108 Adult female	MUSM 2192 Adult male
Total Length (SVL) (mm)	351 (265) [358 (273)]	446 (330)	550 (428)	462 (348)
Tail length (mm)	86 [85]	116	122	114
Tail length/total length	0.24	0.26	0.22	0.25
Maxillary teeth	12	13	12	15
Dorsal scales	15–15–15	15–15–15	15–15–15	15–15–15
Ventrals (+preventrals)	145 (+2) [148; preventrals not recorded]	145 (+1)	177 (+2)	163 (preventrals not recorded
Subcaudals	66 [67]	68	66	68
Anal scale	Single	Single	Single	Single
Preoculars (loreals)	0/0 (1/1)	0/0 (1/1)	0/0 (1/1)	0/0 (1/1)
Postoculars	2/2	2/2	3/3	2/2
Temporals				
Primary	2/2	2/2	2/2	2/2
Secondary	3/3	3/3	3/4	3/3
Tertiary	3/3	3/3	[fragmented]	?/?
Supralabials (touching eye)	6 (3 + 4)/6 (3 + 4)	7 (4 + 5)/7 (4 + 5)	6 (3 + 4)/7 (3 + 4)	6 (3 + 4)/? (3 + 4)
Infralabials	10/9 [10]	10/10	10/10	?/?

of reproductive organs was not undertaken.

New Material and Comparison of Specimens Referred to *Sibynomorphus oligozonatus*

Sibynomorphus oligozonatus has previously been known only from the holotype, EPN 3612. I refer three additional specimens to this taxon: AMNH 110587, BMNH 1935.11.3.108, and MUSM 2192. I was able to make side-by-side comparisons of BMNH 1935.11.3.108 and the holotype and subsequently made side-by-side comparisons of AMNH 110587 and BMNH 1935.11.3.108. Later I determined that MUSM 2192 should be referred to this species. Standard characteristics of each specimen are given in Table 2.

BMNH 1935.11.3.108 (Fig. 2) is an adult female from approximately 70 km SSW of the type locality. It was part of a collection from southern Ecuador obtained for the British Museum by Clodov-

Figure 1. *Sibynomorphus oligozonatus.* Holotype in dorsal and ventral views (EPN 3612; Azuay Province, Ecuador). Subadult male, 265 mm SVL.

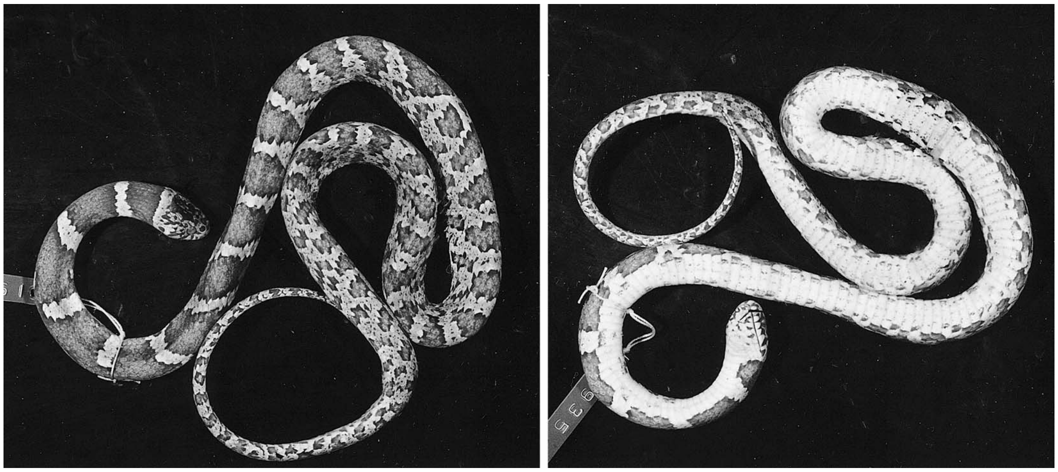

Figure 2. *Sibynomorphus oligozonatus.* Dorsal and ventral views of BMNH 1935.11.3.108 (Loja Province, Ecuador). Female, 428 mm SVL. The specimen illustrates the typical pattern in the known specimens: broad anterior dorsal crossbands, fragmented posterior bands, and relatively unpatterned venter.

eo Carrión (Parker, 1930a, 1930b, 1932, 1934, 1938). Parker (1938) referred several specimens in this collection to "*Dipsas mikanii oreas*" (= *Dipsas oreas*; Cadle, 2005). Rather peculiarly for a moderately sized collection from this region, none of the snakes that Parker referred to *D. oreas* appear to represent that species. Instead, they comprise the single specimen here identified as *Sibynomorphus oligozonatus* and a larger series I identify as *S. petersi* (see subsequent species account).[7] Parker (1938: 444) did not use BMNH collection numbers, but he noted that one of the females "differs from other specimens in having a smaller eye, a higher and narrower rostral, and the first labial in contact with the loreal; it may possibly represent a distinct species." BMNH 1935.11.3.108 matches the locality and characteristics given by Parker, including ventral and subcaudal counts that are virtually identical to mine.

AMNH 110587 is an adult male road-killed specimen collected by Charles W. Myers on 12 February 1974 approximately 25 km northwest of the type locality. MUSM 2192 is an adult male from "Piura, Peru" (department or city not specified, here assumed to refer to the department) collected by Otavio Ruíz with no additional data. MUSM 2192 is soft and in poor condition; its scale counts were determined only with difficulty. (Another specimen possibly referable to *S. oligozonatus,* MUSM 2248, with locality "Piura" but no collector or date, is very soft and deteriorated. Its color pattern was apparently similar to MUSM 2192 but its condition precluded accurate scale counts, etc. It will not be considered further here.)

Because so few specimens of *Sibynomorphus oligozonatus* are known and they exhibit some differences in scutellation and color pattern, I herewith highlight features suggesting that these are conspecific and note some differences among them. Nonetheless, some characteristics of the

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[7] Although *Dipsas oreas* is known from the same region as Carrión's collections (Cadle, 2005), the presence of *Sibynomorphus* in his collection and the apparent absence of *D. oreas* suggest that his collections were from drier, more open habitats (as opposed to humid forested habitats). *Dipsas oreas* is restricted to humid forests (Cadle, 2005), whereas species of *Sibynomorphus* in Ecuador and Peru generally occur in subhumid to arid environments, such as dry deciduous forests or thorn forests, which predominate in this region.

specimens make the interpretation of differences somewhat difficult with so few specimens. For example, the holotype is a subadult male and smaller than the other males, AMNH 110587 and MUSM 2192, whereas BMNH 1935.11.3.108 is a large female (Table 2). The head shape and body proportions of AMNH 110587 were difficult to assess because it is flattened, somewhat desiccated, and has a damaged head. More than likely there would be changes in shape associated with growth as well, rendering comparisons of shape characters (e.g., the distinctive head shape of BMNH 1935.11.3.108) between the small holotype and other specimens problematic. Similarly, MUSM 2192 is soft, in poor condition, and has a damaged head. These factors made it difficult to assess the relative contributions of size, sexual dimorphism, and other sources of variation.

Scutellation and Body Proportions. Two of the males, AMNH 110587 and the holotype, are nearly identical in scutellation (Table 2). Especially significant are the very low ventral counts, approached only by a few specimens of *Sibynomorphus vagrans* among the other species of Ecuador or Peru (male *S. vagrans* have many more subcaudals than either AMNH 110587 or EPN 3612). On the other hand, MUSM 2192 has considerably more ventrals than either of the other two males.

In contrast, the female, BMNH 1935.11.3.108, has considerably more ventrals than two of the males (EPN 3612, AMNH 110587; Table 2). The difference is probably accounted for by sexual dimorphism and perhaps geographic variation, but the disparity in ventral counts (32) is greater than has been reported for males and females of any other species of *Sibynomorphus* (see later comparisons herein; Scrocchi et al. 1993). The closest approach to this difference among the northern species of *Sibynomorphus* is in *S. petersi,* in which the minimum and maximum ventral counts (male and female, respectively) differ by 24.

Other differences among the three specimens are found in the configuration of scales in the loreal region. In AMNH 110587 supralabials 2–4 touch the loreal scale (the first supralabial is well separated from the loreal by the posterior nasal scale), whereas supralabials 1–3 border the loreal in BMNH 1935.11.3.108 (Fig. 3); in MUSM 2192 supralabials 2–3 broadly contact the loreal but on each side, the first supralabial also touches the loreal at a point. In the holotype, supralabials 2–3 border the loreal. In the AMNH specimen, supralabials 4 and 5 border the eye, whereas supralabials 3 and 4 border the eye in the other specimens. Scales in the loreal region vary substantially within some other Dipsadini (Cadle, 2005: 71–73; Peters, 1960: 25), and the variations among the referred specimens of *Sibynomorphus oligozonatus* do not seem extreme. The differences among the specimens in the relationships of the supralabials, loreal, and eye could reflect slightly different head shapes or proportions (see below). Differences among these specimens in other scutellation characters (Table 2) are typical of those observed in other Dipsadini.

BMNH 1935.11.3.108 has one unusual character of the dorsal head plates. Each supraocular is divided by a suture extending from the posterolateral angles of the frontal to the dorsal midpoint of the eye (Fig. 3). These sutures are very regular, well formed, and bilaterally symmetrical (i.e., each supraocular is identically divided). I am not aware of other colubrids with this variation, although Peters (1960: 25) reported fusions among some of the dorsal head plates (e.g., internasals, prefrontals) within *Dipsas.* BMNH 1935.11.3.108 also has more irregular scales in the temporal region than either AMNH 110587 or EPN 3612, but irregularities in this region are characteristic of many species of Dipsadini.

The three specimens differ somewhat in general body form and head shape, but the size differences among specimens and the general conditions of AMNH 110587 and

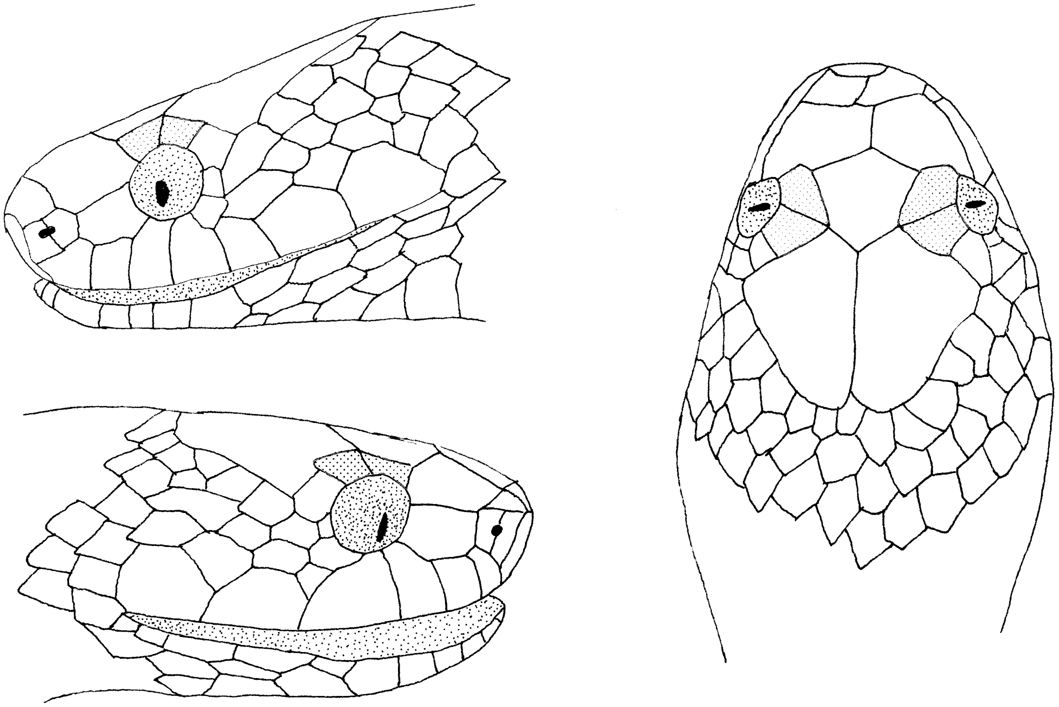

Figure 3. Head scales of *Sibynomorphus oligozonatus* (BMNH 1935.11.3.108) in left and right lateral views and in dorsal view. The lateral views indicate the blunt, short appearance of the snout (see also Fig. 4). The peculiar divided supraocular scales (shaded dorsal head plates) are unique to this specimen.

MUSM 2192 make these comparisons problematic. Judging from BMNH 1935.11.3.108, adult *Sibynomorphus oligozonatus* have a peculiarly foreshortened and very blunt snout (Fig. 4). It is not possible to judge precisely the physiognomy of AMNH 110587, especially the head, because it has been flattened. It seems to have a somewhat longer and more acuminate snout than BMNH 1935.11.3.108, but this could be entirely due to artificial deformation. The head shapes of BMNH 1935.11.3.108 and EPN 3612 are similar; the head of MUSM 2192 is damaged but appears to be particularly blunt.

Figure 4. *Sibynomorphus oligozonatus.* Lateral view of head, BMNH 1935.11.3.108.

Some differences in head size seem apparent between the adult specimens of *Sibynomorphus oligozonatus,* AMNH 110587 (male), BMNH 1935.11.3.108 (female), and MUSM 2192 (male), even accounting for distortion brought about by damage to the AMNH specimen. AMNH 110587 has a larger head in relation to SVL (4.0% or 3.7% by HL–mandible and HL–interparietal, respectively) than the BMNH specimen (3.5% and 2.6%, respectively) or MUSM 2192 (3.0% by HL–interparietal; lower jaws are damaged, precluding accurate measurement of HL–mandible). Sexual dimorphism in head length relative to SVL is widespread in snakes—for example, in nearly half of the species and 43% of the genera in one taxonomically diverse survey (Shine, 1991). However, Shine (1991) found that female snakes commonly had relatively larger heads in most genera (40 of 61 genera, omitting taxa without dimorphism). Thus, if the difference in head proportions between the males and female *S. oligozonatus* truly represents sexual dimorphism, it is of a relatively less common pattern among snakes.

Color Patterns. The color patterns of specimens referred to *Sibynomorphus oligozonatus* are similar (Figs. 1, 2, 5, 6). Dorsally, all specimens have broad anterior crossbands that begin to fragment at about one-third to one-half the body length. After the point of fragmentation, a series of middorsal blotches or saddles tends to alternate with lateral vertical bars or blotches. In BMNH 1935.11.3.108 and MUSM 2192, the middorsal blotches and the lateral bars are larger and more regular than in the holotype or in AMNH 110587; the BMNH and MUSM specimens have more complete crossbands than either of the other specimens. The crossbands of all specimens end on the outer one-quarter of the ventral plates.

In three specimens, there is a tendency, more pronounced in EPN 3612 and AMNH 110587 than in BMNH 1935.11.3.108 or MUSM 2192, for the anterior crossbands to be offset (i.e., corresponding portions of the bands on either side are displaced middorsally). In the BMNH specimen, crossbands 3–5 are offset, whereas in EPN 3612 and AMNH 110587, all anterior crossbands except the first one or two are offset. None of the complete crossbands in MUSM 2196 are offset. In AMNH 110587, BMNH 1935.11.3.108, and MUSM 2196, the central parts of the crossbands tend to be somewhat lighter than peripheral parts (i.e., bands appear dark-edged); this character was not recorded for the holotype.

The venter of all specimens has narrow irregular rectangles of dark pigment encroaching from the dorsum onto the edges of the ventral plates. Central parts of the ventral plates are speckled and flecked with tiny dark specks, which is much heavier in EPN 3612 and AMNH 110587, less so in BMNH 1935.11.3.108, and least in MUSM 2192. Pigmentation becomes denser on the posterior venter in all specimens, but to a lesser extent in BMNH 1935.11.3.108 and MUSM 2192 than in the others. Thus, BMNH 1935.11.3.108 and MUSM 2196 have relatively unmarked venters compared with the holotype and AMNH 110587.

The top of the head in BMNH 1935.11.3.108 is pale yellowish brown with bold black irregular marks all over. Supra- and infralabials in this specimen are pale yellowish with black suture lines (Fig. 4). The dorsal head pattern of the holotype is similar to BMNH 1935.11.3.108, including a pair of irregular bold longitudinal streaks posteriorly and a bold spot on each prefrontal scale. In AMNH 110587, the top of the head is grayish brown to medium brown without bold markings, except for an irregular spot on the anterior end of each parietal. Its markings are generally smaller and less distinct than in the holotype or BMNH specimen. Some suture lines on the supralabials and infralabials in AMNH 110587 are grayish brown, and some other grayish brown stippling is present on the supralabials, but they are not boldly marked as in the holotype or the BMNH specimen. In general, the dark markings on the heads of EPN 3612 and BMNH 1935.11.3.108 are distinctly blackish, whereas those in AMNH 110587 are grayish brown. MUSM 2192 has irregular spotting on top of the head, including a large spot at the anterior end of each parietal.

For several reasons, the identification of MUSM 2192 as *Sibynomorphus oligozonatus* is the most problematic of the four specimens. Its ventral count is much higher (163) than that of either of the other males (145), which brings it closer to the range of ventral counts in male *S. williamsi*

(173–182) (MUSM 2192 was previously identified in the MUSM catalogues as *S. williamsi*). These two species are otherwise very similar in scutellation (Table 1). The imprecise locality for MUSM 2192, "Piura" [Department], is intermediate between the other nearest localities for *S. oligozonatus* (Catamayo Valley of Loja Province, Ecuador) and *S. williamsi* (southern Ancash Department, Peru; see Fig. 43), although it is closer to the former.

Details of the banding pattern in MUSM 2192 compared with the other referred specimens of *S. oligozonatus* and *S. williamsi* convincingly demonstrate that MUSM 2192 should be referred to *S. oligozonatus.* These similarities to *S. oligozonatus* include (contrasting state for *S. williamsi* in parentheses; see Figs. 40–42) (1) abrupt transition from regular dorsal crossbands anteriorly to fragmented crossbands posteriorly (transition is gradual); (2) a narrow pale collar just behind the head, with the dark pigment of the first crossband not encroaching onto the head (pigment of first dark crossband extends up onto the head); (3) crossbands with distinctly darkened edges (bands lack distinctly darker edges); (4) crossbands brown (bands usually distinctly blackish in preservative, although this could be because of preservation or storage); (5) posterior crossbands usually distinctly narrower than interspaces (posterior crossbands as wide as, or wider, than interspaces); and (6) venter relatively immaculate (venter often, but not universally, dusky or with a ladder-like dark pattern or with dark spots posteriorly). Although the head shape of MUSM 2192 is difficult to assess because it is damaged, it seems to be relatively small and foreshortened, as in *S. oligozonatus,* compared with the longer, more acuminate head in *S. williamsi.*

Considering the highly variable coloration and scutellation in some other species of *Sibynomorphus,* the differences among the four specimens I refer to *S. oligozonatus* do not seem extreme, although the disparity in ventral counts (Table 2) between MUSM 2192 and the other males and between the female (BMNH 1935.11.3.108) and two of the males (EPN 3612, AMNH 110587) are remarkable. These specimens should be re-evaluated as additional material of this species accumulates. The following account is based on the collective characteristics of these four specimens.

Diagnosis

Sibynomorphus oligozonatus is a gray to grayish brown snake with broad dark crossbands anteriorly (narrowing and becoming broken into dorsal and lateral blotches posteriorly). Anterior crossbands are much broader than the interspaces and have regular, vertical edges and sometimes are offset. Posterior crossbands are usually much narrower than the interspaces. The venter is unmarked or has irregular dark speckling or spotting concentrated posteriorly. The head is foreshortened and blunt. The species has a low number of supralabials (6 or 7) and maxillary teeth (12–15). Males of *S. oligozonatus* have a low number of ventrals (145 in two males, 163 in another) and relatively long tail (24–26% of total length); these characters in the single known female (177 and 22%, respectively), are typical of some other species of *Sibynomorphus* (see Table 1).

Scrocchi et al. (1993) questioned whether *Sibynomorphus oligozonatus* was diagnosable from *S. vagrans* on the basis of the characters given in the original description. However, these two species differ in head shape and proportions, as well as several scale characters. *Sibynomorphus oligozonatus* has a short head and blunt snout (Fig. 4), lacks preoculars in the known specimens (i.e., the preocular is fused with the prefrontal and only a loreal is present between the eye and posterior nasal), and has six or seven supralabials and fewer than 70 subcaudals. *Sibynomorphus vagrans* has a more elongate head and more pointed snout (compare Fig. 4 with Figs. 30, 31), has a preocular in addition to a loreal (occasionally 2 preoculars and a loreal), and has eight to 10 supralabials and more than 70 subcaudals (Table 1).

Sibynomorphus oligozonatus differs in color pattern from *S. oneilli* (see Figs. 8–10). Both species have dark crossbands that are broader anteriorly than posteriorly (some *S. oneilli* lack bands; see following species account). In *S. oligozonatus,* the anterior crossbands are twice or more as broad as the pale interspaces, whereas on the anterior body in *S. oneilli,* the interspaces are about as broad as, or broader than, the dark crossbands. *Sibynomorphus oneilli* has a bold pattern of dark markings in an irregular checkerboard pattern or paired spots on each ventral plate, whereas the venter of *S. oligozonatus* is relatively unmarked (AMNH 110587 does have irregular dark speckling all over the venter and some larger spots that tend to be concentrated laterally, but this pattern does not resemble the heavily spotted venter of *S. oneilli*; see Figs. 9, 10, 12).

Sibynomorphus petersi occasionally has relatively broad anterior crossbands reminiscent of, but less regular than, those of *S. oligozonatus. Sibynomorphus petersi* has a preocular above the loreal (preocular absent in *S. oligozonatus*) and usually has eight supralabials (six or seven in *S. oligozonatus*). In addition, male *S. petersi* have more ventrals (164–183) than *S. oligozonatus. Sibynomorphus petersi* generally has a strongly patterned venter (Fig. 13 and following) compared with the relatively less patterned venter of *S. oligozonatus.*

Sibynomorphus oligozonatus differs from *S. vagus* in color pattern: broad anterior crossbands having regular, more or less vertical borders in *S. oligozonatus* versus either nonbanded (a vague network or fine reticulations) or with narrow, poorly formed, and irregular crossbands in *S. vagus. Sibynomorphus vagus* has fewer ventrals in females, has a preocular scale, usually has a single primary temporal, and has seven or eight supralabials.

Sibynomorphus oligozonatus differs from *S. williamsi* in having fewer ventrals (males: 145–163 vs. 173–182; females: 177 vs. 181–188), in head shape (*oligozonatus*: head slightly broader than neck, short and blunt; *williamsi*: head broader than neck, longer and acuminate), and in some aspects of color pattern. In *S. williamsi,* the first dorsal crossband usually encroaches broadly onto the nuchal region (see Figs. 41, 42), whereas in *S. oligozonatus,* the first crossband is separated narrowly from the head by a distinct narrow pale collar (Fig. 4). The dorsal bands in *S. williamsi* are bold and distinct the whole length of the body and tail (even when fragmented into a dorsal and lateral series of blotches), whereas in *S. oligozonatus,* the anterior bands are much bolder than the posterior ones. In *S. oligozonatus* the dorsal blotches on the posterior body are slightly to much narrower than the pale interspaces; the posterior dorsal blotches in *S. williamsi* are equivalent to or wider than the pale interspaces.

The color pattern of the BMNH and AMNH specimens of *Sibynomorphus oligozonatus* is reminiscent of some specimens of *Dipsas oreas,* which perhaps led Parker (1938) to refer the BMNH specimen to that species (as "*Dipsas mikanii oreas*"). However, *D. oreas* usually has a pair of large oval dark irregular spots on the dorsoposterior portion (primarily parietal scales) of the head (Cadle, 2005: 101–108), a strongly compressed body, and a relatively much larger eye (compare Fig. 4 with Cadle, 2005, fig. 21). The relative eye diameter of the BMNH specimen of *S. oligozonatus,* the only adult with an undamaged head, was 0.51% of SVL, whereas for 12 adult *D. oreas,* the eye averaged 0.73 ± 0.049% of SVL (range: 0.64–0.78%). Males of *S. oligozonatus* can be distinguished from *D. oreas* by having fewer ventrals (144–163 vs. 167–184 in *D. oreas*) and subcaudals (66–68 vs. 82–91 in *D. oreas*). The female referred to *S. oligozonatus* is similar to females of *D. oreas* except for a slightly lower subcaudal count (66 vs. 70–83) and the previously mentioned aspects of color pattern and body form. See Table 2 and Cadle (2005, table 1).

Description

Size and Scutellation. Tables 1 and 2 summarize taxonomic data for *Sibynomorphus oligozonatus.* Largest male 446 mm total length (330 mm SVL). Largest female 550 mm total length (428 mm SVL). Body somewhat compressed. Tail 24–26% of total length in three males, 22% in one female. Ventrals 145 (two males) to 163 (third known male), 177 in a female; ventrals preceded by one or two preventrals. Anal single. Subcaudals 66–68 in males, 66 in one female. Loreal and prefrontal bordering anterior edge of eye (no separate preocular) (Fig. 3); loreal longer than tall. Postoculars 2 or 3, primary temporals 2, secondary temporals 3 or 4, tertiary temporals (when discrete) 3. Supralabials most commonly 6 (3–4 bordering eye); other patterns 7 (3–4) or 7 (4–5). Infralabials 10 (9 on one side in the holotype). Chin shields in 2–3.5 pairs. Maxillary teeth 12–15 (*N* = 4).

As far as can be discerned with only four specimens, *Sibynomorphus oligozonatus* shows typical colubrid patterns of sexual dimorphism in size (female larger), ventral counts (female greater), and relative tail length (male longer). Despite the difference in relative tail length, subcaudal counts do not differ between the males and the female. Statistical tests were not performed on these comparisons because only four specimens are known.

Color in Life. Orcés and Almendáriz (1989) described the color of the holotype as follows (paraphrased): "Diffuse dark brown spots on the top and sides of the head. Dark brown bands on the anterior part of the body four scales wide, narrowing to one scale wide on the posterior body. Interspaces anteriorly pale brown, becoming grayish at midbody. Venter whitish, finely speckled with brown posteriorly." Charles W. Myers annotated his field catalog for AMNH 110587 with the comment "venter white," meaning simply that the venter lacked any wash colors such as yellow or orange, which are common on the venters of some colubrids (Charles W. Myers, personal communication); the venter of AMNH 110587 does have some dark spotting.

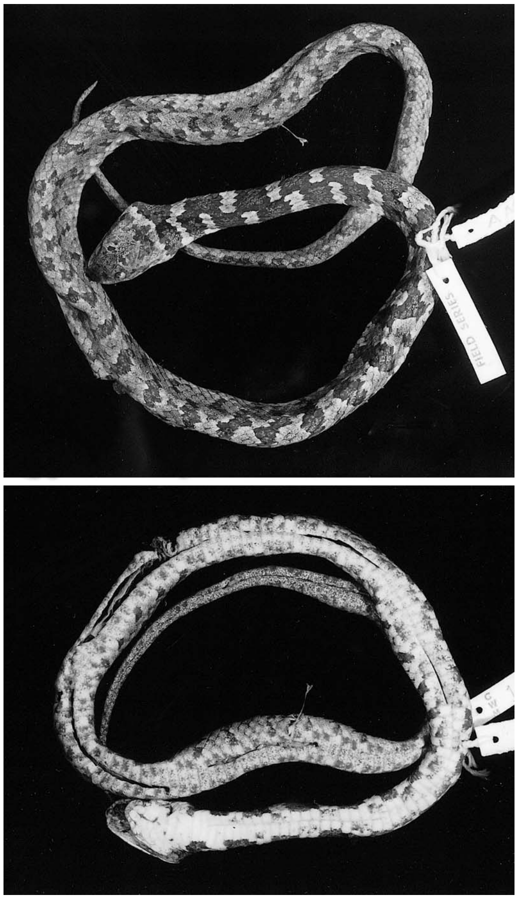
Figure 5. *Sibynomorphus oligozonatus.* Dorsal and ventral views of AMNH 110587 (Azuay Province, Ecuador). Male, 330 mm SVL.

Color in Preservative. The coloration of the four specimens in preservative is very similar (Figs. 1, 2, 5, 6). The dorsal pattern consists of broad anterior crossbands (4–10 dorsal rows wide) that progressively narrow posteriorly, fragmenting into middorsal and lateral blotches by about midbody. The crossbands are brown to blackish brown with a narrow darker border. Interspaces are gray, grayish white, or light (yellowish) brown. The top of the head is pale grayish or brown with bold dark spots and markings in an irregular pattern. The venter is pale gray without bold markings, but can have dark speckling that increases in density posteriorly. The color tones of the crossbands in MUSM 2192 are somewhat lighter brown (with reddish or chestnut tones) than the other specimens, but this could be preservation artifact (? light-induced fading). The coloration in preservative for three specimens is as follows (notes taken 2003 for AMNH 110587; 2004 for the others):

AMNH 110587 (Fig. 5): Dorsal ground color on anterior third of body grayish to grayish white, becoming grayish brown posteriorly. Approximately the anterior third of the body has bold blackish brown crossbands. The anterior five to six crossbands are offset middorsally, have vertical sides (i.e., they appear as squares or vertical rectangles viewed laterally), and tend to have somewhat paler centers than edges (central scales of the crossbands are mottled with dark brown and pale grayish brown, whereas peripheral scales are solid blackish brown). Anterior crossbands are four to five scales wide. Posteriorly the crossbands fragment abruptly into irregular middorsal and lateral blotches. The anterior dorsal crossbands encroach onto the outer quarter of the ventral plates. Dorsal scales in the interspaces between crossbands are finely flecked with minute dark brown specks. Interspaces anteriorly are 2–2.5 scale rows wide, increasing to 3 rows just before the point at which the dorsal crossbands fragment. Venter white, speckled, and irregularly spotted with dark brown, which increases posteriorly.

Top of the head brown (grayish brown on parietals), heavily flecked and spotted irregularly with dark brown. A single larger irregular spot is present at the anterior edge of each parietal. An indistinct narrow (two scales wide) pale grayish nape collar is behind the mouth commissure, followed by the first dorsal crossband.

BMNH 1935.11.3.108 (Figs. 2, 4): Dorsal ground color pale, somewhat yellowish, brown. Crossbands are medium brown with blackish edges <1 dorsal row wide. Under magnification their centers are flecked with minute pale specks, making their centers somewhat lighter than the edges. The first neck band is about 6 to 6.5 scale rows wide. The next two crossbands are 7 to 8 rows wide. Succeeding crossbands narrow to six, five, and four rows before breaking up into a series of dorsal saddles and lateral blotches or bars. All crossbands are complete middorsally and extend ventrally to the outer edges of the ventral plates. On the posterior body, the lateral blotches are very irregular in shape and poorly formed, whereas the dorsal saddles have a more regular shape. The venter is yellowish white with scattered dark markings, which become denser posteriorly and are mostly disposed on the lateral portions of the ventral plates.

The top of head has bold, crisp (sharp edged) irregular blackish reticulations and spots in no distinct pattern. Supra- and infralabials are yellowish with bold black suture lines. Posterior to the region of bold head markings are a pair of scale rows relatively free of markings, forming a narrow pale nape collar; then follows the first crossband.

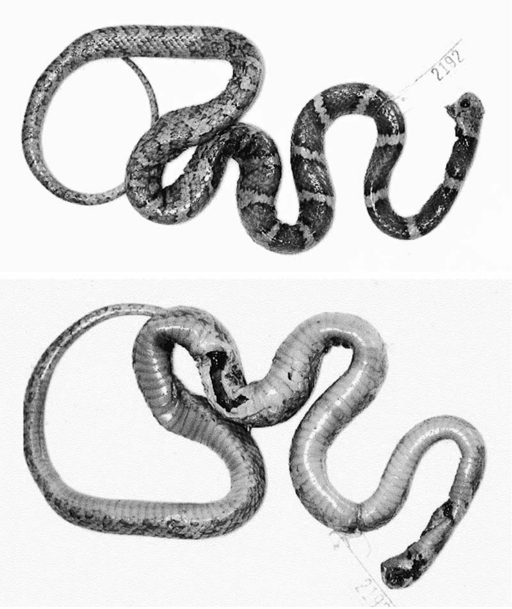

Figure 6. *Sibynomorphus oligozonatus.* Dorsal and ventral views of MUSM 2192 from an unknown locality in Piura Department, Peru. Male, 348 mm SVL.

MUSM 2192 (Fig. 6): Dorsal crossbands are pale, somewhat reddish brown, each with a narrow (<1 dorsal scale row wide) dark brown border. Interspaces grayish. First neck crossband is 11 scale rows wide; then follow 11 to 12 discrete crossbands, progressively narrowing from 7–9 rows wide anteriorly to 4 rows wide posteriorly. Crossbands extend ventrally to the outer edges of the ventral scutes. Pale interspaces are 1.5–2 scale rows wide. The venter is immaculate grayish with a few small punctations on the edges of the plates. The top of the head is pale grayish brown with darker irregular spots (large spots on anterior edges of parietals and on other head scales). Supralabials have a few dark lines, but are generally pale. Infralabials and gular region are pale.

Etymology. The specific epithet, *oligozonatus,* comes from the Greek words *oli-*

go- (few) and *zona* (belt); the suffix *-atus* indicates possession. It refers to the "few transverse bands, much less numerous than is usual in the genus" (Orcés and Almendáriz, 1989: 63).

Hemipenis

The hemipenes of the holotype of *Sibynomorphus oligozonatus* are partially everted, and I first report details observable on them. Then follows a complete description of the everted organ of AMNH 110587. No differences were observed between the portions of these two organs that could be compared.

The hemipenis of the holotype (EPN 3612) is capitate and apparently slightly bilobed. The sulcus spermaticus divides within the capitulum, which is spinulate on the visible proximal portion; the spinules apparently correspond to the fringe of spines on the proximal edge of the capitulum of the everted organ of AMNH 110587 described below. These spinules in the holotype are nonmineralized or poorly mineralized. Proximal to the capitulum, the distal portion of the hemipenial body bears a battery of enlarged spines, which appear to be mineralized only at their tips. A nude pocket bordered on each side by a fleshy lobe is on the lateral side of the hemipenial body proximal to the abovementioned battery of spines.

The right hemipenis of AMNH 110587 was partially everted upon preservation. Full eversion was effected with the use of methods described by Myers and Cadle (2003). Although the organ is fully everted, it is not likely to be maximally expanded. Hence, the entire surface morphology of the hemipenis can be studied, but it is probably not as fully expanded as a fully everted fresh organ (see Myers and Cadle [2003] for discussion). In particular, the basal portion, which was everted before preservation, appears somewhat dehydrated and not fully expanded; a portion of the asulcate side of the capitulum also appears incompletely expanded.

Total length of the everted organ 15 mm, bilobed less than 1 mm. The relative proportions of the capitulum to base could not be assessed with accuracy because the base of the hemipenis is rather nonpliant and is probably not extended to its maximal state. The hemipenis is fully capitate and slightly bilobed. The capitulum is entirely calyculate and calyces are ornamented with fingerlike papillae; some of the more proximal papillae might have mineralized tips. A fringe of small mineralized spines encircles the proximal edge of the capitulum just distal to the overhang demarcating the capitulum; these spines are relatively straight and blunt. The calyces cover all aspects of the capitulum, including the crotch and medial portions of the lobes.

Proximal to the capitulum, a battery of enlarged hooked spines about three spines across encircles the entire organ. Proximal to the spinose midsection, the hemipenis bears scattered minute spinules, which appear to be denser toward the sulcate side of the organ. A very long nude pocket is positioned laterally on the organ and extends from the very base of the organ to the battery of spines. The pocket is bordered on each side by a prominent lobe. A single large hooked spine approximately twice the size of any other spines in the battery is present at the distal end of the sulcate edge of the nude pocket. At the level of the lobe on the asulcate edge of the pocket (i.e., the lip toward the asulcate side of the organ) are two large spines in a transverse row. Of these, the spine closest to the pocket is much larger than the one farther from the pocket, which is positioned nearly in the middle of the asulcate side (the lack of proper inflation of the base of the organ makes the position of this spine in a fully inflated organ difficult to ascertain). A gap ornamented with minute spinules separates these enlarged spines from the battery of spines around the midsection.

The sulcus spermaticus divides just within the capitulum. Its branches extend distally in centrolineal orientation, but ultimately pass to the outer (lateral) edges of each lobe. It is possible that the orientation of the branches could be somewhat different in a maximally expanded organ because of differential tissue expansion. The branches of the sulcus spermaticus end at the peripheral edge of the tip of each lobe (i.e., not continuing to the center of the lobe's apex).

Distribution and Natural History

Sibynomorphus oligozonatus is known from extreme southwestern Ecuador (Azuay and Loja Provinces) on the western slopes of the Andes and from a specimen without specific locality from Piura Department, Peru (Fig. 7). The known elevational range is 1,440 to 2,250 m.

The holotype of *Sibynomorphus oligozonatus* was found at night on the ground in the process of swallowing a small snail (Orcés and Almendáriz, 1989: 63) and in similar ecological conditions as specimens of *S. petersi*: "arid temperate zone with bushy vegetation that includes *algarrobos* and cacti; similar to the Brazilian caatinga and corresponding to the regions that Chapman called the arid temperate zone" (Orcés and Almendáriz, 1989: 63). *Algarrobos* refers to trees of the legume family, probably of the genus *Prosopis,* that are generally characteristic of seasonally dry to arid regions (e.g., mesquite). Chapman (1926: 97–98) described his "Arid Division of the Temperate Zone" thus:

> The aridity of the treeless portions of the Temperate Zone varies from that of valleys with sufficient rainfall to produce pasturage to that of rock-strewn plains where cactus is the prevailing type of vegetation. Generally speaking, the arid Temperate Zone comprises all the unforested areas between 9.000 and 12,000 feet, but where, because of insufficient rainfall, forests of the Subtropical Zone are lacking, the arid Temperate descends considerably lower and may even meet the Tropical Zone.

AMNH 110587 was dead on a road in an area of open grassy slopes in the Río Jubones valley (Charles W. Myers, personal communication, and field notes for 12 February 1974). Myers' notes describe this portion of the valley: "[from about 600 m to above 1,500 m] the Jubones valley has barren, steep, rocky slopes that are mostly covered with short grass and dotted with tree cacti. In places, especially along the river, there is low brush; some patches of sugar cane are grown in small flats near the river. . . . This section of the valley seems to be in rain shadow."

At the type locality (Orcés and Almendáriz, 1989) and in the Río Catamayo valley of southwestern Ecuador (BMNH 1935.11.3.108), *Sibynomorphus oligozonatus* is broadly sympatric with *S. petersi.* These species of *Sibynomorphus* are also broadly sympatric with another dipsadine, *Dipsas oreas,* but *D. oreas* may be segregated by habitat from the species of *Sibynomorphus* (see footnote 7).

Sibynomorphus oneilli Rossman and Thomas

Figures 8–12

Sibynomorphus oneilli Rossman and Thomas, 1979. Type locality: "NNE Balsas on the road to Abra Chanchillo, Departamento de Amazonas, Peru (ca. 1645 m)." Holotype, LSUMZ 33736. Rossman and Kizirian, 1993. Scrocchi et al., 1993. Carrillo de Espinoza and Icochea, 1995: 17.

Sibynomorphus oneilli has been reported in the literature from only two males (including the juvenile male holotype) and a female (Rossman and Kizirian, 1993; Rossman and Thomas, 1979). I examined these specimens and refer 14 additional specimens in the MUSM to *S. oneilli* (see *Specimens Examined and Locality Records*; another specimen provisionally referred to *S. oneilli* is excluded from this account because of its uncertain provenience: see detailed discussion of MUSM 2258 at the end of the species account for *S. vagrans*). The additional specimens significantly amplify knowledge of intraspecific variation and the distribution of *S. oneilli.* Of the three previously known specimens, Rossman and Thomas (1979: figs. 1, 2) illustrated the holotype and Rossman and Kizirian (1993: fig. 1) illustrated KU 212600. The third specimen,

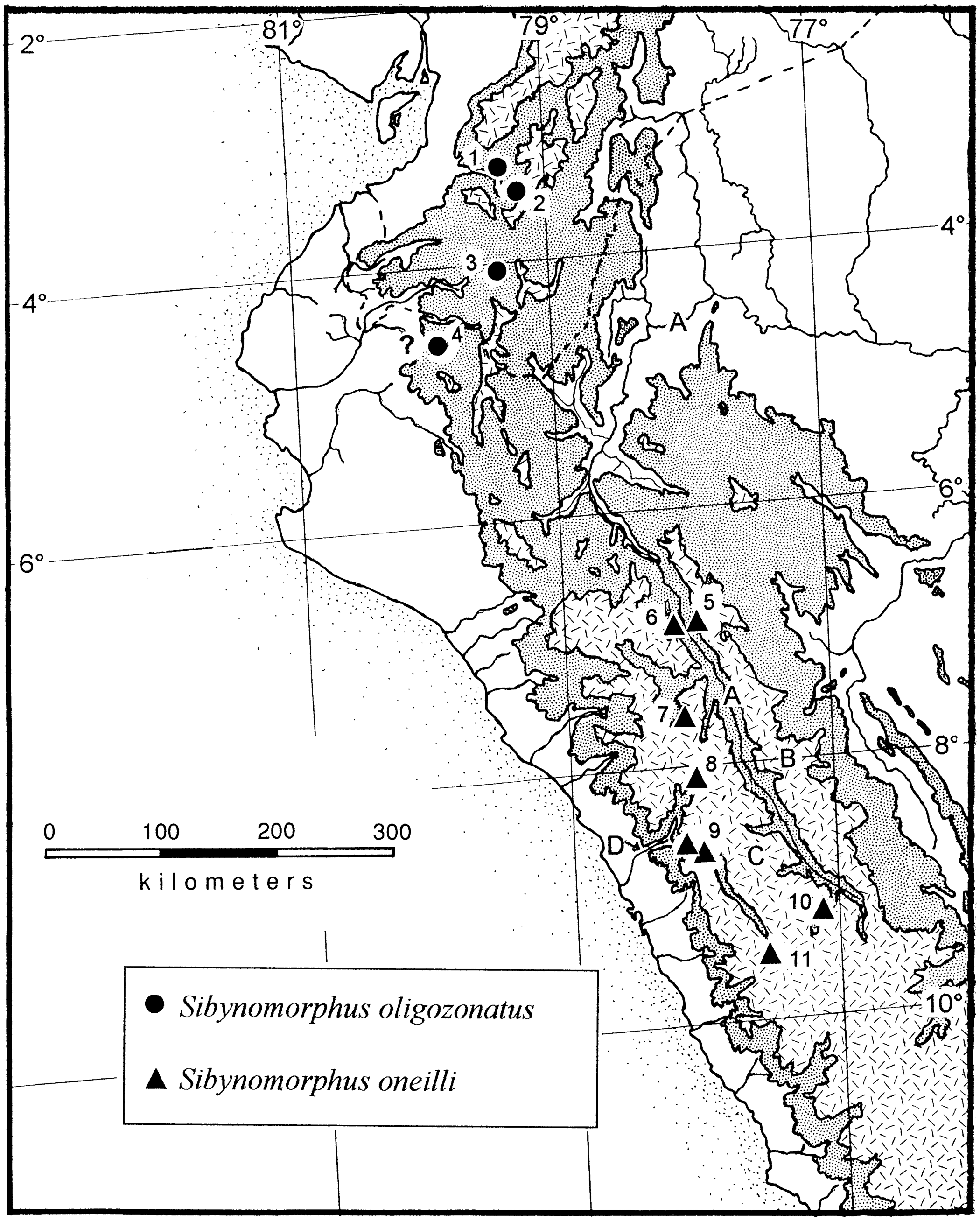

Figure 7. Distributions of *Sibynomorphus oligozonatus* and *S. oneilli* in southern Ecuador and northwestern Peru. All known localities are plotted (a couple of symbols reflect closely contiguous localities). See Figure 43 for amplification of the southern portion of the distribution of *S. oneilli* (Ancash Department, Peru). Stippled area is above 1,000 m; hatched area is above 3,000 m. Numbers are locality records and letters are physical features mentioned in the text, as follows: ***Sibynomorphus oligozonatus***: *Ecuador:* (1) Santa Isabel; (2) Zhila (type locality); (3) Río Catamayo valley; *Peru:* (4) uncertain locality in Piura Department, Peru (symbol arbitrarily placed above the 1,000-m contour in the center of the department). ***Sibynomorphus oneilli***: *Peru:* (5) between Balsas and Abra Chanchillo (type locality); (6) Abra Gelic; (7) Cajabamba; (8) Hacienda Ticapampa; (9) Huaylas and Hacienda Santa Rosa; (10) Yuracyacu; (11) Huaráz. **Physical features:** (A) Río Marañón (the inter-Andean portion is between the Cordilleras Oriental and Occidental; B and C, respectively); (B) Cordillera Oriental; (C) Cordillera Occidental; (D) Río Santa.

KU 212599, and others from the MUSM are illustrated herein (Figs. 8–12)

Notes on the Holotype and Comparisons with Other Specimens

Redescription of the Holotype. The following observations on the holotype (LSUMZ 33736) of *Sibynomorphus oneilli* were made in April 2004 and supplement the original description (Rossman and Thomas, 1979). Notes on the circumstances of its collection are given in the section *Natural History.* The type is compared with other specimens referred to this species, and a discussion of these specimens then follows.

The holotype is 233 mm in total length, 174 mm SVL (tail 25% of total length). It is a juvenile male, as indicated in the original description, but it has a distinct umbilical scar, which suggests that it is a very young juvenile. It is presently in rather poor condition. The specimen seems to have partially cleared since the species was described, perhaps as a result of the quality of its initial preservation and, possibly, exposure to a low concentration of isopropyl alcohol at some point during its history.[8] The clearing has resulted in loss of details of many aspects of the pattern and made some scale counts (e.g., ventrals) difficult to obtain with accuracy. For example, the head markings noted by Rossman and Thomas (1979: 5) are no longer discernible without magnification and careful observation, and the dorsal and ventral markings are very indistinct.

My scale counts for the holotype are very close or identical to those reported by Rossman and Thomas (1979): Dorsal scales 15–15–13, ventrals 168 (0 preventrals), subcaudals 77, anal plate single, preoculars 2/2, postoculars 2/2, primary temporals 1/1, secondary temporals 2/2, tertiary temporals 2/2, supralabials 8/8 (4–5 touching eye on each side), infralabials 9/8, maxillary teeth 16. The posterior dorsal scale reduction to 13 is unusual and seems to result from the "irregular fusions of the vertebral and paravertebral rows posteriorly" (Rossman and Thomas, 1979: 4); "irregular" in this case refers to the vertebral and paravertebral rows that are fused, then separated, several times with no particular regularity. On the posterior body, these fusions result in a "vertebral" row twice as wide as the adjacent rows, whereas anteriorly and at midbody, the vertebral row is scarcely wider than the adjacent paravertebral rows. Occasional reductions to 13 dorsal rows posteriorly occur in several other species of *Sibynomorphus* (e.g., *S. mikanii, S. neuwiedii,* and *S. turgidus*; Peters, 1960).

The top of the head has cleared substantially and, except under magnification, is medium to somewhat darker brown, forming a uniform head cap. Under magnification and with good light, the indistinct blotches on each parietal and the blotch on the frontal scale mentioned in the original description (Rossman and Thomas, 1979: 5) can be seen. The parietal blotches appear as broad elongate streaks parallel to the interparietal suture and extending from the anterior border of each parietal for most of the length of the scale. The uniform brown head cap is followed by a narrow pale collar and the first crossband. The body is grayish brown with narrow darker brown crossbands. The anterior neck band is about 2 scales wide. Subsequent crossbands are 1.5 scales wide, narrowing to less than 1 scale wide for most of the body. The posterior crossbands are very indistinct. Interspaces anteriorly are about 2 scales wide, broadening to 3 scales for most of body. The venter is largely cleared, but apparently had bold

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[8] Details concerning the collection and initial preservation of the holotype are given in the section on natural history. Isopropyl alcohol, the standard storage medium of the LSUMZ collection, causes clearing of museum specimens at concentrations below 45% (Simmons, 2002: 70). The condition of the holotype of *Sibynomorphus oneilli* was not indicated in the original description, but the photographs provided and the description of the color pattern (Rossman and Thomas, 1979: 5) suggest that the clearing occurred subsequent to the original description.

squarish or half-moon–shaped spots aligned to form irregular lines on the lateral edges of the ventral plates.

Comparison of the Holotype with Other Specimens. The holotype of *Sibynomorphus oneilli* has several unusual characteristics compared with all other specimens referred to this species. These include ventral and subcaudal counts (168 and 77, respectively) at the upper extremities of the character ranges, an unusual reduction to 13 dorsal scales posteriorly (unique), 2/2 preoculars (unique), 9/8 infralabials (nearly unique: no other specimen had 8 infralabials, one other specimen had 9/9), and 1/1 primary temporals (nearly unique: one other individual had 1/1; another had one primary temporal on one side).

Some of these characters are unusual not only within *Sibynomorphus oneilli,* but within the genus as a whole. As a consequence of having two preoculars, the loreal is excluded from the border of the eye. The preocular scales appear to be normally formed and not merely the result of formation of an "extra" suture across a portion of the loreal, as occurs occasionally in Dipsadini (e.g., Cadle, 2005, fig. 1). Elsewhere within the genus, two preoculars occur with some frequency in *S. petersi* and *S. vagrans* (Table 1), and in another specimen of *S. oneilli,* the loreal on each side was divided to form two lower preoculars in addition to the usual one. The head scales of the holotype are roughly the same shape and proportions as in other specimens, although the parietals of the holotype extend farther laterally (correlated with it having only a single anterior temporal vs. two in most other specimens). However, it does not appear that an upper (second) anterior temporal is simply fused with the parietals in the holotype. Consequently, the head of the holotype appears somewhat long and narrow compared with other specimens.

The holotype differs in a few details of color pattern from other specimens although color patterns vary considerably within this species. The first dorsal crossband in the holotype is two dorsal rows wide. Subsequent crossbands are 1.5 rows wide, rapidly narrowing to one scale row wide for most of the body. In most other specimens, the anterior crossbands are three to five scale rows wide, narrowing to two scales (next four to five crossbands) and then to one scale row. In the holotype, bold blotches on the venter are confined primarily to the edges of the ventral plates, whereas in virtually all other specimens, the bold markings are distributed across the ventral plates (Figs. 9, 10, 12; Rossman and Kizirian, 1993: fig. 1). The holotype has a longitudinal dark streak on each parietal that parallels the interparietal suture, whereas in other specimens, the head is relatively unmarked or has streaks that parallel the posterolateral edge of the parietals.

New Material of *Sibynomorphus oneilli* from Ancash and Libertad Departments, Peru

After careful consideration of the characters and geographical setting of a series of *Sibynomorphus* in the MUSM from the Río Marañón and Río Santa drainages of the Andes in Ancash and Libertad Departments, Peru, I conclude that they conform to the concept of *S. oneilli* developed herein (Fig. 8).

As detailed in the section on distribution, *Sibynomorphus oneilli* inhabits a region of complex topography, and several major rivers and mountain chains separate the referred populations. Primary among these are the Río Marañón, which separates the type locality from all other known localities, and the Cordillera Blanca, which separates populations of the Amazonian and Pacific versants. Populations of the Pacific versant are known from the Río Santa drainage, a major river of the western Andes. This geographical setting and the relatively few specimens makes the interpretation of character variation within this species difficult. One locality (Yuracyacu) is represented by six specimens (four males, two females), but all other localities are represented by three or fewer specimens. The holotype of *S. oneilli* is the only

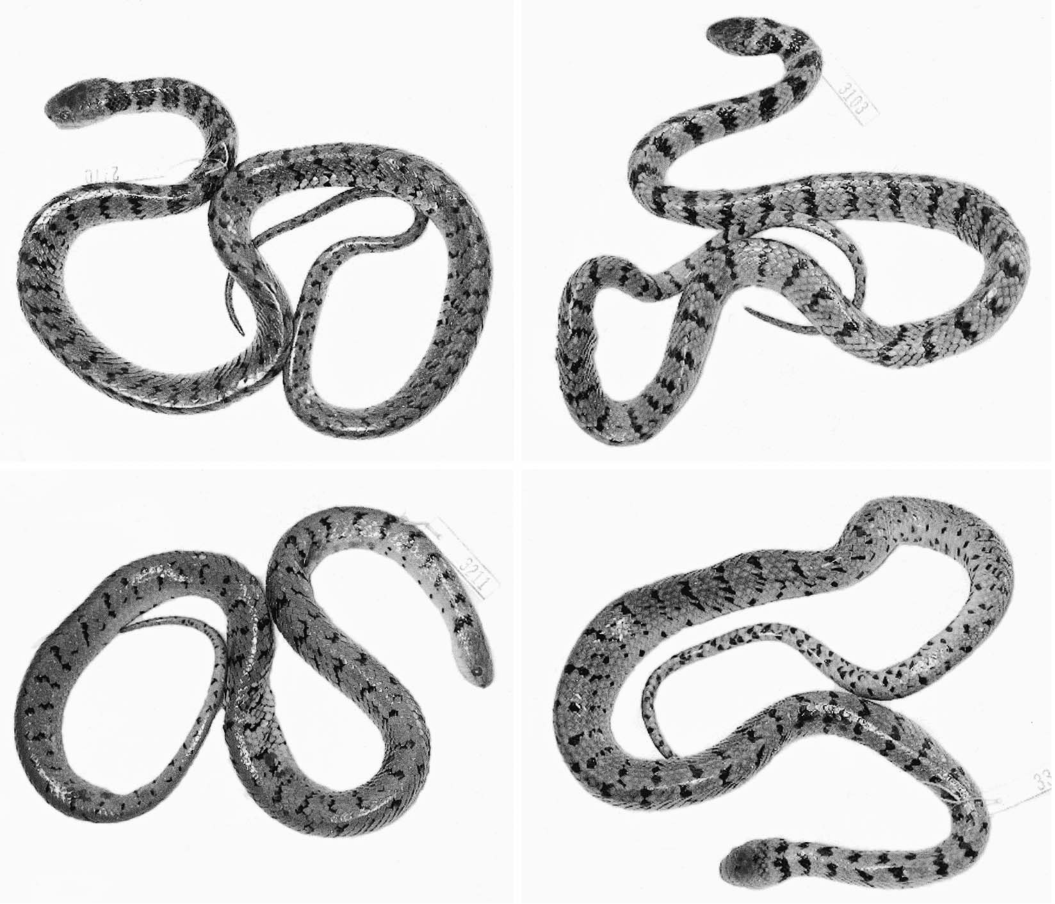

Figure 8. *Sibynomorphus oneilli.* Representative specimens in dorsal view. Top: left, MUSM 2770 (male, 470 mm SVL) from Hacienda Ticapampa (La Libertad Department); right, MUSM 3103 (female, 469 mm SVL) from Cajabamba (Cajamarca Department). Bottom: two specimens from Yuracyacu (Ancash Department): left, MUSM 3211 (female, 413 mm SVL); right, MUSM 3334 (male, 384 mm SVL).

specimen from east of the Río Marañón, and the type locality is the lowest elevation of all known localities (1,646 m). These factors might, in part, explain some of the unusual characters of the holotype. The complexity of the terrain inhabited by these populations enhances the potential for isolation and character differentiation among populations.

The "new" specimens from Ancash Department, herein referred to *Sibynomorphus oneilli,* were perplexing because they extend the range of variation in scutellation and other characters within *S. oneilli.* In some cases, the extended ranges approach the character variation within *S. vagus.* Many of these specimens are much larger (nine of 14 specimens >500 mm total length, with the largest 790 mm total length) than had been known for *S. oneilli* from the three previously known specimens (233–374 mm total length). Further complicating their interpretation was the existence, in the Río Santa valley, of specimens lacking discrete crossbands, a characteristic of many of the known specimens of *S. vagus* (see species account). Thus, whether the "new" specimens represented

S. oneilli, S. vagus, some mixture of the two, or even a new species, was a real question.

All specimens from east of the Cordillera Blanca (10 specimens, including the holotype from east of the Río Marañón) show the banded pattern considered typical of *Sibynomorphus oneilli* (Rossman and Kizirian, 1993; Rossman and Thomas, 1979) (Fig. 8). Of seven specimens from the Río Santa drainage (localities Huaylas, Hacienda Santa Rosa, Hacienda Ticapampa, and Huaráz), three are typically banded (MUSM 2770, 3089, 3395) and one has very narrow and fragmented dorsal crossbands (MUSM 2662). The other three specimens, each from a different Río Santa locality, lack crossbands entirely: MUSM 2687 (Huaylas), 2390 (Hacienda Santa Rosa), and 2660 (Huaráz). Instead, they have a dorsal pattern of fine dark flecks and reticulations reminiscent of the dorsal pattern in *S. vagus* and some specimens of *S. petersi.* Two lines of reasoning led to the conclusion that all specimens from the Río Santa valley and from Yuracyacu in southern Ancash were referable to *S. oneilli.*

First, although the Cordillera Blanca is an impressive mountain range, it is also geologically quite young and probably attained heights over 3,000 m only since the late Miocene (Farrar and Noble, 1976; Simpson, 1979). Geographically, it would not be surprising that populations on either side of the Cordillera Blanca would be closely related to one another. On the other hand, it seems less likely that populations in the Río Santa valley would be closely related to populations on the Amazonian versant far to the north overshadowed by the Cordillera de Huancabamba (the range of *Sibynomorphus vagus*). Populations of the Río Santa are separated from those of Huancabamba not only by rugged mountains, but also by the relatively lower elevations of the Huancabamba Deflection region. This area is a biogeographic discontinuity to many montane elements of flora and fauna that reach their northern or southern distributional limits here (Duellman, 1979; Lynch, 1986; Simpson, 1975, 1979).

Second, the character variation within the sample from the Río Santa valley is more similar to *Sibynomorphus oneilli* than to *S. vagus* (Table 3), despite the similarity of some individuals to *S. vagus* in color pattern. Banded specimens throughout Ancash and southern Cajamarca/Amazonas Departments (e.g., Figs. 8, 9) resemble the regular and fully crossbanded pattern typical of *S. oneilli* in scutellation as well as pattern, rather than the unbanded or anteriorly banded patterns typical of *S. vagus.* A comparison of selected characters of the unbanded specimens of *Sibynomorphus* from the Río Santa valley with both *S. oneilli* and *S. vagus* (Table 3) shows that for ventral counts, unbanded males and females from the Río Santa are within the range of other specimens of *S. oneilli,* but outside the range for *S. vagus.* There are strong frequency differences between *S. oneilli* and *S. vagus* with respect to temporal scale counts. Temporal scale patterns in the unbanded specimens from the Río Santa correspond to the predominant frequencies in *S. oneilli* rather than *S. vagus.* Furthermore, some specimens referred to *S. oneilli* from east of the Cordillera Blanca have fragmented dorsal bands (Fig. 8, lower left), which suggests that there is some lability in the expression of crossbands. I conclude that all available specimens from both sides of the Cordillera Blanca in Ancash Department are referable to *S. oneilli* and that this species is polymorphic in color pattern, as is already well known for some other species of *Sibynomorphus.*

Diagnosis

Sibynomorphus oneilli has a large number (38–63) of dark crossbands on the dorsum throughout the length of the body when discrete crossbands are present (the most common condition) (Fig. 9). In some specimens, the dorsal crossbands are complete only anteriorly; the posterior cross-

Table 3. Comparison of selected characters of noncrossbanded specimens referred to *Sibynomorphus oneilli* from the Río Santa valley with character states in *S. oneilli* and *S. vagus*. Ventral counts summarized for *S. oneilli* and *S. vagus* are ranges followed by mean (in parentheses) and sample sizes (*N*). Temporal counts for these two species treat each side of each specimen as an independent observation. Bilateral counts are separated by a solidus (left/right). The sample of *S. oneilli* includes all specimens except those from the Río Santa valley. See Table 1 for summary statistics of these data.

	Noncrossbanded Specimens from the Río Santa Valley				
	MUSM 2687 Female Huaylas	MUSM 2390 Female Santa Rosa	MUSM 2660 Male Huaráz	*Sibynomorphus oneilli* (except Río Santa)	*Sibynomorphus vagus* (total sample)
Ventrals					
Male	—	—	159	156–168 (163) *N* = 8	144–152 (149) *N* = 5
Female	163	168	—	163–173 (168) *N* = 4	151–158 (154) *N* = 5
Primary temporals	2/2	2/2	2/1	2 (*N* = 18)	1 (*N* = 19) 2 (*N* = 1)
Secondary temporals	3/3	3/3	3/3	2 (*N* = 2) 3 (*N* = 14) 4 (*N* = 4)	2 (*N* = 18) 3 (*N* = 2)
Tertiary temporals	4/3	3/3	4/4	2 (*N* = 2) 3 (*N* = 6) 4 (*N* = 11)	0 (*N* = 0) 1 (*N* = 1) 2 (*N* = 13) 3 (*N* = 5)

bands in these specimens are incomplete middorsally and appear as narrow lateral bars. Several specimens from the Río Santa valley lack discrete bands entirely; instead, the dorsum has an obscure network of dark flecks or reticulations. The anterior crossbands (generally two to three dorsal rows wide) are slightly broader than, or equal in width to, the interspaces, whereas most crossbands are only one dorsal row wide and much narrower than the interspaces. The venter is heavily checkered or spotted with large bold markings (rounded, squarish, or half-moon–shaped) (Fig. 9). Ventrals are 152–168 in males; 163–173 in females. Subcaudals are 62–77 in males; 56–64 in females. Infralabials are 9–13.

Sibynomorphus oneilli differs from other species of *Sibynomorphus* in Ecuador and Peru as follows. In *S. oligozonatus,* S. *vagrans,* and *S. williamsi,* the anterior crossbands are usually twice or more as broad as the interspaces (see illustrations in the species accounts), whereas in *S. oneilli,* crossbands are usually equivalent to, or narrower than, the interspaces (occasionally broader than interspaces but never approaching twice their width). These species also differ from *S. oneilli* in other characters: *S. oligozonatus* has fewer supralabials (6–7) and a less boldly patterned venter (Figs. 1, 2, 4, 6). *Sibynomorphus williamsi* has fewer supralabials (6–7) and a greater number of ventrals (males, 173–182; females, 181–188) than *S. oneilli. Sibynomorphus oneilli* averages about 10 more ventrals and 15 fewer subcaudals than *S. vagrans* when sexes are considered separately (Table 1).

Sibynomorphus vagus differs from *S. oneilli* in temporal scale patterns (Table 1) and by having fewer ventrals (males, 144–152; females, 151–158). *Sibynomorphus petersi* has a greater number of ventrals (164–188, sexes combined) and subcaudals (males, 75–87; females, 65–77) than *S. oneilli* and has different color patterns on the head and body.

Description

Size and Scutellation. Taxonomic data for *Sibynomorphus oneilli* are summarized in Table 1. The largest specimen is a female 790 mm total length (624 mm SVL).

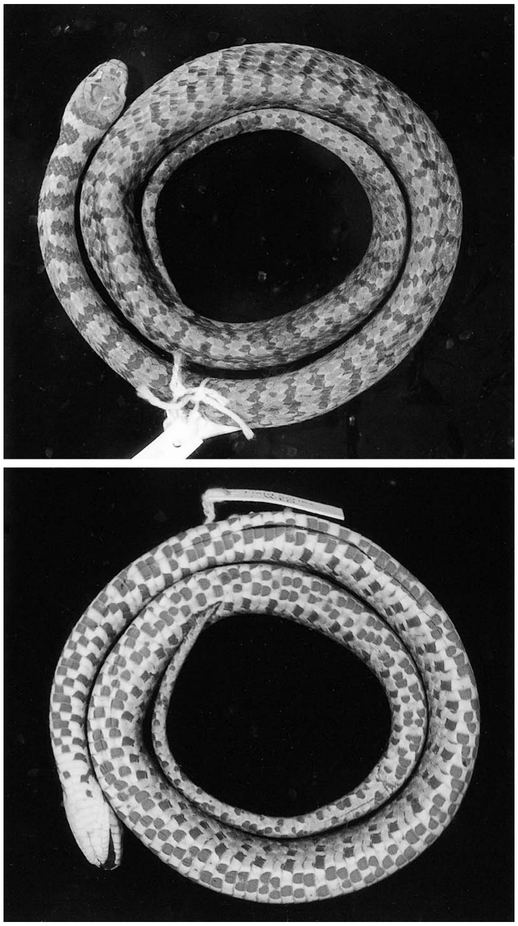

Figure 9. *Sibynomorphus oneilli.* Dorsal and ventral views of KU 212599 (from near Cajabamba, Cajamarca Department, Peru). Female, 374 mm total length.

The largest male is 571 mm total length (440 mm SVL). Body somewhat compressed. Tail 22–26% of total length in males, 20–22% of total length in females. Dorsal scales smooth and in 15–15–15 rows in all specimens except the holotype, in which there is a posterior reduction to 13 scale rows (see above *Redescription of the Holotype*). Vertebral row slightly broader than paravertebral rows. Ventrals 152–168 (averaging 161) in males, 163–173 (averaging 167) in females; 0–4 preventrals precede the ventral plates. Anal single. Subcaudals 62–77 (averaging 68) in males, 57–64 (averaging 61) in females.

Usually, a loreal and a single preocular (superior to the loreal) border the anterior edge of the eye, but the preocular is often fused with the prefrontal (Table 1); loreal squarish or polygonal. The holotype has two preoculars on each side and the loreal is separated from the eye (interposed between the inferior preocular and the posterior nasal). MUSM 3376 has a separate preocular but, in addition, the loreal is divided vertically and horizontally to form a pair of lower preoculars, thus resulting in three preoculars. Postoculars are virtually always 2 (3 on one side of one specimen). Primary temporals usually 2 (occasionally 1); secondary temporals usually 3 (range 1–4), tertiary temporals usually 3 or 4 (rarely 2). Supralabials 6–10 with the most frequent patterns 8 (4–5 bordering eye) or 7 (3–4 bordering eye). Infralabials 9–13 (most frequently 10 or 11). One pair of infralabials in contact behind mental in all specimens. Chin shields in 2 pairs (N = 3), 3 pairs (N = 10), 3.5 pairs (N = 1), or 4 pairs (N = 4). Maxillary teeth 13–16 (N = 13). The pupil is prolate in preservative.

Barring patterns of geographic variation that remain unforeseen because of sampling issues,[9] *Sibynomorphus oneilli* shows typical colubrid patterns of sexual dimorphism in size (females attain larger size), ventral counts (female greater; t = 2.545, df = 15, $p < 0.05$), subcaudal counts (male greater; t = 2.764, df = 12, $p < 0.05$), and relative tail length (males have longer tails) (Table 1).

Color in Life. Unknown.

Color in Preservative. The pattern of the holotype is described above, but its poor state of preservation does not warrant a detailed description (see above *Rede-*

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[9] The female from Santa Rosa is substantially larger than other specimens (790 mm total length). Large size is conceivably characteristic of this population, but that is unverifiable with a single specimen. It could be that the extremely large size of this specimen is due to vagaries of sampling. The next largest specimen, a male, was 623 mm total length.

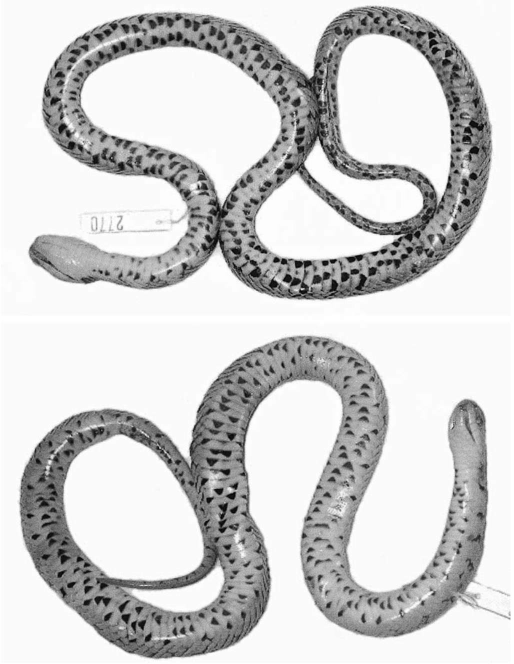

Figure 10. *Sibynomorphus oneilli.* Representative specimens in ventral view. Top: MUSM 2770 (La Libertad Department; male, 470 mm SVL). Bottom: MUSM 3211 (Ancash Department; female, 413 mm SVL).

Figure 11. *Sibynomorphus oneilli.* Dorsal and lateral views of head, KU 212599. The skull of this specimen had been dissected from the skin, hence the appearance of the eyes and tears in the rostral and mental regions.

scription of the Holotype and Rossman and Thomas, 1979: 5). The coloration of *Sibynomorphus oneilli* in preservative, on the basis of the other specimens, follows. Dorsal ground color medium brown or grayish brown, occasionally somewhat reddish brown; grayish when the stratum corneum is removed. Dorsal crossbands and other markings black (Figs. 8, 9). Dorsal crossbands on the body, when present, range from 38 to 63 with no apparent sexual dimorphism; crossbands can be fragmented or even completely absent, as described below. The venter is dull whitish or with fine dark stippling giving a dusky appearance, upon which are bold black squarish or half-moon–shaped spots in a checkerboard pattern. Ventral spots are usually densely arrayed (Figs. 9, 10), but there is a tendency for specimens lacking dorsal bands also to have less boldly patterned venters (see Fig. 12). Gular region immaculate, grayish to white. Dorsal and ventral surfaces of the tail are like the corresponding surfaces of the body, except the dorsal bands are incomplete middorsally.

The top of the head is medium brown, usually with some scattered irregular blackish marks primarily on the parietals and frontal; these marks sometimes include an irregular curved black streak that roughly parallels the posterolateral edge of each parietal (Fig. 11; Rossman and Kizirian, 1993: fig. 1). A narrow dark nape bar is frequently present between the first dorsal crossband and the parietal scales; it extends laterally to just above the posterior supralabials and, when present, can be manifested by dusky shading or a very distinct blackish bar. In a few specimens, the top of the head is unmarked (e.g., MUSM 3211, Fig. 8). Temporal scales are very narrowly edged with black, but without close examination, the impression is that the side of the head is unmarked. The supralabials are dull whitish with some dark stippling (but no discrete markings) along

Figure 12. *Sibynomorphus oneilli.* A nonbanded specimen from Huaylas in the Río Santa valley (Pacific versant, Ancash Department). MUSM 2687 (female, 463 mm SVL).

suture lines. Infralabials are dull whitish, unmarked.

The dorsal pattern varies by individual. The first crossband is interrupted middorsally in many specimens, forming a pair of blotches (much higher than wide) on the side of the neck (Figs. 8 [upper and lower right], 9, 11). Other crossbands on the body are likewise sometimes interrupted middorsally. At least occasionally (e.g., MUSM 3211; Fig. 8, lower left), virtually all of the crossbands are interrupted so that the dorsal pattern consists of a series of irregular narrow vertical streaks on the flanks, and in extreme cases (MUSM 2662), the crossbands are extremely fragmented so as to give the appearance of an irregular pattern. In most specimens, the crossbands on the anterior quarter to third of the body are wider than more posterior crossbands (Figs. 8, 9). Occasionally (MUSM 2770, KU 212600) these anterior crossbands are twice or more the width of the posterior crossbands. Except for these anterior bands, most bands on the body are one scale row or less in width and are much narrower than the interspaces. As described above (*New Material of* Sibynomorphus oneilli *from Ancash and Libertad Departments, Peru*), two females and a male from the Río Santa valley lack crossbands entirely and have irregular dark flecks over the dorsum (Fig. 12).

There seems to be little or no ontogenetic change in color pattern, as four specimens 203–280 mm total length had patterns similar to adults; one of these (MUSM 3089; 232 mm total length) had the highest number of dorsal bands recorded (63), and these were formed by darkened scale edges rather than fully formed bands.

Details of the dorsal patterns of KU 212599 and 212600 are as follows:

KU 212599 (Fig. 9): Approximately 55 crossbands are present on the body. On the neck just behind the head is a pair of lateral blackish blotches 4 to 5 dorsal rows wide. The following crossband (complete across the dorsum) is 3 scales wide and the following 4 crossbands are two scales wide. Subsequent crossbands are no more than a single dorsal row wide, becoming increasingly fragmented posteriorly, but more or less discrete the length of the body. Anteriorly, the crossbands extend down to the first dorsal row or outer edge of the ventrals; posteriorly the crossbands tend to fragment before reaching the first dorsal row. Interspaces between the crossbands are medium reddish brown, 2 to 3 dorsal rows in width anteriorly and usually 3 rows posteriorly. Many dark flecks are present in the interspaces, especially posteriorly.

KU 212600: The body has 38 total crossbands (+2 half-bands in between complete bands) (see Rossman and Kizirian, 1993: fig. 1 for dorsal and ventral photographs of this specimen). Crossbands are complete across the dorsum (except the two half-bands) and extend to the outer edge of the ventral plates, where most fuse more or less completely with one or more of the dense squarish spots on the venter. The first crossband behind the head is 4 scales wide, the next five bands are 3 scales wide, the following five are two scales wide, and the rest are one scale wide. The crossbands are wider middorsally than ventrally; they have irregular edges, but are essentially oriented vertically (slightly curved in some cases). Laterally, between many of the crossbands, and in the vertebral/paravertebral region are scattered irregular black flecks mainly formed by black edging on some of the dorsal scales. Interspaces anteriorly are two scale rows wide, broadening to three on anterior one-third of body, and then to four scale rows wide posteriorly.

Etymology. Sibynomorphus oneilli was named for ornithologist John P. O'Neill, who collected the holotype. The ornithological expeditions of Louisiana State University to Peru, many under the guidance of O'Neill, have also made important contributions to knowledge of the Peruvian herpetofauna.

Distribution

Sibynomorphus oneilli is known from the northern end of the Cordillera Oriental in extreme southern Amazonas Department, Peru, and in the Cordillera Occidental from southern Ancash to southern Cajamarca Department (Fig. 7; see also Fig. 43). Localities are on the Amazonian versant (Río Marañón drainage) and Pacific versant (Río Santa and its tributary, the Río Tablachaca/Tablache) of the Andes. The recorded elevational range is 1,646–3,500 m. In Ancash Department, populations of *S. oneilli* from the Amazonian versant of the Cordillera Occidental are separated from populations of the Pacific versant (Río Santa drainage) by extensive mountains of the Cordillera Blanca well over 4,000 m. The type locality is separated from other known localities by the Río Marañón (but see footnote 15).

As here conceived, populations of *Sibynomorphus oneilli* inhabit one of the most tectonically active and topographically complex regions of the Andes. The species occurs on both sides of the Río Marañón, one of the longest and largest rivers descending from the Andes; it separates the Cordillera Oriental from the Cordillera Occidental, the principal chains of the Andes in northern Peru. The Río Marañón flows northwesterly until near the Ecuadorian border, thence turning east and becoming the major western affluent of the Amazon system. On the Pacific versant, *S. oneilli* occurs in the valley of the Río Santa and one of its tributaries, the Río Tablachaca/Tablache (which forms the border between Ancash and La Libertad Departments). The Río Santa flows northwesterly through the length of Ancash Department, eventually turning westward through the gorge of the Cañon del Pato and emptying into the Pacific Ocean. Lehr et al. (2002: fig. 11) present a photograph of the Río Santa valley upstream from Huaráz, one of the localities for *S. oneilli.* The inter-Andean valleys of the Río Marañón and Río Santa are relatively arid and presently form effective barriers for east–west dispersal of montane flora and fauna (Simpson, 1979).

In addition to large river systems, populations of *Sibynomorphus oneilli* are separated by incredibly rugged mountains. Populations in the Río Marañón drainage are separated from those in the Río Santa valley by the glacier-laden Cordillera Blanca, the highest continuous range in the Andes (see Lehr et al., 2002: fig. 11). This impressive mountain chain contains more than 10 peaks exceeding 6,000 m elevation (the highest being Nevado Huascarán at 6,746 m) and no passes below 4,000 m; most of its area is above 5,000 m (Clapperton, 1993). Vertical descents on either side of the Cordillera Blanca frequently exceed 4,500 m, and its fault zones are young and very active (Noble et al., 1990). Major uplifts in the late Miocene through Pleistocene brought the mountains to their present height (Farrar and Noble, 1976). The Río Marañón and the Río Santa are relatively young rivers that developed in the down-faulted trenches between major uplifts of the Cordillera Oriental and Cordillera Occidental (Río Marañón) or within the Cordillera Occidental (the Río Santa, flanked on the east and west by the Cordillera Blanca and Cordillera Negra, respectively).

Thus, populations referred to *Sibynomorphus oneilli* on either side of major geographic barriers within the species' range (Río Marañón, Cordillera Blanca) were probably isolated, geologically speaking, relatively recently. Nonetheless, the heavily dissected topography enhances opportunities for the isolation of these populations, particularly those of the eastern and western versants, which are separated by inhospitable terrain or unsuitable high-elevation habitats. *Sibynomorphus oneilli* is one of few reptiles known to have populations on both the Amazonian and Pacific versants of the Andes, and most of these have only become known in conjunction with field work in the area in the last quarter century (Cadle, unpublished data).

Natural History

The holotype of *Sibynomorphus oneilli* was collected 8 August 1975 in "semiarid brushland" (Rossman and Thomas, 1979). According to the collector, ornithologist John P. O'Neill (personal communication, 25 April 2006), the holotype was dead in the middle of a gravel highway on an overcast, cool day; the area had scattered bushes and was rather overgrazed. It was placed in a jacket pocket for 24 or more hours before preservation, which could in part explain its poor present condition.

Two specimens (KU 212599–600) were collected in January and March under rocks in agricultural land (Rossman and Kizirian, 1993). Other specimens with dates of collection have been obtained in January, February, March, April, September, October, and December. These months generally correspond to the cooler, wetter part of the year in this portion of the Andes (wet season primarily November–April).

The three smallest individuals have visible umbilical scars: MUSM 3303 (203 mm total length; 155 mm SVL), MUSM 3089 (232 mm total length; 181 mm SVL), and LSUMZ 33736 (233 mm total length; 174 mm SVL). MUSM 3089 was collected in December 1982; LSUMZ 33736 was collected 8 August 1975. The date of collection of MUSM 3303 is unknown.

***Sibynomorphus petersi* Orcés and Almendáriz**

Figures 13–27

Dipsas mikanii oreas: Parker, 1934: 271, 1938: 444 (misidentifications). See later discussion of misidentified literature records.

Dipsas variegata variegata: Peters, 1964: 47 (misidentification). Based on USNM 237040, which was subsequently referred to *Sibynomorphus petersi* (Cadle and Myers, 2003: 7).

Sibynomorphus petersi Orcés and Almendáriz (1989). Type locality: "Zhila (2,250 m) 79°17′26″W, 03°39′45″S [see footnote 19], parroquia Oña, cantón Girón, Provincia Azuay [Ecuador]." Holotype, EPN 2659. Almendáriz and Orcés (2004).

Sibynomorphus vagus: Lehr et al. (2002) (misidentification of SMF 80048, MUSM 20583).

Notes on the Type Series of *Sibynomorphus petersi*

The specimens here referred to *Sibynomorphus petersi* substantially amplify knowledge of variation in this taxon, which was previously reported only from the holotype (EPN 2659) and two paratypes (EPN 1847, 2660) (Orcés and Almendáriz, 1989). I refer other specimens from southern Ecuador and eight Peruvian specimens to this species (see *Specimens Examined and Locality Records*). Of the type series, I have examined only a paratype from the type locality, EPN 2660 (Fig. 13).

According to Orcés and Almendáriz (1989) the holotype is an adult male 763 mm total length, 609 mm SVL, 154 mm tail length (= 20.2% of total length and not the 21.9% reported in the original description); 15 [midbody] dorsal scale rows (vertebral row slightly enlarged); 176 ventrals, 79 subcaudals, single anal; 9 supralabials (4 + 5 touching the eye), 12 infralabials; four pairs of chin shields; 0/1 preoculars, 2/2 postoculars; 3 + 2 + 3/2 + 3 + 3 temporals. These data conform to my own for male *Sibynomorphus petersi* (Table 1), except that the tail is shorter than in any male I examined.

Diagnosis

Sibynomorphus petersi attains a large size (to 771 mm total length in females, 763 mm in males) and has moderately

Figure 13. *Sibynomorphus petersi.* Paratype (EPN 2660, Azuay Province, Ecuador) in dorsal and ventral views. Female, 542 mm SVL.

high ventral (164–188) and subcaudal (65–87) counts. Many features distinguishing this species from others in Peru and Ecuador are aspects of color pattern. *Sibynomorphus petersi* has a dorsal ground color of medium brown (brown or grayish in preservative), generally with narrow, dark brown (sometimes dark gray in preservative), irregular zigzag crossbands that extend ventrally to the lowermost dorsal rows or extreme outer edges of the ventral scales (Figs. 13, 14). Three or four anterior crossbands are sometimes broader than the others. Crossbands may be fragmented into a dorsal and lateral series of blotches, and crossbands or blotches are difficult to discern in some individuals. The venter is whitish with bold black or dark brown squarish or half-moon–shaped blotches or streaks; the ventral ground color is sometimes heavily invested with brown, a reflection of a dense peppering of minute flecks and spots.

The top of the head is brown or grayish brown with dark brown spots, streaks, or other markings in a highly irregular pattern. Nonetheless, one feature of the head pattern seems relatively constant, albeit somewhat variable in precise execution: a large discrete spot is usually present on each prefrontal scale (Fig. 15). The prefrontal spots are usually symmetrically placed but vary in size, shape, and exact position among specimens (see *Color in Preservative and Variation in Pattern*). They are usually round but occasionally are irregular in shape. Dark markings on the head have a narrow pale edge (yellowish in life), which can be obscure in preserved specimens. In many specimens the dark head markings also have a pale core (Fig. 15).

Sibynomorphus petersi differs from other species of the genus in northern South America as follows: *S. vagrans* and *S. vagus* have fewer ventrals (149–159 and 144–158, respectively) and different color patterns (see descriptions and illustrations herein). *Sibynomorphus oneilli* usually has narrow, more or less straight-sided (compared with zigzag) crossbands and has fewer ventrals and subcaudals than *S. petersi* (*S. oneilli* ventrals and subcaudals, male: 152–168 and 62–77; female: 163–173 and 57–64). *Sibynomorphus oligozonatus* has anterior crossbands that are much broader than the interspaces and, in males, fewer ventrals (145–163) and subcaudals (66–68); *S. oligozonatus* has six or seven supralabials, whereas *S. petersi* usually has eight. *Sibynomorphus williamsi* usually has six supralabials (3–4 touching the eye), whereas *S. petersi* usually has eight supralabials (4–5 touching the eye); *S. williamsi* also has distinct bold crossbands the entire length of the body and usually a relatively unmarked venter (when marked, never bold spots or half-moons).

In the collections I surveyed, *Sibynomorphus petersi* was commonly misiden-

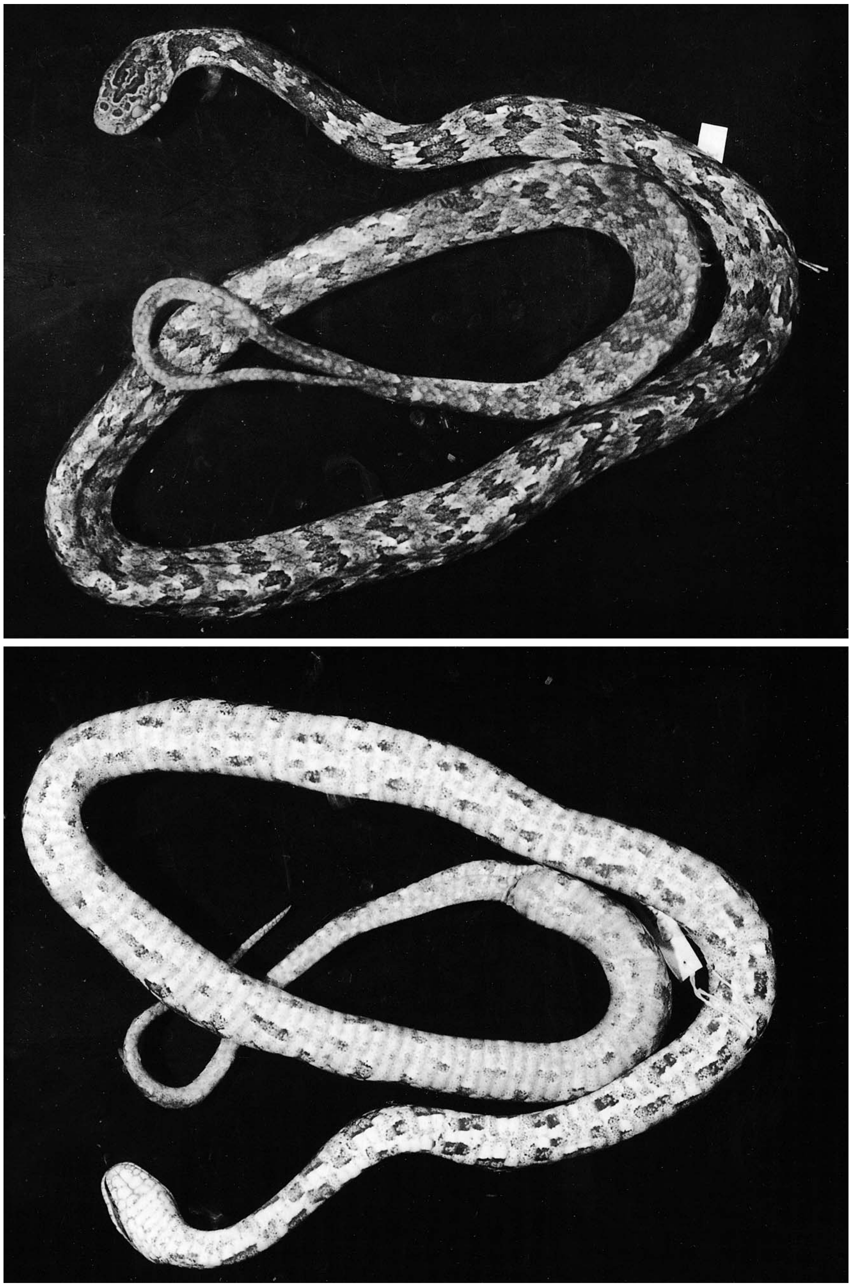

Figure 14. *Sibynomorphus petersi.* Dorsal and ventral views of a specimen from southern Ecuador. EPN 4737 (Loja Province, Ecuador). Female, 580 mm SVL.

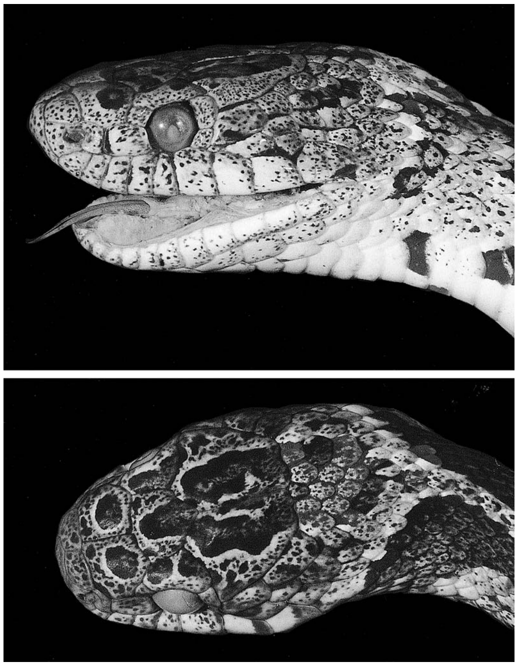

Figure 15. *Sibynomorphus petersi.* Top: Lateral view of head (BMNH 1900.3.30.19 from San Pablo, Cajamarca Department, Peru). Bottom: Dorsal view of head (EPN 4737, Loja Province, Ecuador). Both specimens show the large spot on each prefrontal scale that is characteristic of *S. petersi* despite some variation (see Figs. 19, 22). In most specimens, the spots are bordered by a narrow pale ring, as seen clearly in the lower figure here. Note also the minute dark spots on individual scales.

tified as *Dipsas variegata* or *D. oreas* (see discussion of misidentifications in the literature below). *Sibynomorphus petersi* can be distinguished from all species of *Dipsas* in western Ecuador and Peru by a few key aspects of color pattern, especially details of the banding pattern on the body and patterns atop the head (see Cadle, 2005; Cadle and Myers, 2003). Scutellation characters alone are insufficient for some comparisons because of substantial overlap in scale counts for many species of Dipsadini. Species of *Dipsas* also have a relatively much larger eye than species of *Sibynomorphus*; see Cadle (2005) and Cadle and Myers (2003) for descriptions and illustrations. The following comparisons show, for subadult and adult *S. petersi* and *D. oreas,* the difference in eye size compared with SVL (for these comparisons subadults are ≤351 mm SVL):

S. petersi:
  Adult eye size: 0.552 ± 0.081% SVL (*N* = 4)
  Subadult eye size: 0.701 ± 0.016% SVL (*N* = 2)

D. oreas:
  Adult eye size: 0.730 ± 0.049% SVL (*N* = 12)
  Subadult eye size: 0.840% SVL (*N* = 1)

Misidentifications of Sibynomorphus petersi *in the Literature. Sibynomorphus petersi* was frequently misidentified in museum collections, and some of these records have made their way into the literature. Parker (1934: 271; 1938: 444) identified specimens of *S. petersi* from the collections of Clodoveo Carrión from southern Ecuador as *Dipsas mikanii oreas* (= *D. oreas*). Parker cited only six specimens from the Carrión collection as this species, whereas I located 13 Carrión specimens in the BMNH that were originally identified as *"Dipsas mikanii oreas."* All of these except one are here referred to *S. petersi* (the other is *S. oligozonatus*; see *Specimens Examined and Locality Records*). Three specimens can, with reasonable confidence, be associated with BMNH catalogue numbers on the basis of the sex, locality, and segmental counts provided by Parker (1938): a male and two females from "Catamayo Valley" are, respectively, BMNH 1935.11.3.110 (= *Sibynomorphus petersi*), 1935.11.3.108 (= *S. oligozonatus*), and 1935.11.3.109 (= *S. petersi*). I could not confidently associate BMNH numbers with the other three specimens reported by Parker (1934, 1938).

Specimens of *Sibynomorphus petersi* were commonly misidentified as *Dipsas variegata,* apparently on the basis of earlier reports of that species from Ecuador and Peru (e.g., Peters, 1960, 1964). However, Cadle and Myers (2003) showed that some previously published records of

"*Dipsas variegata variegata*" and "*Dipsas variegata nicholsi*" from Ecuador and Peru were based on misidentifications of other species, including *D. andiana, D. oreas, D. peruana,* and *S. petersi.*[10] Peters' (1964: 47) record of "*Dipsas variegata variegata*" from western Ecuador is based on USNM 237040, which was subsequently referred to *Sibynomorphus petersi* (Cadle and Myers, 2003: 7). Lehr et al. (2002) referred two specimens of *S. petersi,* SMF 80048 and MUSM 20583 from Ancash Department, Peru, to *S. vagus.* They clearly are not that species and one of them is here referred to *S. petersi* (see footnote 22).

Description

Size and Scutellation. Table 1 summarizes basic characteristics of *Sibynomorphus petersi.* The largest specimen is a female 771 mm total length, 595 mm SVL. The largest male is the holotype, 763 mm total length, 609 mm SVL (Orcés and Almendáriz, 1989). Tail 22–28% of total length in males (with the holotype an outlier at 20% on the basis of measurements in the original description), 20–24% of total length in females. Body somewhat compressed. Dorsal scales smooth, in 15–15–15 rows. The vertebral row is slightly broader than, to approximately twice the width of, the adjacent paravertebral rows; the vertebral row seems relatively broader in Ecuadorian compared with Peruvian specimens. Ventrals 164–183 (averaging 173) in males, 173–188 (averaging 179) in females. Ventrals preceded by one to three preventrals. Anal single. Subcaudals 75–87 (averaging 81) in males, 65–77 (averaging 73) in females. Usually a loreal and a single preocular border the eye (preocular superior to the loreal); occasionally two or three preoculars were present, but the preocular was never fused with the prefrontal (Table 1). The loreal varies in shape from squarish (e.g., Fig. 15, top) to more elongate (Fig. 23, bottom). Postoculars 2 (rarely 3). Primary temporals usually 2 (occasionally 1). Secondary temporals usually 3 (range 2–4). Tertiary temporals 2–4. Supralabials usually 8 (range 7–9) with 4–5 bordering the eye. Infralabials usually 10 or 11 (range 9–12). One or two pairs of infralabials in contact behind the mental, with the following frequencies in the sample: first pair of infralabials in contact (11), first two pairs in contact (6), one infralabial contacts two on the opposite side (4). Three pairs ($N = 15$), 3.5 pairs ($N = 1$), or four pairs ($N = 3$) of squarish or polygonal chin shields. Maxillary teeth 14–17 ($N = 10$).

Sexual Dimorphism. Compared with females, male *Sibynomorphus petersi* have significantly fewer ventrals ($t = 2.408$, df

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[10] Cadle and Myers (2003) were specifically concerned with Peruvian and Ecuadorian records of *Dipsas variegata* discussed by Peters (1960, 1964) and Steindachner (1902). We failed to note more recent reports of "*D. variegata*" from southeastern Peru (Doan and Arriaga, 2002; Duellman and Salas, 1991). In 2001, I had examined one of two specimens referred to *D. variegata* from Cusco Amazónico (Duellman and Salas, 1991), KU 214858, and concluded that it is not the same taxon as *D. variegata* Duméril, Bibron, and Duméril from Venezuela and the Guayanan region. On this basis, Duellman (2005: 371) listed the Cusco Amazónico material as "*Dipsas* sp." Doan and Arriaga (2002) apparently collected the same taxon from a site near Cusco Amazónico and referred all the material to *D. variegata.*

KU 214858 (Duellman, 2005: 371 and pl. 183), a female, has more ventrals and a different color pattern than specimens of *Dipsas variegata* from Venezuela and the Guayanan region examined by Cadle and Myers (2003: table 1), although ventral counts recorded in the literature, including those for a syntype reported in the original description, are greater (Cadle and Myers, 2003: footnote 5; Duméril et al., 1854: 478). KU 214858 is similar in color pattern and high ventral counts to specimens tentatively referred to *D. variegata* from the mouth of the Amazon (Cadle and Myers, 2003: footnote 5; Cunha and Nascimento, 1993). This taxon has not turned up in some comprehensive collections from central Amazonia (Martins and Oliveira, 1998). Clearly, the status of these specimens from southeastern Peru referred to *D. variegata* (Doan and Arriaga, 2002; Duellman and Salas, 1991) needs clarification, and *Dipsas variegata* itself needs a thorough range-wide study. These issues do not affect Cadle and Myers's (2003) conclusions on the basis of Peters' (1960, 1964) and Steindachner's (1902) records of "*Dipsas variegata*" from Peru and Ecuador, none of which are that species.

= 22, $p < 0.05$), significantly more subcaudals ($t = 4.760$, df = 18, $p < 0.001$), and greater relative tail lengths. Females attain a greater body size than males. The five largest females were 681–771 mm total length (541–595 mm SVL), and four of these were >700 mm total length. The five largest males were 568–657+ mm total length (422–520 mm SVL) and three of these were >600 mm total length. Large females appear to have somewhat different body proportions than smaller individuals of either sex, but larger samples of well-preserved specimens would be needed to test this observation rigorously. Additionally, because localities for *S. petersi* are represented by few individuals (most frequently one or two specimens per locality), it is difficult to separate divergence in characters because of sex from geographic or other sources of variation. Nonetheless, large females tend to have rather narrow, elongate heads and relatively small eyes; smaller individuals have shorter, more rounded, bulbous heads and larger eyes. Large females have rather stout bodies, especially posteriorly, compared with males (this comparison ignores the two females that were clearly carrying eggs).

Sex differences in head size and shape and body size and shape, such as those apparent in *Sibynomorphus petersi,* are relatively common in snakes (reviews in Bonnet et al., 1997; Shine, 1989, 1993). The head shape differences most often reflect intersexual dietary differences (e.g., Camilleri and Shine, 1990), whereas body shape differences, in which females have a stouter, robust body, most likely reflect the reproductive needs of female snakes to accommodate eggs or fat body stores (Lourdais et al., 2006).

Corresponding to the relatively longer SVLs of females compared with males, there is sexual dimorphism in the number of crossbands on the body. Females averaged 38 ± 8.01 bands on the body (range: 31–59, $N = 12$; ignoring a clear outlier at 59, the range is 31–44 with a mean of 36.0 ± 4.74). Males averaged 31.2 ± 1.69 bands (range: 29–35; $N = 10$). The overall means are significantly different (unequal variances, $t'_s = 2.949$, $t'_{0.05} = 2.203$, $p < 0.05$), as well as the comparison ignoring the female outlier (unequal variances, $t'_s = 3.049$, $t'_{0.02} = 2.77$, $0.01 < p < 0.02$).

Superimposed on this pattern of sexual dimorphism is geographic variation in the number of crossbands (Peruvian specimens tend to have greater numbers of crossbands; see below), but even considering only Ecuadorian specimens, females average about four more bands on the body than males.

Geographic Variation. Notable geographic trends in scutellation or body proportions are few in *Sibynomorphus petersi,* as shown for ventrals, subcaudals, and relative tail lengths in Table 4. None of these characters show statistically significant differences between Ecuadorian and Peruvian samples when sexes are compared separately. Three of six Peruvian specimens have a single anterior temporal on each side (the others have two), whereas all Ecuadorian specimens have either two or three anterior temporals. No other scutellation differences among Ecuadorian and Peruvian specimens were noted. Perhaps significantly, the only specimen of *S. petersi* from the Amazonian versant, MUSM-JEC 12884, has the lowest ventral count (164) of all specimens (range in the rest of the sample: 170–188; $N = 23$). No other characters of this specimen were unusual (unfortunately, it is a badly damaged road kill).

In addition to the sexual differences indicated above, the number of body crossbands varies geographically, but sample sizes are too small to thoroughly analyze the trend. The only Peruvian male with a full complement of crossbands has 35 bands on the body, whereas the range among Ecuadorian males was 29–32. Three Peruvian females had 41, 44, and 59 crossbands, whereas the range among Ecuadorian females was 31–38 and one outlier at 43. Thus, it seems likely that for

TABLE 4. GEOGRAPHIC COMPARISON OF SELECTED CHARACTERS IN *SIBYNOMORPHUS PETERSI*. THE TWO MALES FROM PERU HAD BROKEN TAILS, SO NO SUMMARY STATISTICS ARE AVAILABLE FOR SUBCAUDALS AND RELATIVE TAIL LENGTHS FOR MALES FROM PERU. NONE OF THESE CHARACTERS SHOW STATISTICALLY SIGNIFICANT DIFFERENCES BETWEEN ECUADORIAN AND PERUVIAN SAMPLES IN SEPARATE COMPARISONS BY SEX..

	Ecuador	Peru	Total Sample
Ventrals			
Male	170–183 174.3 ± 4.85 (*N* = 9)	164–176 170.0 ± 8.48 (*N* = 2)	164–183 173.5 ± 5.39 (*N* = 11)
Female	173–188 178.8 ± 5.06 (*N* = 8)	174–182 178.2 ± 3.35 (*N* = 5)	173–188 178.5 ± 4.33 (*N* = 13)
Subcaudals			
Male	75–87 81.0 ± 3.66 (*N* = 8)	65+ to 74+ (*N* = 2)	75–87 81.0 ± 3.66 (*N* = 8)
Female	65–77 73.3 ± 4.43 (*N* = 8)	70–74 72.5 ± 1.91 (*N* = 4)	65–77 73.0 ± 3.69 (*N* = 12)
Tail length/total length			
Male	0.22–0.28 0.25 ± 0.02 (*N* = 8)	0.21+ to 0.26+ (*N* = 2)	0.22–0.28 0.25 ± 0.02 (*N* = 8)
Female	0.20–0.24 0.22 ± 0.01 (*N* = 7)	0.20–0.24 0.22 ± 0.02 (*N* = 4)	0.20–0.24 0.22 ± 0.01 (*N* = 11)

both sexes, northern specimens tend to have fewer crossbands than southern ones.

Color in Life. The color pattern of *Sibynomorphus petersi* in life consists of various shades of brown (yellowish brown to dark brown) or gray. The dorsum is usually distinctly crossbanded, but three individuals from Peru have very indistinct crossbands. Bands are characteristically narrow and undulating or zigzag. The venter is heavily marked with bold spots, and the top of the head has complex dark markings, including the consistent presence of a large spot on each prefrontal (details below). The following color notes are available for individual specimens:

FMNH 232569 (Fig. 16 female, Río Zaña Study Site, 494 mm SVL): Dorsum medium rich brown with dark brown markings: a middorsal series of irregular spots and a lateral series forming oblique incomplete crossbands. Dorsal ground color lighter anteriorly than posteriorly. Head medium rich brown with dark irregular spots and markings on most scales. Gular region cream with dark brown peppering on lower labials (upper labials also have this peppering but the ground color is darker). Venter whitish anteriorly with large dark spots forming irregular, roughly parallel, series of broken lines on each side. Entire venter peppered with dark brown, which becomes denser posteriorly. Ventral surface of tail also peppered with dark brown. (Field notes of J. E. Cadle)

KU 121309 (Fig. 17. male, southern Ecuador, 351 mm SVL): Ground color medium brown extending to bottom of lower scale row; dorsum spotted and barred with darker brown, often edged with black; top of head medium brown with black spots; upper labials gray brown; chin white and dark brown; iris gray at top and bottom with broad brown band through it; tip of tongue black, remainder red. (Field notes of John D. Lynch)

KU 142804 (Fig. 18. male, southern Ecuador, 377 mm SVL): Dorsum brown with darker brown crossbars faintly outlined with creamy tan. Venter creamy white with black spots. Iris tan. (Field notes of William E. Duellman)

LSUMZ 27374 (male, northern Peru, 520 mm SVL): Dorsal ground color gray, markings black or very dark gray (gray-brown). Light flecking and isolated scales on edges of bands white. Venter paler gray with black spots and white spots, more extensive anteriorly. (Field notes of Richard Thomas for RT 3059)

Color in Preservative and Variation in Pattern. In preservative, the pattern elements (crossbands, head markings, ventral markings) remain distinct. In preserved specimens that have not lost the stratum corneum, the ground colors, crossbands, and other markings retain their brown color tones, although they are duller than in

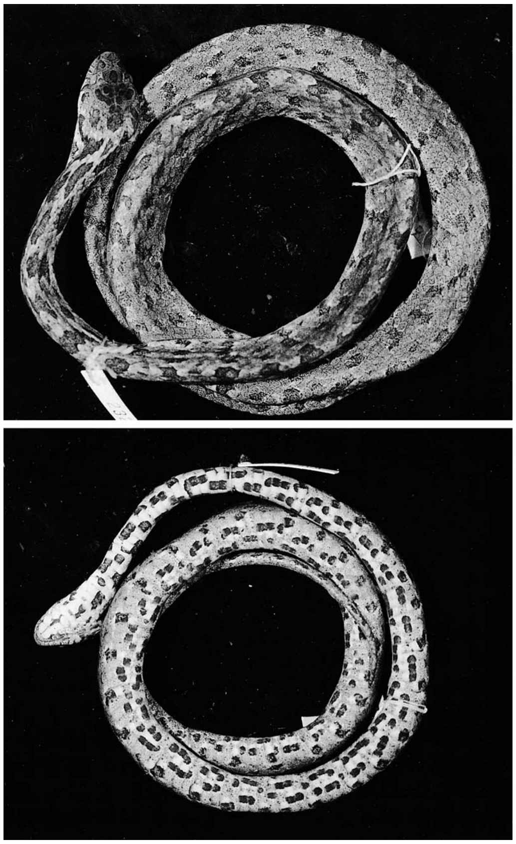

Figure 16. *Sibynomorphus petersi.* Dorsal and ventral views of FMNH 232569 (Río Zaña Study Site, Cajamarca Department, Peru). Female, 494 mm SVL. The crossbands in this specimen are fragmented into a series of irregular vertebral and lateral spots.

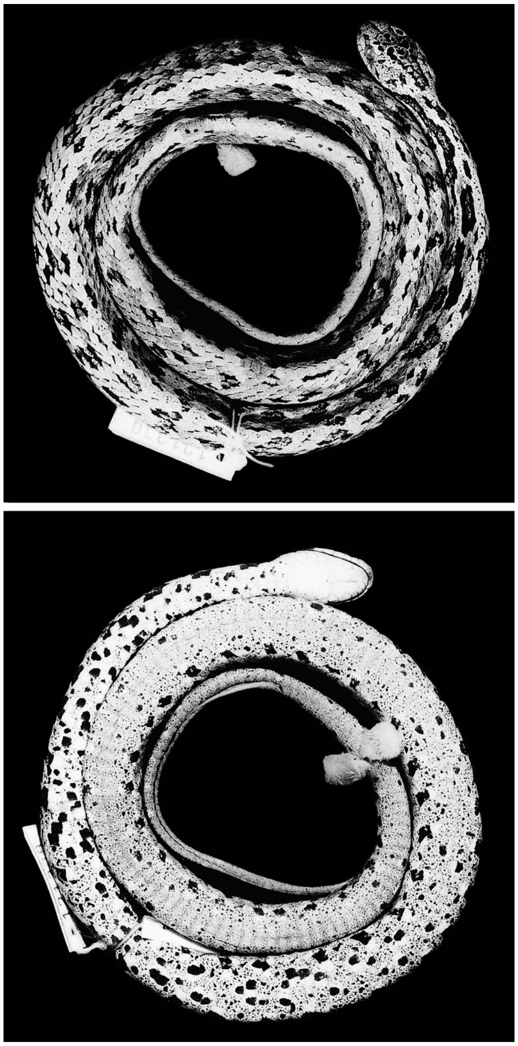

Figure 17. *Sibynomorphus petersi.* Dorsal and ventral views of KU 121309 (Loja Province, Ecuador). Male, 351 mm SVL.

life. With loss of the stratum corneum, the brown tones present in life are gray (in some older specimens, the ground color of such specimens is ash white). There is both sexual dimorphism and geographic variation in the number of crossbands on the body, as covered in previous sections.

Most specimens of *Sibynomorphus petersi* have a series of narrow zigzag or wavy crossbands that are complete across the dorsum (i.e., not alternating side to side). These crossbands usually have a very narrow light border and jagged edges (Fig. 14). A band on the nape and the following two to four crossbands are usually, but not always, broader than the others (Fig. 14). These anterior crossbands are sometimes incomplete across the vertebral line. Crossbands on the neck are occasionally absent and replaced by a broad longitudinal streak on each side (Fig. 18). In some individuals, the crossbands are fragmented laterally into a series of spots that can maintain the appearance of crossbands or are so fragmented that individual bands

Figure 18. *Sibynomorphus petersi.* KU 142804 (Loja Province, Ecuador). Male, 377 mm SVL. The dark streak on the side of the neck is characteristic of many specimens of *S. petersi.*

are difficult to discern, as described for three Peruvian specimens below.

The top of the head in *Sibynomorphus petersi* is brown or grayish brown with dark brown markings. A large discrete spot is present on each prefrontal (Fig. 19); although it varies in size, position, and shape, it is a constant feature of the pattern. Despite the variation in form, the prefrontal spots are sufficiently diagnostic of this species that specimens that otherwise differ greatly in pattern retain this character (compare Figs. 15, 19, 22, and the photos of corresponding dorsal patterns). Other large spots or reticulations are present on the frontal, parietals, and supraoculars; these can fuse with one another to form larger patterns (Fig. 19, lower right). In virtually all cases, the dark head markings have a narrow pale edge.

The venter has a whitish ground color with bold black or dark brown squarish or half-moon–shaped spots. These spots vary

Figure 19. *Sibynomorphus petersi.* Dorsal views of heads. Top: left, KU 142804; right, KU 121309; both from Loja Province, Ecuador. Bottom: left, FMNH 232569; right, BMNH 1900.3.30.19; both from Cajamarca Department, Peru. These specimens show the characteristic prefrontal spots in *S. petersi* and some of the variation in the size, shape, and position of the spots.

in density, from series arrayed at the lateral edges of each ventral plate (Fig. 14) to denser arrays all across the venter and occasionally arrayed into larger patterns of streaks (e.g., Figs. 13, 16). The venter is often heavily peppered with fine dark brown. The dorsal bands do not encroach onto the ventral plates or encroach only to their extreme lateral edges.

Individual scales in *Sibynomorphus petersi* are typically finely flecked with minute dark brown spots, which are best seen under magnification. These spots seemingly appear on any scales of the body (dorsal and ventral) or head, with some variation in their density among specimens. Figure 15 (top) shows the pattern on head scales particularly well; for some of the variation, see Figures 17 (bottom), 19, 22, and 23.

Three Peruvian specimens, SMF 80048 (Fig. 20), FMNH 232569 (Fig. 16), and stomach contents associated with a *Micrurus mertensi,* ANSP 31806 (see Fig. 26), lack discrete crossbands over most or all of the body. In FMNH 232569 and ANSP 31806, a series of vertebral spots marks the position of the crossbands, and indistinct lateral bars are visible when the specimens are submerged in alcohol in good light. These unbanded specimens otherwise retain characteristic pattern elements of this species, as elaborated below. Other Peruvian specimens are banded with some variation: bold bands present the whole length of the body and tail (e.g., Fig. 21) to specimens with narrow, somewhat fragmented bands (e.g., Fig. 27).

The color pattern in preservative of SMF 80048 (Figs. 20, 22), one of two southernmost specimens of *Sibynomorphus petersi* known and one of three unbanded specimens, is as follows: Dorsal pattern indistinct, with no discrete bands. Ground color (dorsally, ventrally, and on head scales) brown, each scale on all of these areas finely speckled with minute dark brown specks. A large round dark brown spot on each prefrontal positioned toward the midline (Fig. 22). A similar, but more smudged spot on the anterior end of each parietal, more smudged on the right than on the left side. Dark suture lines to many dorsal scales give the appearance of irregular flecking on the dorsum. Posteriorly these dark edges tend to align into diagonal lines, but anteriorly they are more irregular. Nowhere are there regular lines or bands. The gular region is yellowish and unpatterned except for a very few minute flecks. The venter is heavily marked with irregular to half-moon–shaped dark brown spots, more or less aligned into irregular rows. In addition, very fine dark flecks cover the venter. The ground color of the venter is paler and more yellowish brown than the dorsum (medium brown).

The smallest specimen examined (USNM 237040 from southern Ecuador, 184 mm SVL) still has an unfused umbilical scar. It has irregular crossbands over the dorsum similar to some adult patterns and otherwise does not differ substantially from the color pattern of adults. Thus, there is little or no ontogenetic change in color pattern.

To summarize, several features of the color pattern of *Sibynomorphus petersi* are relatively constant and are helpful in identifying this species: (1) Narrow zigzag crossbands with irregular edges, and often a longitudinal lateral neck bar. (2) A spot, usually rounded and of varying size and position, on each prefrontal scale. These spots are sometimes positioned toward the midline near the suture between the prefrontals and sometimes more laterally; they are usually on the posterior half of the prefrontals (Figs. 15, 19, 22, 23). Like other markings on top of the head, these spots are often surrounded by a narrow pale border. Even in specimens that otherwise differ greatly in pattern, including those lacking definitive crossbands on the dorsum, these spots are invariably present (Fig. 22). (3) Minute dark brown speckling on individual dorsal and ventral scales (e.g., Fig. 15, top). In specimens with less distinct dorsal bands, the bands are usually

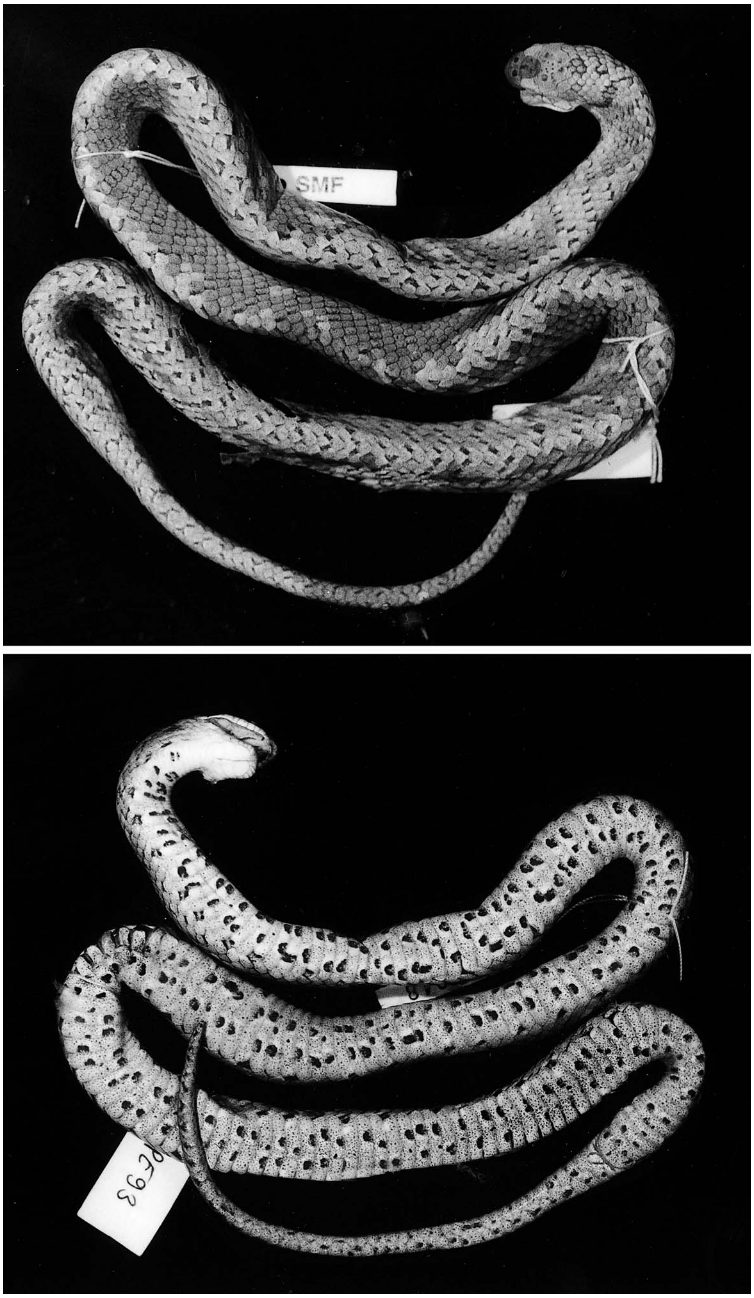

Figure 20. *Sibynomorphus petersi.* Dorsal and ventral views of SMF 80048 (Ancash Department, Peru). Female, 492 mm SVL. This is one of two southernmost specimens of *S. petersi* known. The specimen entirely lacks discrete crossbands, instead having a dorsal pattern of fine streaks and reticulations.

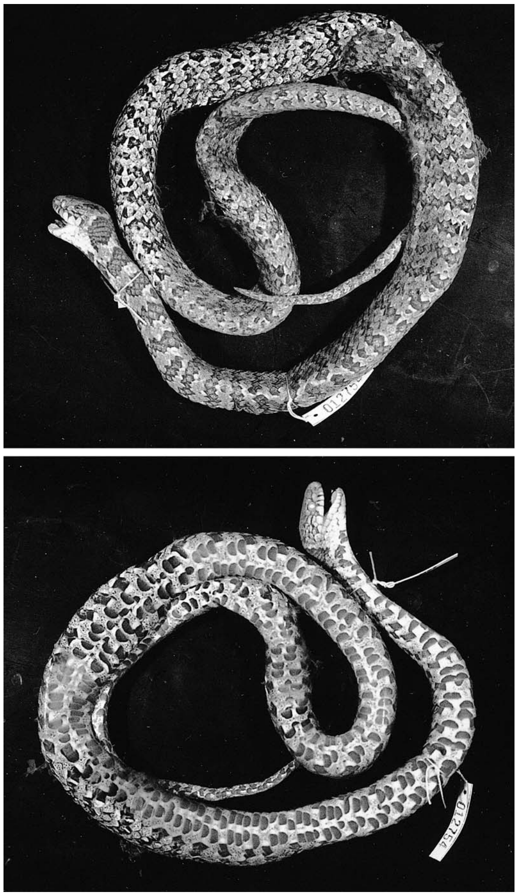

Figure 21. *Sibynomorphus petersi.* Dorsal and ventral views of MCZ 178047 (Bosque Cachil, Cajamarca Department, Peru). Female, 543 mm SVL. This specimen is more completely banded than most specimens of *S. petersi.*

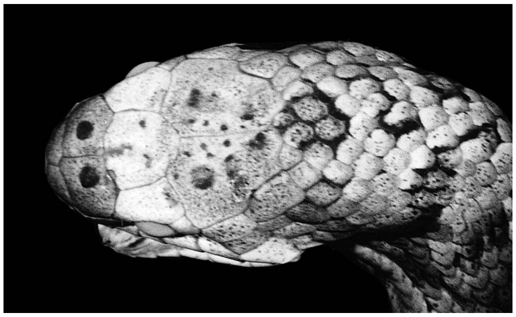

Figure 22. *Sibynomorphus petersi* from Ancash Department, Peru. Dorsal view of head (SMF 80048). The head is relatively unpatterned compared with most *S. petersi* (compare Figs. 19, 23) but still retains the characteristic prefrontal spots.

Figure 23. *Sibynomorphus petersi.* Dorsal and lateral views of head (MCZ 178047). The prefrontal spots in this specimen are exceptionally large and show the surrounding pale ring particularly well. Also visible are the minute dark specks that pepper individual scales on most specimens of *S. petersi* (especially visible on the posterior dorsal head scales and lateral scales around the jaw angle).

indicated as a discrete increase in the density of this characteristic dark peppering. (4) The venter is heavily marked with bold half-moons or squarish spots (Fig. 21), often in longitudinal arrays. In addition, the venter is often heavily invested with fine dark brown minute spots.

Etymology. Sibynomorphus petersi was named for James A. Peters, former curator in the Division of Amphibians and Reptiles at the National Museum of Natural History.

Hemipenis

Field-everted hemipenes were available for two specimens of *Sibynomorphus petersi*: KU 142804 (Loja Province, Ecuador) and LSUMZ 27374 (Piura Department, Peru). These organs are virtually identical and the following detailed description is based on KU 142804.

The hemipenis of KU 142804 is nonbilobed (single) and fully capitate (Fig. 24).

Figure 24. Hemipenis of *Sibynomorphus petersi* in sulcate view (KU 142804).

Total length of the organ is approximately 13 mm. Length of the capitulum on the sulcate side approximately 7 mm. The sulcus spermaticus divides within the capitulum and has more or less centrolineal branches, but each branch ultimately passes somewhat laterally to end at the outer (lateral) periphery of the tip of the organ. Proximally, the hemipenis has minute spines all over, although these are sparse, especially on the asulcate side. A battery comprising about three rows of enlarged hooked spines completely encircles the midsection of the organ just proximal to the capitulum. These spines are larger adjacent to the sulcus spermaticus than on the asulcate side.

The capitulum is completely ornamented with papillate calyces. Calyces are well developed, but proximally, the longitudinal connections between them tend to break down so as to give the appearance of weakly developed, but densely arrayed, flounces. The calyces are surmounted by large blunt papillae. Because the proximal calyces tend to be poorly formed, there is the appearance of about three rows of papillae (or papillate flounces) encircling the base of the capitulum. Probing with a fine needle suggests that these proximal papillae might be somewhat mineralized.

A very large nude pocket (3.5 mm long) is present on the lateral side of the organ (i.e., midway between the sulcate and asulcate surfaces); it extends from the very base of the organ to the battery of spines on the midsection. The pocket has thickened borders, which are especially prominent at the middle of the pocket. A small, but distinct, fleshy lobe is present on the asulcate side of the pocket slightly more distal than its midpoint. Distally, the pocket is bordered by two large hooked spines on one side and a similar spine on the other. These spines are larger than any of those in the midsection battery and are positioned at the proximal border of the battery. In LSUMZ 27374, the spines at the distal edge of the nude pocket are not as closely associated with the pocket as in KU 142804. In particular, the large pair of spines on the asulcate edge of the nude pocket could be viewed in either specimen as having no special association with the nude pocket.

Distribution and Natural History

Sibynomorphus petersi is known from southwestern Ecuador (Azuay and Loja Provinces) and northern Peru south to southern Ancash Department (10°09′S) (Fig. 25; see also Fig. 43). The Ecuadorian localities and all Peruvian localities except one are on the Pacific versant of the Andes. MUSM-JEC 12884 documents that the species also occurs east of the continental divide in the Río Chotano drainage, which flows northward and joins the Río Huancabamba to form the Río Chamaya, a western affluent of the Río Marañón. The documented elevational range is 1,457–2,250 m for Ecuadorian localities and 1,250–3,120 m for Peruvian localities.

Two specimens of *Sibynomorphus petersi* were obtained at the Río Zaña Study Site (Cajamarca Department, Peru). FMNH 232569 was found at midmorning recently killed on a trail through secondary growth (brushy hillsides, agricultural land) on 2 May 1987 (early dry season). The freshness of the specimen on a hot day suggests that it might have been active during the day when killed. Another spec-

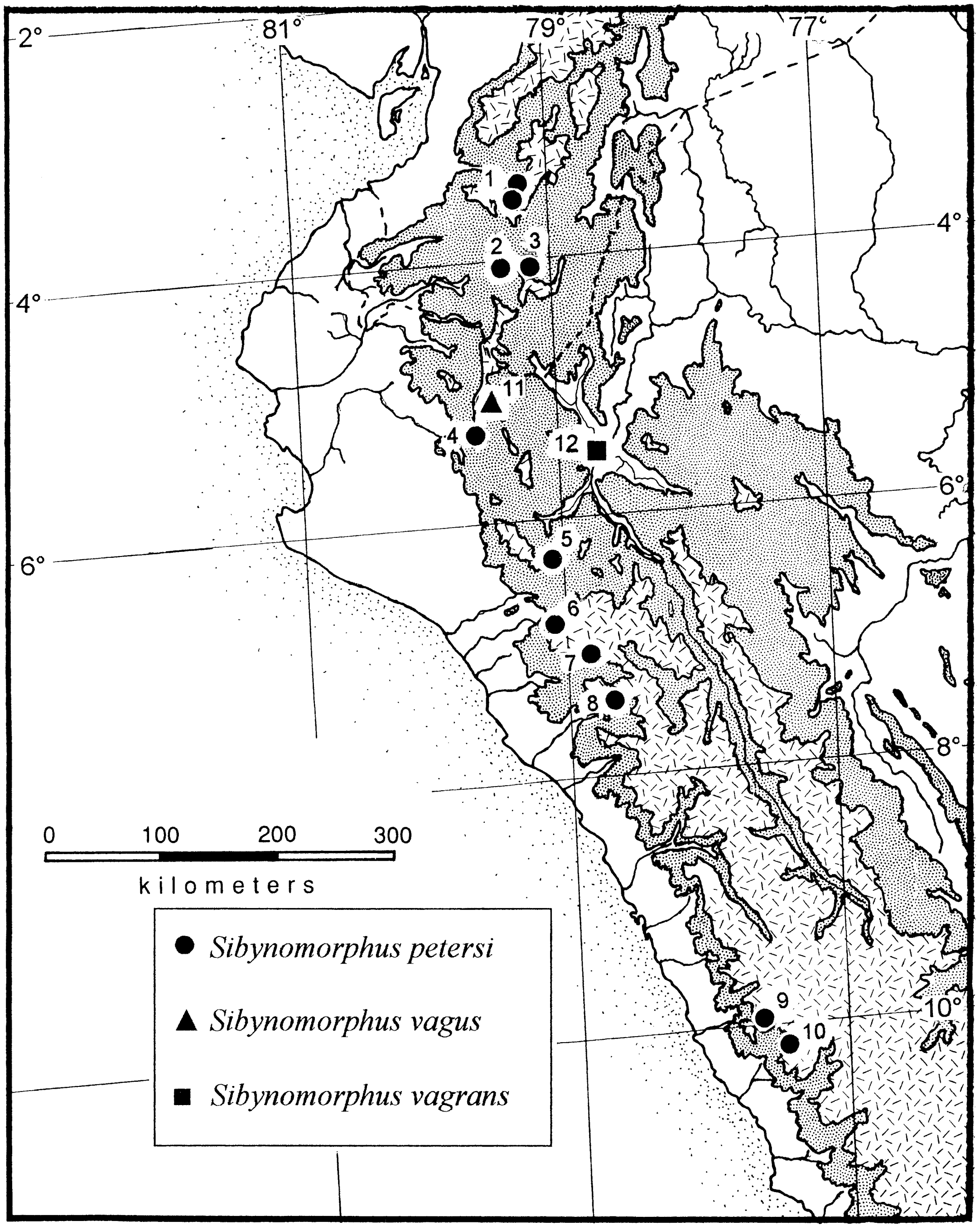

Figure 25. Distributions of *Sibynomorphus petersi, S. vagrans,* and *S. vagus* in southern Ecuador and northwestern Peru. All known localities are plotted (locality 3 represents multiple contiguous localities). See Figure 43 for amplification of the southern portion of the distribution of *S. petersi* (Ancash Department, Peru). Stippled area is above 1,000 m; hatched area is above 3,000 m. Numbers are locality records, as follows: ***Sibynomorphus petersi*:** *Ecuador*: (1) Zhila (type locality, north) and El Tablón (south); (2) Río Catamayo valley; (3) Loja city and vicinity (multiple localities); *Peru*: (4) Canchaque; (5) Paraguay, Río Chotano (Amazonian versant); (6) Río Zaña Study Site; (7) San Pablo; (8) Bosque Cachil; (9) Malvas; (10) Cajacay. ***Sibynomorphus vagus*:** *Peru*: (11) Huancabamba. ***Sibynomorphus vagrans*:** *Peru*: (12) Bellavista.

imen from the Río Zaña Study Site had been swallowed head first by a *Micrurus mertensi,* ANSP 31806 (Fig. 26). The *Micrurus* is 573 mm SVL (total length 652 mm) and the *Sibynomorphus* (not separately catalogued) is approximately 465 mm SVL (total length 613 mm); the specimen was collected by a local resident in early November 1988 (late dry season/transition to rainy season).[11] MCZ 178047 was collected 12 October 1992 at Bosque Cachil at the edge of the humid forest; Cadle and Chuna (1995) and Sagástegui et al. (“2003” [2004]) describe this forest.

MUSM-JEC 12884, a road kill in poor condition, was collected 10 August 1994 near Paraguay in the Río Chotano valley (Cajamarca Department, Peru) and is the only specimen from the Amazonian versant (Fig. 25). This area once harbored extensive montane humid forests, but by 1994, these forests had been reduced to scattered patches, mainly on steep hillsides and in riparian strips. Otherwise, pasture and agricultural land were extensive. The area was dissected by rocky streams with occasional waterfalls. My field notes described the forest as “rich tropical montane humid forest with abundant tree ferns and large bromeliads. Canopy 20–30 m high, with some palms. Abundant epiphytes with a diversity of orchids. Secondary growth forest on some steep hillsides in areas of former landslides.” MUSM-JEC 12884 was collected in a deforested area.

Ancillary field data accompany a few other specimens of *Sibynomorphus petersi.* KU 142804 was collected 23 July 1971 at the base of an agave plant growing on a mud fence by day. KU 121309 was collected 12 June 1968 underneath a rock buried in soil along the edge of a stream. LSUMZ 27374 was found 1 December 1974 by day under a log in a partly overgrown pasture (Richard Thomas, field notes). SMF 80048 was collected 2 February 1997 under a rock exposed to the sun (Lehr et al., 2002: 383).

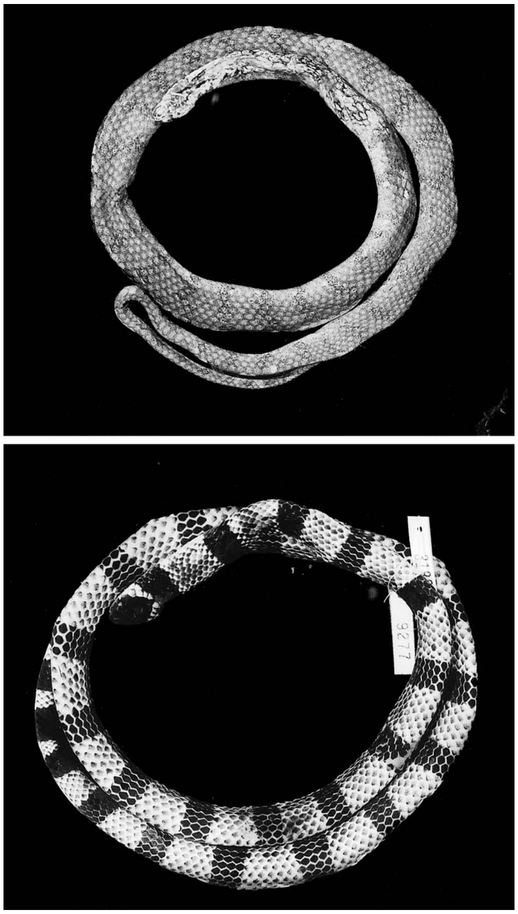

Figure 26. Prey and predator: *Sibynomorphus petersi* (top) from the stomach of *Micrurus mertensi* (bottom; ANSP 31806). Both photos are to the same scale. Approximate total length of the *Sibynomorphus* is 613 mm. Total length of the *Micrurus* is 644 mm. The dorsal crossbands in the *Sibynomorphus* were visible only under alcohol and in good light.

The first specimen of *Sibynomorphus petersi* to make its way into collections from Peru is BMNH 1900.3.30.19 (Figs. 15, 19, 27), collected at San Pablo, Caja-

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[11] The *Sibynomorphus* is intact except that scales covering the head and approximately the anterior 25–30 mm of the body are digested away. The specimen has very indistinct crossbands and the diagnostic aspects of head pattern could not be evaluated. Ventral counts and body measurements were determinable within narrow limits because the exposed vertebral column and skull were still intact; however, no head scales remained.

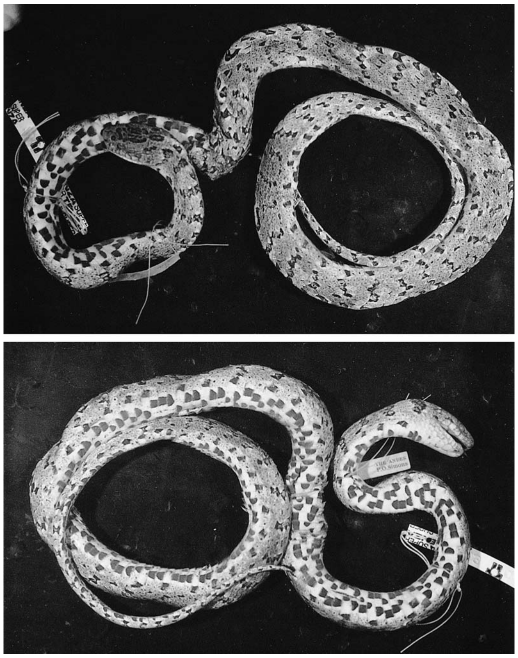

Figure 27. *Sibynomorphus petersi.* Dorsal and ventral views of BMNH 1900.3.30.19 (San Pablo, Cajamarca Department, Peru). Female, 595 mm SVL.

marca Department by Perry O. Simons on 5 November 1899 (the date comes from Simons' itinerary published by Chubb, 1919; see Cadle, 1998: footnote 6). Simons' South American herpetological collections were described by Boulenger (1899, 1900, 1901, 1902a,b), but he mentions no snakes other than *Philodryas simonsii, Homalocranium marcapatae* (= *Oxyrhopus marcapatae*), and two species of *Elaps*: *E. simonsii* (= *Micrurus pyrrhocryptus*) and *E. regularis* (= *M. annellatus*). I visited San Pablo and vicinity 16–17 August 1994, and my field notes indicate that "all natural habitat in the broader area has been destroyed—now only agricultural land, secondary forest, and some brushy vegetation along fence rows . . . few streams. . . . Vegetation included much *Eucalyptus* and *Opuntia* as well as cultivated agaves. Terrain [was] very steep and at this time very dry."

Two females from southern Ecuador (BMNH 1924.6.24.110, 550 mm SVL, 720 mm total length; BMNH 1933.6.24.110, 541 mm SVL, 711 mm total length), dates of collection unknown, each contained five large eggs (determined by palpation). The smallest specimen examined (USNM 237040, 184 mm SVL) still has an unfused umbilical scar and was collected 2 August 1954.

The region of southern Ecuador and northern Peru from which *Sibynomorphus petersi* is known has a complex topography and, consequently, a diversity of environments, including relatively arid inter-Andean valleys (e.g., Río Catamayo) and humid forests on the Andean slopes (Chapman, 1926). Few specific data are available for the ecological distribution of *S. petersi* within this region, although some localities (e.g., the Río Catamayo valley of southern Ecuador and the slopes of the Andes in southern Ancash Department, Peru) are relatively more arid than others (e.g., Río Zaña Study Site and the single known locality on the Amazonian versant). Orcés and Almendáriz (1989: 59) reported the following concerning the Ecuadorian localities for *S. petersi* (see also the species account for *S. oligozonatus*):

> The places . . . ecologically correspond to the life zone of Lower Montane Dry Forest . . . that Chapman called Arid Temperate. Annually, rainfall reaches 500 to 1000 mm. Geographically, to this zone belong the dry plains and canyons of the inter-Andean valleys (toward the interior basins), at altitudes between 2000 and 3000 m above sea level, in the edges of the Lower Montane spiny steppes and Lower Montane humid forest. The natural vegetation . . . has been replaced by cultivated land and there remain few areas covered by *algarrobos.*

In Peru, several localities for *Sibynomorphus petersi* are associated with remnants of humid forests occupying the western Andean slopes or (one specimen) the more humid eastern slopes. Three localities (Canchaque, Río Zaña Study Site [= Bosque Monteseco], and Cachil) are among the best studied and most diverse humid forests on the western slopes of the Andes in Peru (Dillon et al., 1995; Sagástegui et al., "2003" [2004]). Although these are humid forests (with abundant epiphytes and other indicators), the region experiences a pronounced dry season as well. Cadle and McDiarmid (1990: 765–766) and Cadle (2005: 70–71) gave general descriptions and climatic regimes of the Río Zaña Study Site, and Cadle and Chuna (1995: 21–24) described Bosque Cachil.

The two specimens of *Sibynomorphus petersi* from the Río Zaña Study Site are from an area of transition (1,250–1,400 m) between the humid forests on the slopes (above about 1,500 m) and the dry forest characteristic of lower elevations (<1,000 m). Whether *S. petersi* occurs at lower elevations within the dry forest zone is unknown. Despite intensive sampling within humid forests between 1,500 and 2,500 m at the Río Zaña Study Site,[12] the species was not obtained at these elevations, suggesting that it might be more characteristic of the transition zone or the dry forest itself. The three specimens from the Río Zaña Study Site and Bosque Cachil were collected in the early and late dry season (May, October, November). The only specimen from the Amazonian versant, MUSM-JEC 12884, was collected 10 August 1994; the Amazonian versant is more continually humid than the Pacific versant.

A specimen collected by Richard Thomas (LSUMZ 27374) was obtained as part of faunal studies undertaken by the LSUMZ beginning in 1974, when Thomas and Theodore A. Parker III established a camp near the summit of the Cordillera de Huancabamba (3,050 m) and worked on the western slope of the cordillera in late November and early December (approximately the transition between the dry and rainy seasons). LSUMZ 27374 was collected at 2,073 m. Parker et al. (1985: 170), under the name "Cruz Blanca,"[13] described the general environment:

> The west slope was covered by a mixed evergreen forest (including *Clusia, Oreopanax, Podocarpus,* and *Polylepis*). . . . Human pressure on this habitat is increasing . . . and forest is being cleared from above and below. Only scattered patches of forest exist below 2150 m. A mule trail descends about 1000 m from Cruz Blanca through mature forest, continuing downward through cleared lands to Canchaque. We worked the forest along this trail almost daily during our visits. Treeline forest is dominated by *Polylepis,* with a canopy 4 to 6 m high. Taller trees cover the lower slopes and stream valleys. Arboreal bromeliads are conspicuous, but tree ferns are absent (or very scarce), and *Chusquea* bamboo is uncommon. . . . Foggy, cloudy weather occurred regularly on all three visits.

Lehr et al. (2002) characterized Malvas and Cajacay (Ancash Department; SMF 80048, MUSM 20583), two localities from which they obtained specimens, as "montane steppe." Their photograph (Lehr et al., 2002: fig. 10) of the environment at Malvas shows open, mountainous terrain with shrubs, agaves, and eucalyptus trees. Lehr et al. (2002) described montane steppe as having "an arid climate with increases in precipitation and decrease in temperature during the [austral] summer. . . . The vegetation is sparse and forest negligible in extent."

Sibynomorphus petersi is sympatric with *S. oligozonatus* in southwestern Ecuador (see account for *S. oligozonatus*). *Sibynomorphus petersi* is also broadly sympatric with another dipsadine, *Dipsas oreas,* and the two species' geographic ranges are very similar (Fig. 25; Cadle, 2005: fig. 23). *Sibynomorphus petersi* and *D. oreas* are known to be sympatric at two localities on the western slope of the Andes in northern Peru: the Río Zaña Study Site (Cajamarca Department) and between Canchaque and the summit of the Cordillera de Huancabamba (Piura Department). However, the

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[12] Field work at the study site covered 55 days during the early dry season (May–June 1989) and 18 days during the rainy season (January 1991). A basecamp was established at 1,800 m within the humid forest and collections were made from about 1,000–3,000 m, with greater emphasis between 1,500 and 2,500 m.

[13] These forests are referred to under the name "Canchaque" or "Bosque Canchaque" in much of the floral and faunal literature on this area (e.g., Cadle, 1991; Dillon et al., 1995; Sagástegui et al., "2003" [2004]).

two species might be segregated by habitat, with *S. petersi* occurring in more mesic to arid habitats than *D. oreas* (see footnote 7).

Sibynomorphus vagrans **(Dunn)**
Figures 28–32

Pseudopareas vagrans Dunn, 1923: 187. Type locality: "Bellavista [Cajamarca Department], Peru." Holotype, MCZ 17284.

Pseudopareas vagus vagrans: Amaral, "1929"a [1930]: 33; "1929"b [1930]: 201; "1929"c [1930]: 75.

Sibynomorphus vagrans: Peters, 1960: 161, pl. IVe; 1965: 13. Orcés and Almendáriz, 1989. Scrocchi et al., 1993. Carrillo de Espinoza and Icochea, 1995.

Sibynomorphus vagrans is known only from the type series collected by G. K. Noble, all from Bellavista and originally catalogued in the Museum of Comparative Zoology. Noble's series originally comprised the holotype and 26 paratypes, of which some were exchanged to other collections (see footnote 25). I am aware of one other specimen from a "Bellavista" whose reference to *S. vagrans* is highly questionable (MUSM 2258); it is discussed separately at the end of this species account and is not included in the diagnosis and description of *S. vagrans* presented here.

Notes on the Holotype of *Sibynomorphus vagrans*

The holotype of *Sibynomorphus vagrans* (MCZ 17284) is an adult female in good condition, 557 mm total length, 425 mm SVL. Tail (132 mm) 23% of total length. Dorsal scales in 15–15–15 rows, 156 ventrals, anal scale single, and 73 subcaudals. Preoculars 1/2, postoculars 2/2, temporals 1 + 2 + 3 on each side. Supralabials 10 with 4–6 touching the eye on the left, 8 with 4–5 touching the eye on the right. Infralabials 12/12. One pair of infralabials is in contact behind the mental and there are three pairs of polygonal chin shields.

Diagnosis

Sibynomorphus vagrans is a brownish or grayish snake with a variable number (5–10) of broad dark crossbands anteriorly, much wider than the interspaces, and a posterior pattern consisting of an obscure network-like pattern, irregular flecks, or narrow, somewhat indistinct, irregular crossbands (much narrower than interspaces) (Fig. 28). The venter is unmarked (most specimens) or has a few dark spots that never form dense arrays. This species has a relatively low number of ventrals (149–155 in males, 154–159 in females) and relatively high number of subcaudals (80–87 in males, 72–79 in females). The top of the head is ornately patterned and the nape has a narrow pale collar with a characteristic obtuse angular shape.

Sibynomorphus vagrans is distinguished from all other species of the genus in northern South America by its combination of relatively low ventral counts and high subcaudal counts (Table 1). *Sibynomorphus vagus* is similar to *S. vagrans* in ventral counts but lacks well-defined crossbands anteriorly (and they are narrower than interspaces when present), lacks a pale nape collar, and has fewer subcaudals (60–65 in males, 56–60 in females). In addition, *S. vagrans* has a longer tail on average (25–29% of total length in males, 23–26% of total length in females) than *S. vagus* (23–24% in males, 20–21% in females).

Distinct broad anterior crossbands similar to those of *S. vagrans* are found only in *S. oligozonatus* and *S. williamsi*. *Sibynomorphus oligozonatus* differs from *S. vagrans* in having a foreshortened snout (compare Fig. 4 and Figs. 30, 31), fewer subcaudals, and fewer supralabials (6–7 vs. 8–9 in *S. vagrans*). *Sibynomorphus williamsi* differs from *S. vagrans* in having 6 supralabials (3–4 touching the eye) compared with 8 (usually) with 4–5 touching the eye in *S. vagrans,* higher ventral counts (173–188), lower subcaudal counts (56–73), and in *S. williamsi,* the dorsal crossbands are distinct virtually the entire length of the body (sometimes dorsal saddles and alternating lateral blotches posteriorly). *Sibynomorphus oneilli* differs

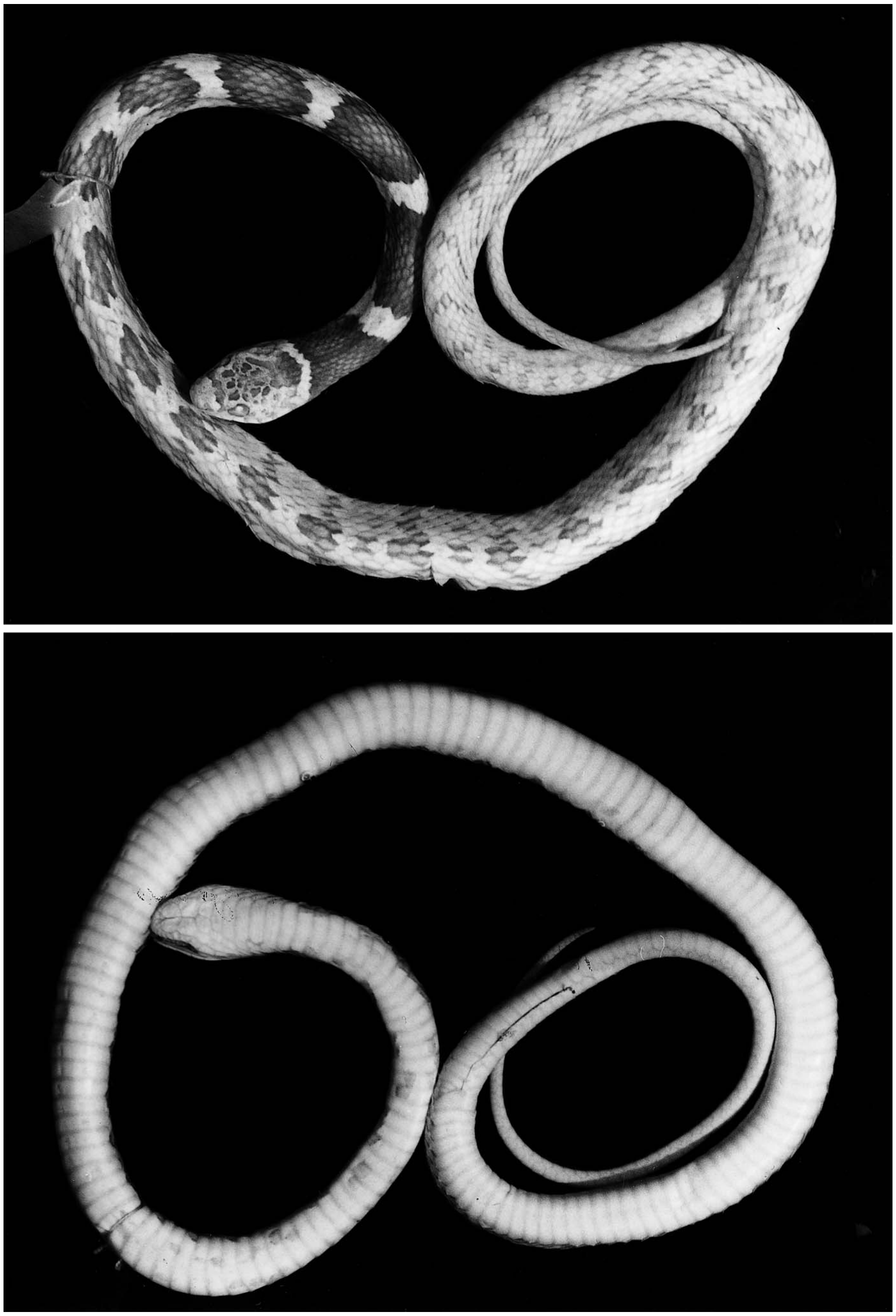

Figure 28. *Sibynomorphus vagrans* Paratype (MCZ 17439). Male, 387 mm SVL.

from *S. vagrans* in having more ventrals (≥152 in males, ≥160 in females), fewer subcaudals (62–77 in males, 57–64 in females), a shorter tail (22–26% of total length in males, 20–22% in females), a less ornately patterned head, narrower anterior dorsal crossbands, and a venter heavily marked with bold black spots. *Sibynomorphus petersi* differs from *S. vagrans* in having more ventrals (>160), a primarily brown dorsum with narrower crossbands (when present), interspaces brown (compared with whitish in *S. vagrans*), and a venter densely patterned with dark brown markings.

Description

Size and Scutellation. Descriptive data for *Sibynomorphus vagrans* are presented in Table 1. The largest specimen is the female holotype, 557 mm total length, 425 mm SVL. The largest male is 543 mm total length, 387 mm SVL. Tail 25–29% of total length in males, 23–26% of total length in females. Body moderately compressed. Dorsal scales smooth and in 15–15–15 rows. The vertebral row is not enlarged or only very subtly enlarged compared with paravertebral rows. Ventrals 149–155 (averaging 151) in males, 154–159 (averaging 157) in females (but see Table 1, footnote 2). Anal single. Subcaudals 80–87 (averaging 83) in males, 72–79 (averaging 74) in females. The loreal and a single preocular border the eye in most specimens (preocular superior to the loreal); the loreal is longer than tall. In three specimens, the loreal is vertically divided, resulting in a small triangular or trapezoidal preocular in addition to the usual one between the eye and the prefrontal scale. Postoculars 2 or, rarely, 3. Primary temporals usually 2 (occasionally 1 or 3). Secondary temporals 2 or 3. Tertiary temporals usually 3 (occasionally 4). Supralabials usually 8 (rarely 9 or 10) with 4–5 bordering the eye (rarely 4–6 or 3–5). Infralabials usually 11 or 12 (range 9–13). One pair of infralabials in contact behind the mental in all specimens ($N = 18$). Generally 3 pairs of chin shields (16 specimens); occasionally 2 pairs (2 specimens) or 2.5 pairs (1 specimen). Maxillary teeth 15–17 ($N = 9$). The pupil is prolate (Myers, 1984) in preserved specimens.

Peters (1960: 162–163), who examined five specimens not seen in this study (see footnote 25), noted individual variations in scutellation within *Sibynomorphus vagrans* that were not observed in my sample. The only consequential difference between Peters' (1960) description and the one here is that Peters indicated the range of subcaudals for male *S. vagrans* as 74–87 (my data: 80–87). There are a few discrepancies between my description and Peters' (1960) on one hand, and the original description (Dunn, 1923: 187–188). Dunn reported a range in ventral counts (sexes combined) of 142–155, whereas Peters' count (149–160) and mine (149–159) are nearly identical. Dunn reported the maxillary tooth count as "about 12 equal teeth," whereas my counts for nine specimens were 15–17 and Peters' for 11 specimens were 14–18. Dunn reported that one specimen had a divided anal scale; this specimen is probably MCZ 17444, which has a partially divided anal plate.

Sibynomorphus vagrans exhibits typical patterns of sexual dimorphism for colubrids. In comparison to females, males have significantly fewer ventrals ($t = 6.692$, df = 17, $p < 0.0001$), significantly more subcaudals ($t = 7.892$, df = 17, $p < 0.0001$), and greater relative tail lengths (Table 1).

Color in Life. Unknown. Dunn (1923: 188) used the expression "belly yellow" in describing the holotype, which might reflect the ventral color still apparent when he described the species. The venter of the type series as of 2003 was grayish white.

Color in Preservative. The color pattern of *Sibynomorphus vagrans* is very consistent among the specimens examined. All specimens have a series of five to 10 broad, bold dark brown crossbands anteriorly that become narrower and increasingly frag-

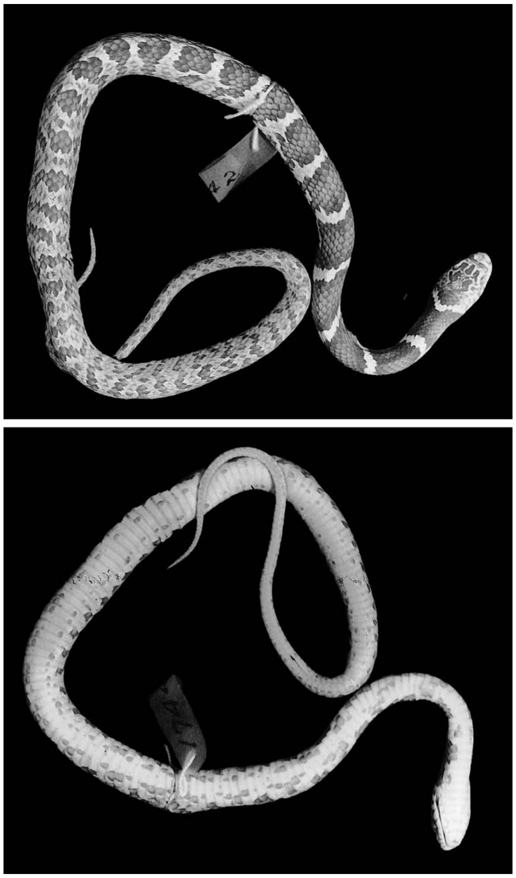

Figure 29. *Sibynomorphus vagrans* Paratype (MCZ 17442). Male, 230 mm SVL.

mented posteriorly (Figs. 28, 29). The anterior crossbands are widest middorsally (generally spanning 5–9 middorsal scale rows) and narrower laterally (spanning 3–6 dorsal rows). The bands in some specimens have a distinctly darker brown narrow border (Figs. 28–30). Bands extend ventrally to the outer edge of the ventral scales. The first dorsal crossband is separated from the dark spotting on the top of the head by a distinct narrow (2 scales or less) whitish collar just posterior to the mouth commissure; the collar connects to the pale gular region on each side and forms a characteristic obtuse angle middorsally with the vertex directed posteriorly (Fig. 30). In MCZ 17447, the first crossband behind the head is interrupted middorsally and thus forms an elongated blotch on each side of the neck; the crossbands in other specimens are complete across the dorsum. The dorsal ground color is dull grayish brown. The venter of most specimens is immaculate (dull grayish or whitish), but some specimens have a variable amount of dark brown flecks or spots, especially concentrated toward the outer edges of the ventral scales.

The top of the head is ornately marked with irregular dark brown spots and blotches (Fig. 30). A consistent feature of the head pattern is a broad, irregular band extending across the posterior edge of the prefrontals, curving over the canthus, and extending ventrally to the top half of the loreal scale (Figs. 30, 31). This band is interrupted at the suture line between the prefrontals in some specimens (Fig. 30, lower left) and occasionally on the lateral portion of the prefrontals on one or both sides (Fig. 30, upper right). Nonetheless, it is a consistent feature of head pattern in all the specimens examined. The supralabial sutures are outlined with dark brown in all specimens and the same is true for the infralabial sutures in most specimens; in a few specimens, the sutures of the chin shields and other gular scales are also marked.

Three small juveniles (MCZ 17446, 17451–52; SVLs of 181, 163, and 147 mm, respectively) do not differ in color pattern from adults. MCZ 17451–52 still have obvious umbilical scars, so the pattern probably does not change ontogenetically.

Etymology. Dunn (1923: 187) did not elaborate on the meaning of his species epithet, saying only that *Sibynomorphus vagrans* was "a species closely allied to [*S. vagus*] but quite distinct." To reflect his supposition that the two species were closely related, Dunn might have used the name *vagrans* (originally of Anglo-French and Germanic origin) because it is a latinized cognate associated with the Latin word *vagus* (meaning wandering or roaming or indefinite; from *vagor,* to wander).

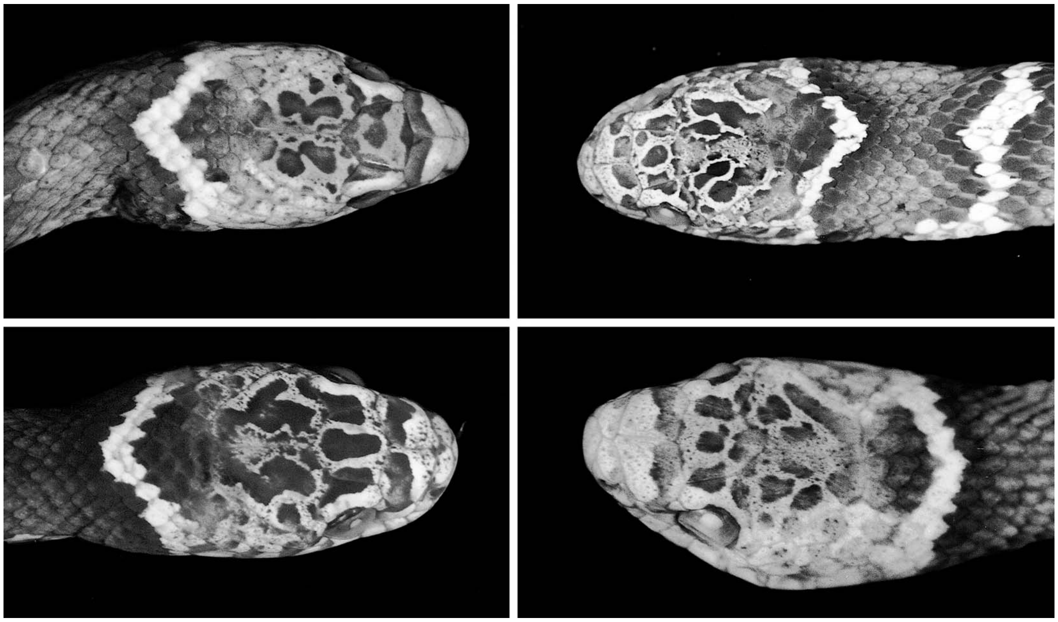

Figure 30. *Sibynomorphus vagrans.* Dorsal views of heads. Top: MCZ 17436 (left), MCZ 17440 (right). Bottom: MCZ 17442 (left), MCZ 17439 (right). These illustrate the ornate patterning atop the head of this species and two characteristic features of the pattern: an angular pale nape collar and a narrow dark band across the posterior portions of the prefrontal scales. The prefrontal band is complete in MCZ 17436 (top left) and shows varying degrees of interruption in the other three (see also Fig. 31).

Figure 31. *Sibynomorphus vagrans.* Lateral views of heads. MCZ 17436 (top), MCZ 17442 (bottom). The ventrolateral portion of the dark prefrontal band is visible immediately in front of the preocular and extending to the upper edge of the loreal (see Fig. 30, left upper and lower).

However, the similarity between the two species ends there if my supposition that the name of *S. vagus* refers to its color pattern (see *Description* in its species account), because the color pattern of *S. vagrans* bears little resemblance to that of *S. vagus.*

Hemipenis

Inverted Hemipenis. The following description of the hemipenis of *Sibynomorphus vagrans* is based on the inverted organ of MCZ 17438, an adult male, 381 mm SVL. The organ extends to the suture between subcaudals 6 and 7. It is slightly bilobed, dividing at the level of the proximal edge of subcaudal 6. Total length of organ 12.5 mm, bilobed distally for approximately 1 mm. The major retractor muscle is divided proximally for 1–1.5 mm.

The hemipenis is capitate, and the capitulum bears well-developed papillate calyces. The sulcus spermaticus is on the dorsal surface of the inverted organ and divides just within the capitulum; its tips end just short of the distal tip of the organ. The undivided portion of sulcus spermaticus is 5–5.5 mm in length; the divided portion is 6–6.5 mm in length. Proximal to the capitulum is a broad battery of robust spines encircling the entire organ; the battery is about three spines in width adjacent to the sulcus, broadening to about four or five spines in width on the asulcate side. The battery is separated from the capitulum by a narrow gap on the asulcate side, whereas the battery approaches the capitulum adjacent to the sulcus spermaticus. Proximal to the battery of enlarged spines, the hemipenis is ornamented with minute spinules, including the borders and lobes adjacent to a basal nude pocket.

The basal nude pocket is 4 mm long and extends from the base of the organ to the battery of spines. The pocket is located in the dorsomedial wall of the inverted organ and thus is probably somewhat lateral in the everted organ. On its asulcate edge, the pocket is bordered by a prominent lobe on its proximal half and a somewhat smaller lobe on the sulcate edge.

Everted Hemipenis. The left hemipenis of MCZ 17439 (adult male, 387 mm SVL) was everted from a preserved specimen according to techniques described by Myers and Cadle (2003) (Fig. 32). Before eversion, the hemipenis extended to the distal half of subcaudal 8. It was slightly bilobed, dividing at the suture line between subcaudals 7 and 8. Total length of the uneverted organ was 15.5 mm, divided for approximately 1 mm. The retractor muscle was divided for about 1 mm, each tip inserting onto a lobe of the hemipenis. After eversion, the hemipenis measured 16 mm total length. The divided portion of the sulcus spermaticus was 7.5 mm in length.

Figure 32. Hemipenis of *Sibynomorphus vagrans* in sulcate (left) and asulcate (right) views (MCZ 17439). This hemipenis was manually everted with the use of methods detailed by Myers and Cadle (2003).

The everted hemipenis is nonbilobed or only very slightly bilobed, fully capitate, and with the sulcus spermaticus dividing within the capitulum. The lobes appear asymmetrical in the preparation (Fig. 32), but this very likely reflects a puncture in one of the lobes and its consequent lack of full inflation. The capitulum is ornamented with well-developed calyces surmounted by spinulate papillae. Proximal spinules are longer and apparently more mineralized than distal ones. A fringe of spinules borders the proximal overhang of the capitulum.

The sulcus spermaticus is more or less centrolineal but the tip of each branch passes somewhat laterally to lie nearly on the lateral sides of the lobes. The tips of the branches end on the outer periphery of the lobes, short of the center of the apex of the organ. Proximally, the hemipenis is ornamented with minute spinules. The midsection of the hemipenial body is ornamented with a battery of large, relatively straight spines encircling the organ; this battery is about three spines across adjacent to the undivided portion of the sulcus spermaticus and about four spines across on the asulcate side. Individual spines are relatively long, narrow, straight, and hooked only at their tips (in contrast to the robust, strongly hooked spines typical of many colubrid hemipenes, including other *Sibynomorphus*). Proximal to the battery of spines on the asulcate side, but not clearly separated from the battery, are two large, hooked spines that are larger than those in the battery. A similar large spine is present near the undivided portion of the sulcus spermaticus.

A large nude pocket (total length 4 mm) is present basally on the lateral surface of the hemipenis; its distal end is bordered by the large hooked spines just mentioned. The pocket is also bordered on each side by a well-developed lobe, the asulcate lobe somewhat larger than the sulcate lobe. The entire basal portion of the organ below the encircling battery of spines (including the lobes on either side of the nude pocket, but not the pocket itself) is ornamented with minute spinules.

Distribution and Natural History

Sibynomorphus vagrans is known only from the type locality, Bellavista, Cajamarca Department, Peru, which lies at 421 m elevation in the subhumid inter-Andean valley of the Río Marañón (Amazonian versant) (Fig. 25). Dixon and Huey (1970: 38) described the general environment around Bellavista as "thorn scrub . . . [with] standing dead *Cereus* [columnar cactus]", although Dixon (personal communication, March 2007) stated that the area was wet enough to support coffee plantations; Dixon did not obtain *S. vagrans* at Bellavista 21–28 November 1968. Noble (1921) included a photographic appendix which shows "The [Río] Marañón at Bellavista"; his caption states that "the valley of the Marañón above Tutumberos [Amazonas Department on the Río Marañón a few kilometers downstream from Bellavista] is decidedly barren except for the cane and the dense thickets that crowd the river banks" (Noble, 1921: 493). All known specimens of *S. vagrans* were obtained by G. K. Noble, who collected around Bellavista in September 1916. Two specimens (MCZ 17451–52; SVLs 163 and 147 mm, respectively) have obvious umbilical scars and probably represent young of the year.

Sibynomorphus vagrans comes from a region frequently traveled by field biologists in northern Peru (e.g., Dixon and Huey, 1970; Dixon and Wright, 1975) because it lies along the main route from the coast to the upper Río Marañón, the stepping stone to the northern Peruvian Amazon. That the species is known only from specimens collected at the type locality nearly a century ago suggests that it might have a very localized distribution. Supporting this suggestion is that Noble did not obtain *S. vagrans* at another locality close to Bellavista—Perico—only about 35 km from Bellavista on the same side of the Río Marañón. The MCZ catalogues record more than 750 reptiles obtained by Noble at Bellavista and more than 300 at Perico.

According to his field notes and Noble (1921), Noble used local resident collectors ("frog hounds") to obtain specimens on the 1916 expedition to Peru. He obtained 27 specimens of *Sibynomorphus vagrans* at Bellavista (it was the most abundant snake in the collection), which suggests that the species was relatively common at that time. These specimens account for more than twice as many as the next most abundant snake represented in the Bellavista collection (12 specimens of *Leptodeira septentrionalis*; see Duellman, 1958: 80), and 41% of the total number of snakes from that locality (66 specimens representing seven species of snakes according to the online catalogue of the MCZ collection).

An Enigmatic Specimen from "Bellavista" Referred to *Sibynomorphus oneilli*

Apart from the type series, MUSM 2258 (Fig. 33) is the only specimen known to me that has been referred to *Sibynomorphus vagrans* (as reflected in the MUSM catalogues). According to the MUSM catalogues, MUSM 2258 was taken from the stomach of a "*Micrurus mertensi*" (MUSM

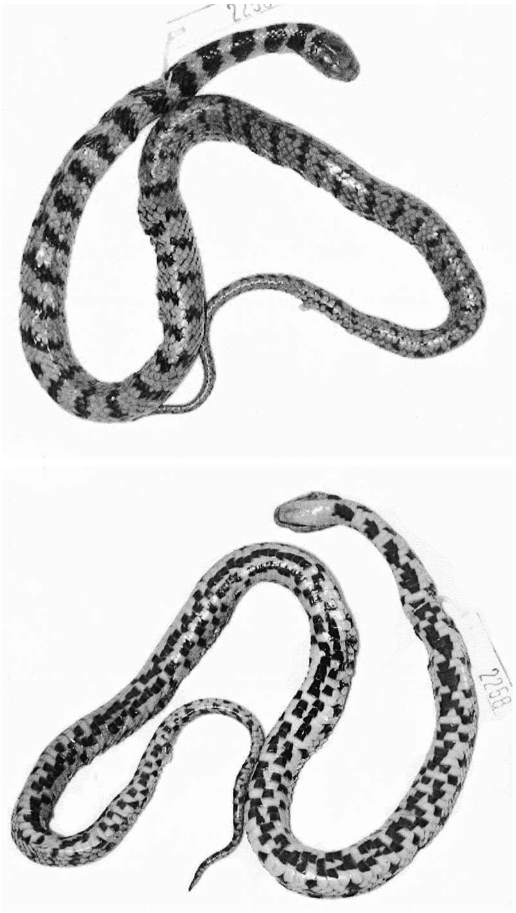

Figure 33. *Sibynomorphus* cf. *oneilli* from "Bellavista" (Peru) of unknown location (MUSM 2258). Male, 328 mm SVL.

2256) collected 25 July 1958 from "Bellavista"; the catalogue entry for the department "Cajamarca" might have been added at a later time. The specimen is problematic because many of its characteristics are unlike specimens of *S. vagrans* of the type series (Table 1) and, in fact, are more like *S. oneilli.* However, no species of *Micrurus* is recorded from the range and elevations known for *S. oneilli,* as judged from distribution maps and elevational data in Campbell and Lamar (2004). Only two known localities for *S. oneilli,* the type locality at 1,646 m and Hacienda Santa Rosa at 1,800 m, are at elevations that seem likely at all to harbor *Micrurus* species, although it is certainly possible that *S. oneilli* occurs at lower elevations as well. Resolving the identity of the *Sibynomorphus* should go hand in hand with study of the *Micrurus* and the locality. I have been unable to undertake a thorough study of MUSM 2256 in comparison with other Peruvian *Micrurus,* and, like the *Sibynomorphus,* it has some unusual characteristics. I herewith present my assessment of these specimens but leave the ultimate resolution of this problem to others.

The locality for the two specimens, "Bellavista," could refer to the well-known herpetological locality in the Río Marañón valley of Cajamarca Department, the type locality of *Sibynomorphus vagrans.* However, a search of the GeoNet Names Server for "Bellavista" in Peru recovered 70 entries, of which several were within the conceivable ranges and elevations of *S. vagrans* and *S. oneilli.* Moreover, the identity of MUSM 2256 as "*Micrurus mertensi*" seems questionable if the locality is the "Bellavista" of the type locality of *Sibynomorphus vagrans. Micrurus mertensi* is a snake of the Pacific coastal region of northern Peru (Campbell and Lamar, 2004), whereas the very similar species, *M. peruvianus,* is found in the upper Río Marañón valley and, indeed, is known from the "Bellavista" of Noble's collections (specimens in MCZ). Nonetheless, MUSM 2256 has some characteristics that are more similar to *M. mertensi* than *M. peruvianus,* and the relationship (or conspecificity) of these two very similar species is unclear (Campbell and Lamar, 2004).

MUSM 2256 is a male tricolored coral snake (without triads), 655 mm total length, 567 mm SVL, 225 ventrals, 46 subcaudals, 1 + 1 temporals, 7 supralabials (3–4 touching the eye), 7 infralabials, 1 preocular, and 2 postoculars. The size is more than 100 mm longer than the maximum reported for *M. peruvianus* but is typical for *M. mertensi.* The ventral count is 23 more than the maximum for male *M. peruvianus* and 4 more than the maximum reported for male *M. mertensi* (data from Campbell and Lamar, 2004). Without further comparative study of *Micrurus* from northern Peru, I do not feel confident in making a call on the identity of MUSM 2256.

The *Sibynomorphus,* MUSM 2258 (Fig. 33), is a male, 425 mm total length, 107 mm tail length (25% of total), with 15–15–15 dorsal rows, 157 ventrals (+2 preventrals), 72 subcaudals, anal single, 8 (4–5)/7 (3–4) supralabials, 11/10 infralabials (the first pair in contact behind the mental), a small preocular on each side superior to loreal, loreal and preocular in contact with eye, 2/2 postoculars, 2/2 primary temporals, 2/3 secondary temporals, and 2 pairs of chin shields.

MUSM 2258 is distinctly banded the whole length of the body with 39 black crossbands (Fig. 33). The anterior crossbands are broader than the posterior ones; a series of crossbands at midbody is interrupted middorsally and tend to alternate. The first (neck) band is 4 scales wide; then follow two bands that are 3 scales wide, whereas most of the crossbands on the body are 1–1.5 scales wide. Interspaces are 1–2 scales wide anteriorly; most of the interspaces are 3 scales wide, occasionally 4. The top of the head is gray with an irregular smudged spot on each parietal; the remainder of head is immaculate grayish. The gular region is grayish and unmarked. The venter is heavily checkerboarded with black squarish and trapezoidal markings on a grayish white ground color (Fig. 33).

MUSM 2258 differs from the type series of *Sibynomorphus vagrans* in several scale and pattern characteristics. Compared with male *S. vagrans,* MUSM 2258 has 2 more ventrals and 8 fewer subcaudals than the next closest respective counts among male specimens of *S. vagrans* (Table 1). The supralabial pattern on one side, 7 (3–4 touching the eye), was observed in no other specimen of *S. vagrans,* although these patterns are highly variable within species. Perhaps the most striking differences between MUSM 2258 and specimens of *S. vagrans* are notable differences in the dorsal and ventral patterns. For these comparisons, the contrasting characters of *S. vagrans* are indicated in parentheses: in MUSM 2258 the body is distinctly crossbanded for its entire length (distinctly banded only anteriorly; compare Figs. 28, 29, 33); the anterior broad crossbands are 3–4 scales wide (generally 5 or more but occasionally 3 or 4); the top of the head is mostly uniform grayish (top of the head ornately patterned with dark irregular markings; Fig. 30); the venter is densely patterned with bold black markings on a pale ground color (venter immaculate or with scattered obscure dark spots). The band across the prefrontal scales typical of *S. vagrans* (see above description) is indistinct in MUSM 2258 and could only be discerned with close inspection; it would certainly not have been noticed had I not been looking carefully for it, whereas in typical *S. vagrans,* this band is very obvious (as noted also by Peters, 1960: 162). MUSM 2258 also lacks the pale angular nape collar characteristic of *S. vagrans*; although MUSM 2258 has a pale nape collar, it is more rounded than is characteristic of *S. vagrans* and is separated middorsally from the parietal scales only by slightly more than 1 nuchal scale, compared with about 3 scales in *S. vagrans.*

On the other hand, all of the scutellation characteristics of MUSM 2258 are typical of *Sibynomorphus oneilli* (Table 1), including ventral and subcaudal counts that are at the approximate midrange of the corresponding counts of male *S. oneilli.* Moreover, the color pattern of MUSM 2258, including details of the dorsal crossbands, the heavily patterned venter, the uncomplicated pattern atop the head, and details of the pale nape collar, are much more similar to other specimens of *S. oneilli* (see above species account) than to *S. vagrans.* In conclusion, were it not for uncertainties concerning the locality and its association with a *Micrurus* of uncertain identity, I would unhesitatingly refer

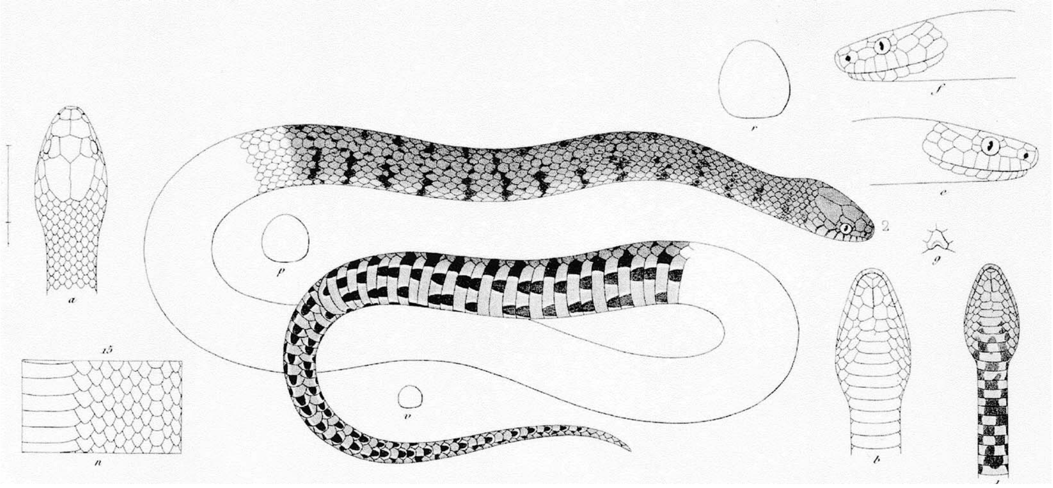

Figure 34. *Sibynomorphus vagus.* Illustration of the holotype from Jan and Sordelli (1860–1881: 37^{e} Livraison, pl. VI, fig. 2).

MUSM 2258 to *Sibynomorphus oneilli* rather than to *S. vagrans.* Further research on the identity of the *Micrurus* and possible identities of the "Bellavista" where the specimens were collected is needed to confidently resolve the present ambiguities.

Sibynomorphus vagus (Jan)
Figures 34–39

Leptognathus vagus Jan, 1863: 100–101. Holotype (Fig. 34), a specimen in the Museo Civico di Storia Naturale, Milan (not examined; probably destroyed during the bombing of 1943), Jan and Sordelli, 1860–1881: 37^{e} Livraison, pl. VI, fig. 2. Type locality: "Hong Kong." Cope (1868: 136) examined the holotype and stated that it is "probably South American."

Leptognathus vaga: Cope, 1868: 136. [brief description of the holotype; see below]

Pareas vagus: Boettger, 1888: 145.

Pseudopareas vagus: Boulenger, 1896: 462. Werner, 1922: 200. Dunn, 1923: 187.

Pseudopareas vagus vagus: Amaral, "1929"a [1930]: 33; "1929"b [1930]: 201; "1929"c [1930]: 75.

Sibynomorphus vagus: Peters, 1960: 164, 1965: 14. Rossman and Thomas, 1979. Rossman and Kizirian, 1993. Orcés and Almendáriz, 1989. Scrocchi et al., 1993. Carrillo de Espinoza and Icochea, 1995.

Notes on the Holotype of *Sibynomorphus vagus*

The holotype of *Sibynomorphus vagus,* illustrated by Jan and Sordelli (1860–1881) (Fig. 34), was a specimen in Milan's Museo Civico di Storia Naturale. Jan's (1863: 100–101) diagnosis of *Leptognathus vagus* appeared in a key to the genus, in which *L. vagus* was diagnosed by the following characteristics: [15] scale rows, loreal in contact with the eye, and 8 supralabials. Jan and Sordelli's (1860–1881) illustration of the holotype shows the following characteristics: body slightly compressed; smooth dorsal scales in 15 rows anteriorly and at midbody; supralabials 8 with 4–5 touching the eye on each side, 2–4 bordering the loreal; infralabials 10/10, the first pair in contact behind the mental; three pairs of polygonal chin shields (the first pair somewhat elongate) followed by three preventrals (the first with a partial suture); loreal and preocular bordering the anterior edge of the eye (preocular superior to loreal); loreal longer than tall; postoculars 2/2; primary temporals 1/1, secondary temporals 2/2, tertiary temporals 2/2 (with the upper secondary temporal fused with the upper tertiary temporal on the left side); anal single; subcaudals 50. The anterior body has a series of irregular lateral vertical markings one scale row or less in width and separated by 2–3 rows. Middorsally is a series of smaller irregular flecks that are aligned with or slightly offset from the lateral series. Top of the head without distinct pattern (stippled uniformly); a slight concentration of dark pigment is on suture lines of the posterior supralabials. The ventrals and subcaudals are heavily patterned with bold half-moon markings; on the posterior body, these tend to align into longitudinal rows on the outer portion of the ventrals.

The characters of the holotype as derived from Jan and Sordelli's illustration are consistent with the variation within the sample of *Sibynomorphus vagus* I examined (Table 1) except for the low number of subcaudals. On this basis, Dunn (1923) inferred that the holotype must be a female, which seems a reasonable assumption. Cope's (1868: 136) brief description of the holotype contains two remarks at variance with the illustration by Jan and Sordelli. Cope stated that "of the preoculars nothing can be said" (the illustration shows the preocular and loreal contacting the eye) and "four pairs of genials" (the illustration shows three pairs of genials, but the first preventral has a partial suture and may have been the fourth pair of genials recognized by Cope).

Cope (1868) first suggested that the holotype of *Sibynomorphus vagus* came from South America, but no other specimens were reported until Dunn (1923) described the series obtained by G. K. Noble at Huancabamba, Peru (Piura Department), in 1916. Dunn (1923: 187) merely stated that Noble's specimens "apparently represent the type of the genus [*Pseudopareas*]." Only half a dozen specimens of *S. vagus,* all from the vicinity of Huancabamba, have been obtained since Noble collected his specimens (see *Specimens Examined and Locality Records*).

Dunn (1923) undoubtedly associated Noble's series with the illustration by Jan and Sordelli because of the close match to details of scutellation and pattern. However, those details also largely match specimens of the later-described *S. oneilli* with fragmented dorsal crossbands, as described herein (see species account and Table 1). The subcaudal count in Jan and Sordelli's illustration (Fig. 34) is equally low for both *S. oneilli* and *S. vagus.* Only the details of the temporal scale patterns in the holotype of *S. vagus* (1 + 2 + 2) more closely match specimens from Huancabamba than they do specimens of *S. oneilli,* as indicated in the discussion of nonbanded specimens of *S. oneilli* from the Río Santa valley and comparisons of them to *S. vagus* (see Tables 1 and 3 and the species account for *S. oneilli*). Thus, even though the differences in temporal scales between these two species are not absolute, the preponderance of characters discernible in the illustration by Jan and Sordelli (1860–1881) matches *S. vagus* sensu Dunn (1923) more closely than *S. oneilli.* Confirmation of the ventral count and sex of the holotype would provide corroboration (see Table 1), but that might be impossible if the specimen was destroyed during the bombing of 1943, as was the case with most or all of the older specimens in the Museo Civico di Storia Naturale.

Diagnosis

Sibynomorphus vagus is characterized by a relatively low number of ventrals (144–152 in males, 151–158 in females) and subcaudals (60–65 in males, 56–60 in females), a dorsal pattern lacking well-defined crossbands or with narrow irregular crossbands (much narrower than interspaces anteriorly), and a venter heavily marked with large squarish spots, often concentrated laterally on the ventral plates (Figs. 34, 35). The top of the head is relatively unmarked or has an obscure pattern. Dorsal crossbands, when present, are usually not well defined, are often present only anteriorly, and usually have irregular borders.

Sibynomorphus vagus differs from other species of the genus in northern South America except *S. vagrans* and *S. oligozonatus* in having a low number of ventral scales. *Sibynomorphus vagrans* is similar

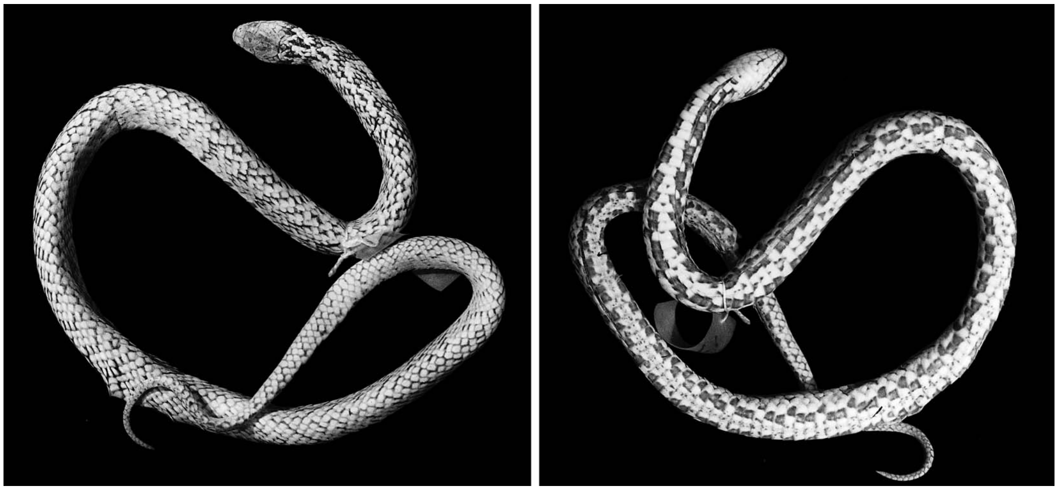

Figure 35. *Sibynomorphus vagus* from Huancabamba, Cajamarca Department, Peru (MCZ 17422). Male, 291 mm SVL.

to *S. vagus* in ventral counts (Table 1) but has bold, well-defined anterior crossbands that are much broader than the interspaces (Figs. 28, 29), has more subcaudals (80–87 in males, 72–79 in females), and has a longer tail than *S. vagus* (Table 1). *Sibynomorphus oligozonatus* differs from *S. vagus* in having well-defined bold anterior crossbands that are much broader than the interspaces (Figs. 1, 2, 4, 5) and a relatively unpatterned venter (heavily marked in *S. vagus*), and in lacking a preocular scale (present in *S. vagus*). *Sibynomorphus petersi* and *S. williamsi* have >160 and >170 ventrals, respectively (sexes combined), and different color patterns. Male and female *S. oneilli* have 152–168 and 163–173 ventrals, respectively.

Description

Size and Scutellation. Descriptive data for *Sibynomorphus vagus* are presented in Table 1. The largest specimen is a male, 483 mm total length, 368 mm SVL; the largest female is 408 mm total length, 326 mm SVL. Tail 23–24% of total length in males, 20–21% of total length in females. Body only slightly compressed. Dorsal scales in 15–15–15 rows, smooth. The vertebral row is very slightly broader to about 1.5 times as broad as the paravertebral rows. Ventrals 144–152 (averaging 149) in males, 151–158 (averaging 154) in females. Anal single. Subcaudals 60–65 (averaging 63) in males, 56–60 (averaging 57) in females. Loreal and preocular bordering eye (preocular superior to the loreal). Loreal longer than tall. Postoculars 2 (rarely 1). Primary temporals usually 1 (rarely 2). Secondary temporals 2 (rarely 3). Tertiary temporals usually 2 (range 0–3). Supralabials 7 or 8, usually with 4–5 bordering the eye (occasionally 3–4). Infralabials usually 9 or 10 (range 8–11). One pair of infralabials in contact behind the mental (8 specimens), or a single infralabial contacts two on the opposite side (2 specimens). Chin shields in 2 pairs ($N = 1$), 3 pairs ($N = 7$), or 4 pairs ($N = 2$). Maxillary teeth 14–16 ($N = 5$). The pupil is prolate (Myers, 1984) in preserved specimens.

Sexual Dimorphism. The largest specimen is a male (Table 1), but with only two adult females and three adult males, it seems likely that this is a sampling artifact rather than an uncommon pattern of sexual dimorphism (none of the other species of *Sibynomorphus* show this unusual pattern, although *S. petersi* comes close). Other sexually dimorphic characters in *Si-*

bynomorphus vagus follow the typical colubrid patterns. Compared with females, male *S. vagus* have significantly fewer ventrals ($t = 2.680$, df = 8, $p < 0.05$), significantly more subcaudals ($t = 7.200$, df = 6, $p < 0.001$), and greater relative tail lengths (Table 1). Dunn (1923: 187) commented that females have less ventral spotting than males, but that difference is not apparent considering the new material (see also Rossman and Kizirian, 1993, fig. 2).

Color in Life. Unknown. Cope (1868: 136) might have seen the relatively freshly preserved holotype, which he described as "above wood-brown, with indistinct cross series of spots. Below yellowish, tessellated with brown."

Color in Preservative. The dorsal ground color is gray to grayish brown. Anteriorly, there may be a series of ill-defined, irregular, narrow (one scale row in width) crossbands; poorly defined reticulations; or a vague dark network (Figs. 35, 36). Posteriorly, the dorsum can be unicolor grayish, with a poorly defined obscure network, or poorly defined crossbands can extend for a variable length along the body (see Rossman and Kizirian, 1993: fig. 2). The venter is usually boldly marked with dark squarish or half-moon–shaped markings or spots on a gray to grayish brown ground color; in some specimens (e.g., MCZ 17420), these markings are reduced to small dark spots mainly concentrated on the anterior venter. The top of the head is gray to grayish brown, usually with a few scattered darker spots, especially on the posterior head plates. The lateral surface of head is generally unmarked and lacks extensively darkened suture lines on the labial scales (Figs. 37, 38).

There seemingly is no substantive ontogenetic change in color pattern, as several small individuals, including one with a visible umbilical scar (MCZ 17426; 137 mm SVL), do not consistently differ from larger ones in pattern.

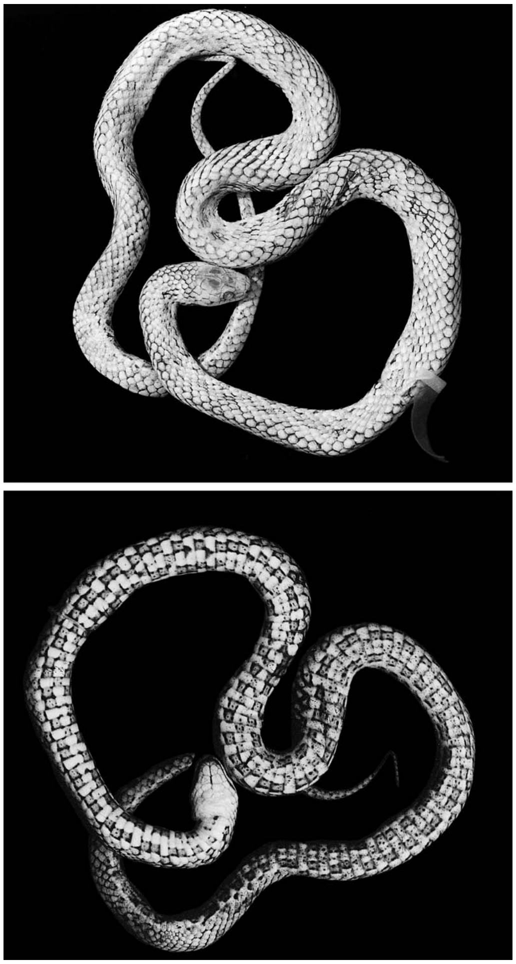

Figure 36. *Sibynomorphus vagus* from Huancabamba, Cajamarca Department, Peru (MCZ 17421). Male, 368 mm SVL.

Etymology. The common meaning of the specific epithet, *vagus,* is wandering or roaming. However, the word can also mean diffuse or indefinite (as in vague). I suspect this is a reference to the diffuse dorsal pattern of *Sibynomorphus vagus* compared with other species of *Leptognathus* known at the time of its description—as seen especially by comparing the illustration of *S. vagus* with the other species illustrated on the same plate by Jan and Sordelli (1860–1881): *Dipsas incerta, S. mikanii,* and the Asian colubrid *Pareas laevis* (all in the genus *Leptognathus* at the

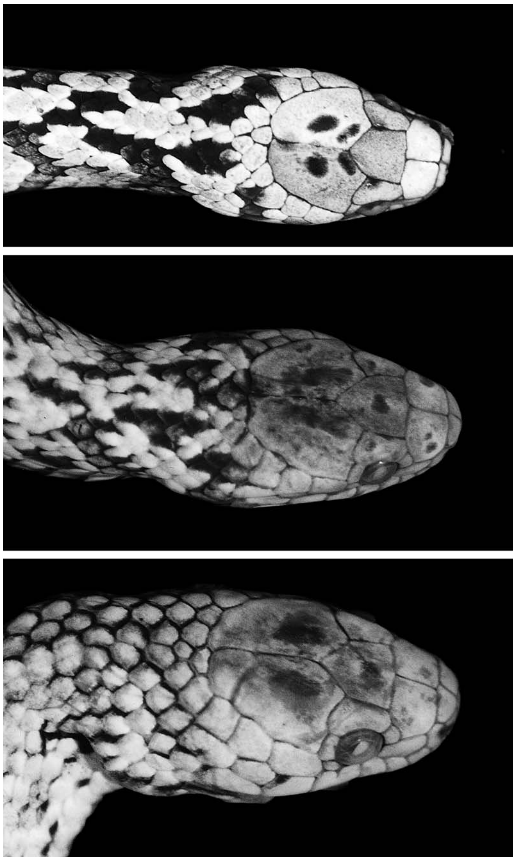

Figure 37. *Sibynomorphus vagus.* Dorsal views of heads. Top to bottom: KU 219121, MCZ 17422, MCZ 17421. The dark spots or smudges on the parietal scales are characteristic of most specimens of *S. vagus.*

time); these are much more boldly marked than *S. vagus.*

Hemipenis

Inverted Hemipenis. The following description of the inverted organ of *Sibynomorphus vagus* is based on MCZ 17422 (adult male, 291 mm SVL). The hemipenis extends to the level of the suture between subcaudals 10 and 11. It is slightly bilobed, dividing at the level of the suture between subcaudals 9 and 10. Total length of the organ 15 mm, divided distally for 2 mm. The major retractor muscle is divided for approximately 1–1.5 mm at its insertion.

Figure 38. *Sibynomorphus vagus.* Lateral views of heads. KU 219121 (top), MCZ 17422 (bottom).

The organ is ornamented with minute spines basally and distally is fully capitate. The capitulum is ornamented with papillate calyces. The sulcus spermaticus (in the dorsal wall of the organ) divides within the capitulum at the level of the distal portion of subcaudal 4; its branches end at the distal tips of the lobes. The undivided portion of the sulcus spermaticus is 6 mm long; its divided portion is 7.5 mm long.

Proximal to the capitulum, a battery of spines completely encircles the hemipenial body. The battery is three spines in width adjacent to the sulcus spermaticus and broadens to four or five spines wide on the asulcate side. A very long basal nude pocket, 4.5 mm in length, extends in the dorsomedial wall of the organ (lateral surface in the everted condition) from the base of the hemipenis to the battery of spines. The distal end of the pocket is nested within the battery of spines. The asulcate edge of the pocket is bordered by a prominent lobe extending from the base to the midpoint of the pocket. The lobe is a narrow flange of tissue proximally, and is most prominent at about the midpoint of the

Figure 39. Hemipenis of *Sibynomorphus vagus* in sulcate view (MCZ 17421). This hemipenis was manually everted with methods detailed by Myers and Cadle (2003).

pocket. The hemipenis proximal to the encircling battery of spines is ornamented with minute spines everywhere except within the nude pocket.

Everted Hemipenis. The left hemipenis of MCZ 17421 (adult male, 368 mm SVL) was everted from the preserved specimen with the use of techniques described by Myers and Cadle (2003) (Fig. 39).

Before eversion, the hemipenis extended to the suture between subcaudals 9 and 10. It was slightly bilobed, dividing at the suture between subcaudals 7 and 8. Total length of the organ was 15.5 mm, divided for approximately 2 mm. The retractor muscle was divided for approximately 1.5 mm, each tip inserting onto a lobe of the hemipenis. At the distal end of the inverted hemipenis, a fold of the tissue that would form the apex of the everted organ extends between the inverted lobes. Consequently, the distal end of the inverted organ was rather trilobed, with a fold of the capitular tissue extending posteriorly between the branches of the divided retractor muscle, and larger than either lateral lobe (i.e., tissue that would become the lobes of the everted organ). The folding of the apical tissue is perhaps only a convenient way of accommodating tissue that is incorporated into the expanding apical region of the everted organ; it has no apparent counterpart in the everted organ. This peculiar structure was not noted in the above-described inverted hemipenis (MCZ 17422).

The everted organ was 15 mm in length and the sulcus spermaticus was divided for 7 mm. The hemipenis is fully capitate, with only a very slight indication of bilobation (perhaps nonbilobed if fully expanded and inflated, which was not attempted because of the delicacy of the preparation). The sulcus spermaticus divides within the capitulum and its tips are more or less centrolineal in orientation, but they pass somewhat laterally and end at the lateral edges of the apex of the organ. The capitulum is ornamented with well-developed papillate calyces. Proximal to the capitulum is a battery of large hooked spines encircling the organ, three to four spines across all around. A large basal nude pocket (3.5 mm in length) is on the lateral side of the organ. It is bordered on its asulcate side by a large lobe and toward its distal end by a pair of large spines, one on each edge. These spines are larger than any in the battery encircling the organ. The base of the hemipenis below the battery of spines, including the lobes bordering the nude pocket (but not the tissue within the pocket) is ornamented with minute spines.

The hemipenes of *Sibynomorphus vagus* and *S. vagrans* are very similar to one another but differ in the shape of their enlarged spines. The spines on the organ of *S. vagus* are comparatively shorter and more robust, and the entire spine forms a curved hook, whereas the enlarged spines on the hemipenis of *S. vagrans* are rather narrow, somewhat straight, and hooked only at their distal tip.

Distribution and Natural History

Sibynomorphus vagus is known only from the vicinity of Huancabamba, Piura

Department, Peru (Fig. 25). The documented elevational range is 1,810 to 1,920 m. Huancabamba lies in the steep valley of the Río Huancabamba, a tributary of the Río Marañón and thus is on the Amazonian versant (and not the Pacific slopes as occasionally stated; e.g., Rossman and Thomas, 1979: 6).

Noble (1921) described the general environment surrounding Huancabamba during August 1916 (when the series in the MCZ was collected) as follows:

> Huancabamba lies on a slope overlooking a mountain torrent. The country on either side is steep and barren. Still, there are pockets of less dry areas and in these we found tropical animals and plants. Huancabamba seemed to be the mingling point of several diverse biotas. Bananas and cacti grew side by side . . . the dominant facies of the fauna seemed tropical, although much out of place in such a barren region.

Parker et al. (1985: 171) described the area in June/July 1980:

> Huancabamba lies in a narrow rain-shadow valley. . . . Although this arid valley is densely settled and intensely cultivated, a few small remnants of desert scrub remain within walking distance of the city. The vegetation [of this desert scrub] is composed of dense shrubbery and scattered *Acacia* trees and clumps of columnar cacti. The farmlands above this dry terrain eventually give way to humid forest at about 2150 m.

Noble's field notes (AMNH Herpetology Department archives) indicate that he worked in and around Huancabamba from 7 to 27 August 1916. There are references in his notes during this period to collecting birds (most references), small mammals, and frogs (including *Gastrotheca*), but no mention of snakes. His entry for 27 August includes the comment "There are so few birds or beasts of interest about Huancabamba that I have decided to move on to some place else."[14]

Some literature records for "*Sibynomorphus vagus*" are questionable or erroneous. Lehr et al. (2002: 134) referred two specimens from the Pacific slopes of southern Ancash Department, Peru (SMF 80048, MUSM 20583) to *S. vagus*; these specimens are *S. petersi* (see above species account). Specimens from Ancash, Cajamarca, La Libertad, and San Martín Departments were also identified as *S. vagus* (Carrillo de Espinoza and Icochea, 1995). These records were presumably based on the specimens I refer to *S. oneilli* (see species account in *New Material of* Sibynomorphus oneilli *from Ancash and Libertad Departments, Peru*), but I did not see specimens from San Martín.[15]

Very little is known of the natural history of *Sibynomorphus vagus.* Six specimens were taken from under rocks in a semiurban setting ("outside a tourist hotel") or in a cleared field in January 1991 (Rossman and Kizirian, 1993). KU 135180 was collected 10 May 1970, and the MCZ series was collected in August 1916. The smallest specimen examined, MCZ 17426 (SVL 137 mm), has the umbilical scar beginning to fuse.

Sibynomorphus williamsi **Carrillo de Espinoza**
Figures 40–42

Sibynomorphus williamsi Carrillo de Espinoza, 1974: 3. Holotype, MUSM 2170 (original number "Of. 0492" given in the original description)[16] (Fig. 40). Type locality: "Jicamarca. Radio-observatorio. Dis-

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[14] The AMNH Herpetology Archives contain only Noble's notes for July–August of the 1916 Harvard Peruvian Expedition, with coverage to just past Huancabamba. The whereabouts of the remainder of the notes (through September, covering the important Noble localities Bellavista and Perico) is unknown. A possible repository is the archives of Harvard University, but their existence was not pursued during this study. The portion of the notes at AMNH contain almost no information on the collections, essentially being a diary of the journey rather than actual field notes.

[15] If the specimen(s) from San Martín are found and also prove to be *Sibynomorphus oneilli,* it would be only the second record, in addition to the holotype, from east of the Río Marañón.

[16] The herpetological collections of the MUSM originally used separate numbering systems for different taxonomic groups; hence "Of.," referring to "Ofidios." With reorganization of the collection commencing in the 1980s, all specimens were renumbered in a continuous series.

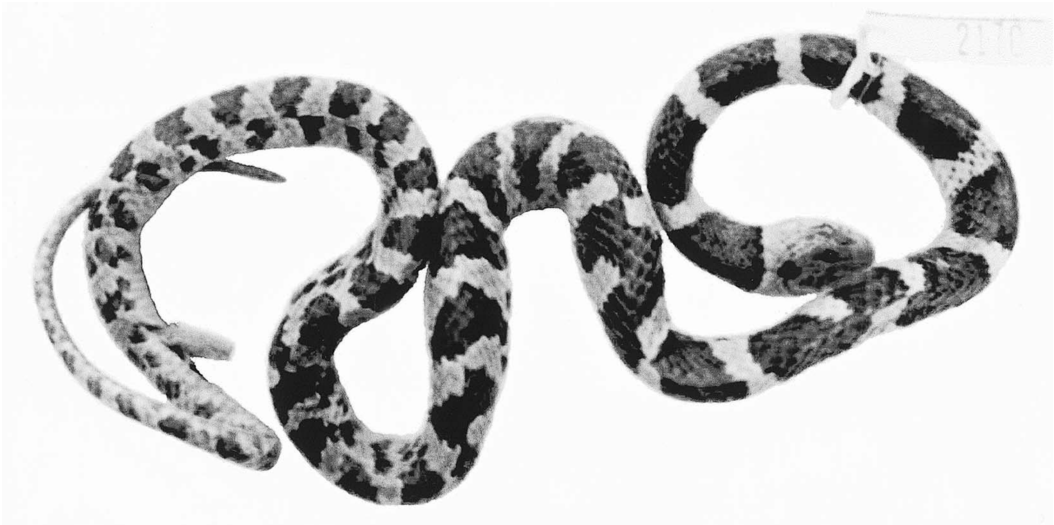


Figure 40. *Sibynomorphus williamsi.* Holotype (MUSM 2170) from Jicamarca (vicinity of Lima). Male, 404 mm SVL.

> trito Lurigancho, Provincia Lima, Departamento Lima" [Peru].

Sibynomorphus williamsi has heretofore been reported only from coastal "lomas" formations in the Department of Lima (Carrillo de Espinoza, 1974); see *Distribution and Natural History* below. Specimens in the MUSM show that the species has a broader distribution in the central coastal region of Peru, including Andean foothills and slopes.

Notes on the Holotype of *Sibynomorphus williamsi*

The type series of *Sibynomorphus williamsi* consisted of a male holotype (MUSM 2170) and six female paratypes. I studied the holotype and four of the six paratypes. Three of the paratypes were from the type locality (MUSM 2173–74; the other not seen), one from the Lomas de Lurín (MUSM 2171), one from the Lomas de Pachacamac (not seen), and one from the Lomas de Lachay (MUSM 3400). These localities, except the Lomas de Lachay, are in the immediate vicinity of the city of Lima; the Lomas de Lachay are on the coast approximately 80–90 km NW of Lima (see Fig. 43).

The holotype of *Sibynomorphus williamsi* (MUSM 2170; Fig. 40) is an adult male in good condition, 530 mm in total length, 126 mm tail length (tail 24% of total length). It has 15–15–15 dorsals, 174 ventrals (+2 preventrals), single anal, 67 subcaudals, 0 preoculars (loreal and prefrontal border the anterior edge of the eye), 3/2 postoculars, 6/6 supralabials with 3–4 bordering the eye on each side (the third supralabial on the right side is divided horizontally to form a "subocular"), 10/11 infralabials, 3 + 4 + 4 temporals on each side, 3 pairs of polygonal chin shields, 1 pair of infralabials in contact behind the mental, and 13 maxillary teeth. It has 35 dorsal crossbands or blotches. The right hemipenis is everted.

I am unable to reconcile my data for the holotype with some scale counts and measurements given by Carrillo de Espinoza (1974: 4, table 1), who reported 186 ventrals, 63 subcaudals, and 10/10 infralabials in the holotype, and body measurements of 545 mm ("cuerpo"), 118 mm ("cola"), and 20 mm ("cabeza"). The high number of ventrals and low number of subcaudals (see *Description*) suggest that data for one of the female paratypes were mixed up with those of the holotype, but data presented for the paratypes (Carrillo de Espinoza, 1974: table 1) do not closely match my data either. Nonetheless, our observations of the holotype are of the same specimen, as indicated by the sex and locality of the specimen and other details, such as the divided right third supralabial (shown in Carrillo de Espinoza, 1974: fig. 4), the everted right hemipenis, and details of banding pattern (Fig. 40; Carrillo de Espinoza, 1974: fig. 1).

Diagnosis

Sibynomorphus williamsi is characterized by a high number of ventral scales (173–182 in males, 181–188 in females), usually 6 supralabials with 3–4 bordering the eye, a relatively short tail (21–24% of total length in males, 19–22% in females), and a head distinctly wider than the neck, with the first dorsal crossband usually extending up onto the wide posterior part of the head. The dorsum is strongly crossbanded from head to tail (35–48 bands; posterior bands might be broken into dorsal and lateral blotches, offset to varying degrees, but they retain their boldness). Anterior crossbands can be twice the width of posterior crossbands, but they are always wider than the pale interspaces, which are 1–2 scale rows wide the length of the body.

Sibynomorphus williamsi differs from other species of the genus in western South America as follows (see also previous species accounts). *Sibynomorphus vagrans* and *S. vagus* have fewer ventral scales (≤160 in each case) and different color patterns. *Sibynomorphus oligozonatus* has a short, blunt snout; a head that is not distinctly wider than the neck; and fewer ventrals in males (145–163 in three specimens). In *S. williamsi,* the dorsal crossbands (including posterior blotches) are bold the entire length of the body (Figs. 40, 41), whereas in *S. oligozonatus,* the anterior crossbands are much more well defined than the posterior blotches. *Sibynomorphus petersi* and *S. oneilli* differ from *S. williamsi* in color patterns (see their species accounts) and in having 8 supralabials with 4–5 touching the eye.

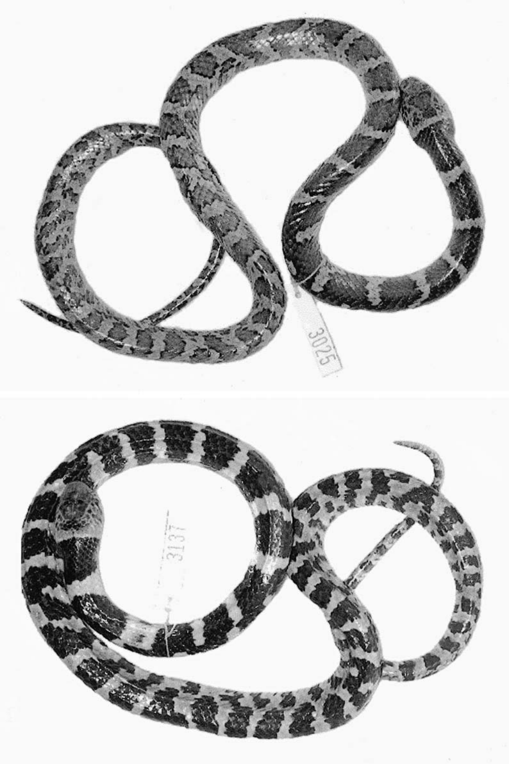


Figure 41. *Sibynomorphus williamsi.* Representative specimens in dorsal view. Top: MUSM 3025 from Ancash Department (female, 427 mm SVL). Bottom: MUSM 3137 from Lima Department (male, 435 mm SVL).

Description

Size and Scutellation. A summary of character data for *Sibynomorphus williamsi* is presented in Table 1. The largest specimen is a female 718 mm total length, 561 mm SVL; largest male is 563 mm total length, 435 mm SVL. Tail 21–24% in males, 19–22% of total length in females. Body somewhat compressed; the head is distinctly wider than the neck. Dorsal scales in 15–15–15 rows. Vertebral row not, or only scarcely, enlarged. Ventrals 173–182 (averaging 177) in males, 181–188 (averaging 184) in females. One to three preventrals precedes the ventral plates. Anal single. Subcaudals 67–73 (averaging 69) in males, 56–66 (averaging 62) in females. Loreal and prefrontal bordering anterior edge of eye (no separate preocular); loreal longer than tall. The first supralabial usually makes broad contact with the loreal (occasionally only narrow contact); supralabials 2 and 3 also border the loreal. Postoculars 2 (occasionally 3). Primary temporals 2 or 3, secondary temporals usually 3 or 4 (rarely 2), tertiary temporals usually 3 or 4 (rarely 5). Supralabials 6 with 3–4 touching the eye (rarely 7 with 3–4 touching the eye). Infralabials usually 10 (range 8–11). One pair ($N = 17$ specimens) or two pairs ($N = 1$) of infralabials in contact behind the mental. Chin shields in three pairs ($N = 11$) or two pairs ($N = 3$). Maxillary teeth 12–14 ($N = 6$).

The consistency of the fused preocular–prefrontal is remarkable in this species compared with some other Dipsadini (e.g., *Sibynomorphus oneilli, S. petersi, S. vagrans,* and various *Dipsas* spp.; Table 1; Cadle, 2005; Cadle and Myers, 2003). No separate preocular is present in any specimen. Three specimens have unusual configurations of the loreal and surrounding scales: in MUSM 19236, the loreal is expanded posteriorly so that the prefrontal contacts the eye very narrowly; MUSM 3137 and MUSM 2173 show the same condition on one side only; additionally, on the contralateral side of MUSM 2173, the loreal contacts the supraocular, occluding contact between the prefrontal and eye. A few other variations were observed: one specimen (MUSM 19236) has an irregular row of suboculars on the left side separating the supralabials from the eye, and a single subocular on the right side of the holotype is formed by horizontal division of the third supralabial (see Carrillo de Espinoza, 1974, fig. 4). No consistent or substantive differences in either scutellation or color pattern were noted between the Ancash and Lima Department series. *Sibynomorphus williamsi* shows typical patterns of sexual dimorphism for colubrids. In comparison to females, male *S. williamsi* have significantly fewer ventrals ($t = 4.560$, df = 13, $p < 0.001$), significantly more subcaudals ($t = 4.365$, df = 12, $p < 0.01$), and greater relative tail lengths (Table 1).

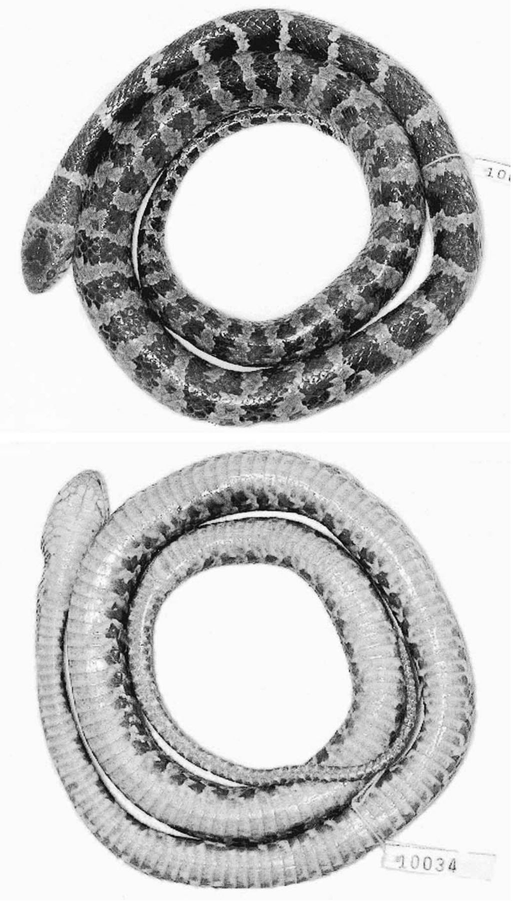


Figure 42. *Sibynomorphus williamsi*. Dorsal and ventral views of a specimen from Lima Department, MUSM 10034. Female, 531 mm SVL.

Color in Life. Unknown. In a relatively recently preserved specimen (MUSM 10034; Fig. 42) the dorsal crossbands are blackish and the interspaces are medium brown with darker brown spots and stippling. The venter is grayish brown, invested with dark grayish irregular markings across each ventral plate.

Color in Preservative. Sibynomorphus williamsi exhibits a consistent color pattern. The dorsum is strongly crossbanded anteriorly, although the bands tend to break up into dorsal and lateral blotches, sometimes offset, on the posterior half to two-thirds of the body. The first dorsal crossband extends well up onto the wide part of the head in most specimens (Figs. 41, 42). At their widest point (dorsal half), individual crossbands are 6 to 9 dorsal scale rows wide on the anterior part of the body, reducing to 3 or 4 rows wide posteriorly. Ventrally, individual crossbands are 2 to 4 rows wide, and they extend onto the lateral edges (up to approximately one-third) of the ventral plates. The interspaces are very narrow (1 or 2 scale rows wide) the length of the body. The total number of crossbands is 35–48. The dorsal crossbands and interspaces are highly contrasting in most specimens, apparently very dark brown or black in life with much paler interspaces. Ventral patterns of the specimens examined were of three forms: (1) pale whitish with fine dark peppering; (2) rather dusky, especially posteriorly; or (3) whitish or dusky with a posterior series of large rounded or squarish spots on the lateral edges of the ventral scales. Occasionally dark pigment was concentrated in narrow lines across the belly, creating a ladder-like appearance.

The head of *Sibynomorphus williamsi* is brown to grayish with blackish markings. Usually some of the labial scale sutures are lined with black and often irregular dark spots are present on the top and sides of the head, especially the parietal scales.

The color pattern of the two smallest individuals, MUSM 3400 (243 mm total length, 198 mm SVL) and MUSM 2867 (199 mm total length, 159 mm SVL), is similar to that of adults, which indicates that little, if any, ontogenetic change in color pattern occurs. The venter of these specimens is very dusky and with a dark ladder-like pattern formed by a dark irregular line across each ventral. The tops of their heads are also very dark.

Etymology. Sibynomorphus williamsi was named for Ernest E. Williams, former curator of herpetology and professor of biology at the Museum of Comparative Zoology, Harvard University.

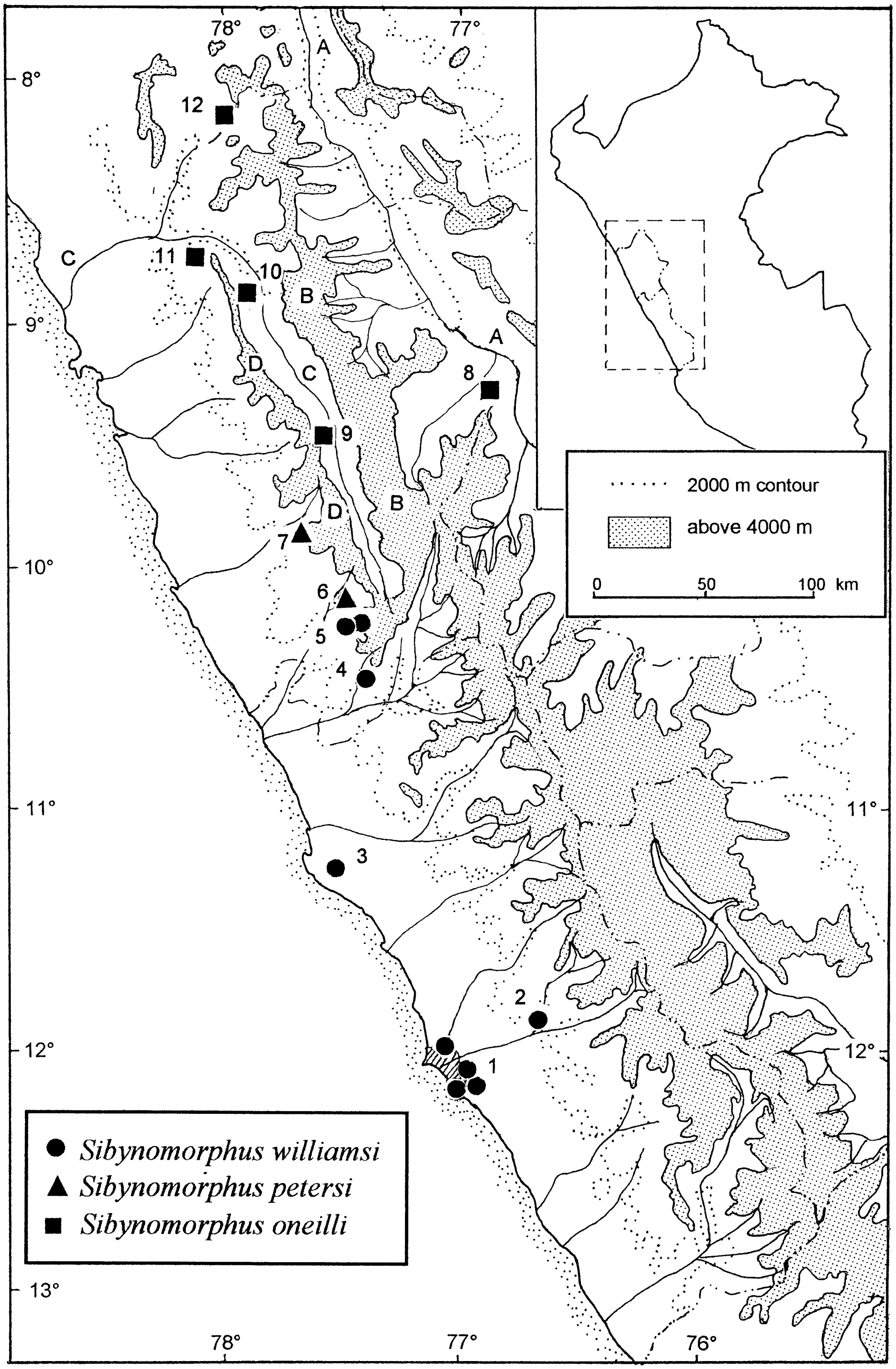
Hemipenis

The following description of the hemipenis of *Sibynomorphus williamsi* is based on the fully everted right organ of the holotype (MUSM 2170); a sketch of the organ was given in the original description (Carrillo de Espinoza, 1974). Total length of the organ 12 mm, bilobed distally for about 1.5 mm.

The hemipenis is slightly bilobed, fully capitate, and with the sulcus spermaticus dividing within the capitulum. The capitulum is set off from the proximal portion of the organ by a well-developed capitular groove. Calyces bearing fleshy papillae ornament the capitulum, but the papillae on the more proximal calyces are spinulate (i.e., have mineralized tips). The sulcus spermaticus divides within the proximal edge of the capitulum and its branches are centrolineal, but distally they pass to the lateral edges of the hemipenial lobes and end at their peripheral distal tips. Proximal to the capitulum is a central section ornamented all around the organ with three to four rows of stout spines. On the asulcate side of the hemipenis is a pair of enlarged spines just proximal to the midsection battery. The basal area below the central spinose section is ornamented with mi-

→

Figure 43. Distributions of *Sibynomorphus williamsi, S. petersi,* and *S. oneilli* in Lima and Ancash Departments, Peru, and adjacent La Libertad Department (locality 12 only). Inset shows the area covered by the larger map (outlined department boundaries are Lima to the south, Ancash to the north). Numbers refer to specimen localities and letters to physical features as follows: **Localities**: ***S. williamsi***: (1) Lima and vicinity: Canto Grande, Lomas de Atocongo, Lomas de Lurín, Jicamarca (type locality), Lomas de Pachacamac; (2) Santa Eulalia; (3) Lomas de Lachay; (4) Huanchay; (5) Yumpe (west) and Huayllacayán (east). ***Sibynomorphus petersi***: (6) Cajacay; (7) Malvas. ***Sibynomorphus oneilli***: (8) Yuracyacu; (9) Huaráz; (10) Huaylas; (11) Hacienda Santa Rosa; (12) Hacienda Ticapampa. **Physical features:** (A) Río Marañón; (B) Cordillera Blanca; (C) Río Santa; (D) Cordillera Negra.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2000 m contour
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50
100 km
● *Sibynomorphus williamsi*
▲ *Sibynomorphus petersi*
■ *Sibynomorphus oneilli*

nute spines. A large basal nude pocket is present on the lateral surface of the organ, but is positioned almost on the asulcate side (i.e., it seems displaced far more toward the asulcate side of the hemipenis than in other species of *Sibynomorphus*). The pocket is 5.5 mm long and has a lobe at its distal end on the asulcate edge and a large spine at the distal end on the sulcate edge.

Distribution and Natural History

Sibynomorphus williamsi is known from coastal "lomas formations" from the vicinity of Lima north to the Lomas de Lachay, from the Andean foothills east of Lima, and from the Andean slopes of southern Ancash Department, Peru (Fig. 43). The known localities span 10 m to at least 2,990 m, but possibly as high as 3,626 m elevation—an extraordinary elevational range matched in few other snakes of which I am aware. The uncertainty in the upper elevational extent is based on specimens from Huayllacayán, Ancash Department, which could have come from lower elevations than the town itself (see footnote 27). However, there is a dichotomy in the elevational range of localities in Lima Department (10–1,036 m) compared with Ancash Department (1,857–?3,626 m). This might reflect either collection biases or environmental differences, but the absence of information on microhabitats or capture circumstances for *Sibynomorphus williamsi* precludes adequate evaluation.

The new records of *Sibynomorphus williamsi* in the Andean foothills and slopes are significant in showing that the species is not restricted to the coastal lomas formations but could have a broader distribution in the Peruvian coastal region and western Andean slopes. Given the extreme environmental conditions that pertain to much of the Peruvian coastal region, a snake such as *S. williamsi* might be infrequently encountered on the surface and could be overlooked through much of the region. Perhaps significantly, many specimens have come from the heavily populated region around Lima where chance encounters are more likely to record the species' presence.

No detailed observations seem to have been recorded for the circumstances of capture for any specimen of *Sibynomorphus williamsi.* The lomas formations, from which some specimens have come (e.g., the lomas of Lurín, Jicamarca, Pachacamac, and Lachay), are plant communities with a highly endemic flora characteristic of the Peruvian and Chilean coastal region (Rundel et al., 1991). These communities develop where there is sufficient topographic relief to intercept the low, dense clouds characteristic of the winter months, thus providing local mesic environments in this otherwise arid region. The formations from the vicinity of Lima and north are floristically among the most diverse lomas because of the increased moisture in this part of the coast compared to farther south. Fog drip at the Lomas de Lachay, from which *S. williamsi* is known, can reach nearly 700 mm per year (Rundel et al., 1991), which is far more than the amount of actual precipitation. Plant communities at Lachay are a diverse assemblage of herbaceous and semiwoody vascular plants, lichens, terrestrial and arboreal bromeliads, and dense stands of small trees with abundant epiphytes (mosses, lichens, ferns) (Rundel et al., 1991: 32). The topography interacts with the prevailing climate to produce a wide array of microenvironmental conditions, including moist woody ravines, lichen-covered rocky terrain, and sandy shrub habitats. Whether *S. williamsi* is restricted to particular microhabitats within this region is unknown. Also, the Lomas de Lachay are topographically and environmentally more diverse than some other lomas localities for *S. williamsi* (at Lachay the lomas reach nearly 1,000 m elevation). For example, the Lomas de Lurín and Lomas de Pachacamac are of much lower relief and with much simpler and more xeric vegetation communities.

Referring to localities in the vicinity of Lima from which the type series was obtained, Carrillo de Espinoza (1974: 5) stated that *Sibynomorphus williamsi* was "a species adapted to a xerophytic environment where *Tillandsias* and other deciduous plants grow; of nocturnal habits, possibly semiarboreal because of the compressed nature of its body." She did not elaborate on the observations suggesting nocturnal habits. One locality for *S. williamsi,* Santa Eulalia (Lima Department, 1,036 m), has been characterized as a semidesert (Koepcke, 1961: 35).

Because they are above the level of interception of the winter clouds and fogs characteristic of the Peruvian coast, the localities for *Sibynomorphus williamsi* in Ancash Department (Fig. 43) are notably more arid than the localities at lower elevations in Lima Department. The region has been characterized as montane or bush steppe (Koepcke, 1961; Lehr et al., 2002).

Three specimens from Lima Department with dates of collection were taken in January, February, and October. Six specimens from Ancash Department were collected in February, March, or April. These months, particularly January–April, correspond to the warmer, drier months along the central coastal region of Peru. Dense clouds form along the Peruvian coast from May to October, often with a ceiling of only 150–300 m (Rundel et al., 1991: 9), and cool weather prevails.

One female (MUSM 10034, month of collection not recorded; 531 mm SVL; Fig. 42), contained six eggs, as determined by palpation through the body wall. The smallest individual, MUSM 2867 (157 mm SVL) was collected 9 January 1978.

Leptognathus atypicus Cope, 1874: Incertae Sedis

Leptognathus atypicus Cope, 1874a: 65–66. Holotype unknown. Type locality: "some portion of the Peruvian Andes, from an elevation of twelve thousand feet."

Pseudopareas atypicus: Boulenger, 1896: 463. Werner, 1922: 200.

Sibynomorphus turgidus (part): Amaral, "1929"a [1930]: 33. Peters, 1960: 158, 1965: 13. Peters and Orejas-Miranda, 1970: 278.

The identity of *Leptognathus atypicus* Cope (1874a) has not been conclusively resolved. Neither Peters (1960: 160) nor I located its holotype in the Academy of Natural Sciences of Philadelphia, and it is not among the Cope types acquired by the American Museum of Natural History (Charles W. Myers, personal communication, 1998; see Myers 1982: footnote 7) or the National Museum of Natural History (Cochran, 1961).

Cope's description of *Leptognathus atypicus* in its entirety follows (Cope, 1874a: 65–66):

> Belonging to sec[tion] vi of my monograph of this genus [Cope, 1868: 107–108], that is, with smooth equal scales, and short geneials separated by but one pair of labials from the symphyseals. The body is rather stout, and, unlike most of the genus, nearly cylindric; the neck is not contracted, but the head is wide and flat, and the muzzle short. Scales rather wide; in fifteen rows. Rostral plate subtriangular; a subquadrate loreal; no preocular; postoculars 2; temporals 2 × 3. Frontal and parietals broad and short, the latter truncate. Superior labials six, eye over third and fourth, fifth and sixth elongate. Inferior labials ten, mostly transverse; four pairs of geneials, all except the first broader than long. Tail short, m. .047 in length, from a total of m. .243.
>
> Color pale, with black transverse spots, which are wide anteriorly (the second covers seven transverse rows of scales) and become gradually narrower, having a width of only two cross-rows on the hinder part of the body. Posteriorly their lateral ends are broken off, and alternate with the dorsal portion. A few small blotches on the ends of the gastrosteges.

The description is cursory, even for Cope. For example, he reported neither ventral nor subcaudal counts. Several characters (15 [midbody] scale rows, a rather stout, cylindrical body, a short muzzle, a loreal but no preocular, and a pale dorsum with wide black blotches anteriorly, narrower posteriorly) suggest a species of *Sibynomorphus,* but it is conceivable that it could also be a species of *Dipsas.* Cope's (1868) concept of *Leptognathus* included species now apportioned among *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas,* and his "sections" of the genus were not based on characters now considered to be systematically informative, that is, "smooth equal scales, and short geneials separated by but one pair of labials from the symphyseals [= mental scale]."

Amaral ("1929"a [1930]: 33) considered *Leptognathus atypicus* identical to *Sibynomorphus turgidus,* and Peters (1960: 158) formally placed it in the synonymy of *S. turgidus,* where it has remained since (e.g., Peters and Orejas-Miranda, 1970). Both authors were perhaps guided by Cope's referral of the species to his "section vi" of *Leptognathus,* which, at the time *L. atypicus* was described, included only *S. turgidus* (Cope, 1868: 108). Peters (1960: 160) noted that the differences between *S. turgidus* and the type of *L. atypicus* as described by Cope, particularly labial counts, appeared as variants within his sample of *S. turgidus.* Peters (1960: 160) also questioned Cope's locality because of the high elevation (3,660 m), which was perhaps understandable because the only montane species of *Sibynomorphus* known at the time, *S. vagus,* was known only from <2,000 m elevation.

Nonetheless, because scutellation and color patterns within this group of snakes are highly variable, Cope's brief description precludes a rigorous determination of the identity of *Leptognathus atypicus.* For example, with little amplification, the characters given by Cope also describe *Sibynormorphus oneilli, S. oligozonatus,* and *S. williamsi,* which were unknown to Peters, and these are more logical on geographic grounds than *S. turgidus.* The known upper elevational limits for these species are, respectively, about 3,500, 2,250, and (possibly) 3,600 m (see previous species accounts). One character in Cope's description, six supralabials with the third and fourth touching the eye, is uniquely shared by *S. oligozonatus* and *S. williamsi* among the northern species of *Sibynomorphus* (Table 1). Given the lack of details in Cope's description, the identity of *L. atypicus* will remain questionable unless the type is rediscovered.

I see no reason to question the type locality of *Leptognathus atypicus* as Peters did, although the elevation (3,660 m) is exceptionally high for a species of *Sibynomorphus* or the related genus *Dipsas.* Nonetheless, we still have much to learn about snake distributions in the Andes. For example, the discovery of a new population of *S. oneilli* extended the known elevational range of that species from 1,645 m to over 3,000 m (Rossman and Kizirian, 1993), and *S. williamsi* might occur well over 3,000 m (but see footnote 27).

Ancillary information in Cope's description lend credibility to the locality data. Cope (1874a) stated that the type of *L. atypicus* was presented to the ANSP "along with two fishes." Cope (1874a) described one of the fishes as *Protistius semotilus* (now *Basilichthys semotilus*) and stated that the other was *Trichomycterus dispar* (Tschudi). The holotype of *Protistius semotilus* is still extant (ANSP fish collection 14404), and both species of fish occur in the Andes of Peru. Thus, unless there was a mislabeling or mix-up before these specimens were presented to Cope, it seems likely that the type of *L. atypicus* is also from Peru.

Other circumstantial details suggest, but cannot prove, that Peru might be the origin of *Leptognathus atypicus.* Cope's work on the South American herpetofauna in the 1870s was dominated by the collections of the naturalist James Orton (1830–1877), primarily from Peru. Orton's second expedition in 1873 traversed the Peruvian Andes, including a "side excursion" to Lake Titicaca (Orton, 1875: xiv). Indeed, Cope (1874a: 70–72) included an appendix describing two reptiles denoted explicitly as sent by Orton, and a paper later the same year (Cope, 1874b) described the bulk of Orton's 1873 collections. In addition to the holotype of *Protistius semotilus,* the ANSP fish collection has two specimens of *Trichomycterus dispar* collected by Orton in 1873 at Tinta (Cuzco Department; ANSP 21251, 21355), which could well be the specimens of that species to which Cope referred (Cope, 1874a: 66) (one reading of the expression "two fishes" is “two kinds, or species” of fishes, rather than two specimens). *Trichomycterus dispar* is not mentioned in the later paper covering most of the fish collection (Cope, 1874b). It is plausible, and perhaps likely, that the holotype of *L. atypicus* was sent to Cope by Orton and that it was obtained on his 1873 expedition to Peru.

HEMIPENIAL MORPHOLOGY IN *SIBYNOMORPHUS* AND OTHER DIPSADINI

As outlined in the following section, I consider the Dipsadini to comprise species in four nominal genera of Neotropical molluscivores: *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas.* These are part of a larger clade, the Dipsadinae (sensu Zaher, 1999), essentially the Central American xenodontine clade of Cadle (1984a,b, 1985) with slightly different composition and many taxa listed “incertae sedis” by Zaher (1999). This is not equivalent to the Dipsadinae of Peters (1960), a much smaller clade whose composition is discussed in the next section. As part of Dipsadinae, *Sibynomorphus,* along with species of several other genera (e.g., *Dipsas, Atractus, Leptodeira,* and *Imantodes*), is a South American representative of a clade with a great diversity of species throughout tropical Mesoamerica.

The Dipsadinae has been characterized on the basis of hemipenial synapomorphies. I here summarize the morphology of the hemipenes of *Sibynomorphus,* as gleaned from the previous species accounts, put their variation in the context of other Dipsadinae and Dipsadini, and characterize interspecific variation in hemipenial morphology among species of *Sibynomorphus.* Myers and Cadle (1994) suggested three hemipenial characters as synapomorphies of Dipsadinae, despite some variation within this group and convergent occurrences in other clades of colubrids (Zaher, 1999): (1) unicapitation, (2) either unilobed or slightly bilobed, and (3) sulcus spermaticus dividing distally within the capitulum.

Hemipenes of at least 27 species of Dipsadini, including species of all four genera, have been described (Cadle, 2005; Cadle and Myers, 2003, and herein), although the descriptions vary in the degree of detail presented. Nonetheless, as inferred from these published descriptions and illustrations, hemipenes of the Dipsadini are very similar in ornamentation. Cadle and Myers (2003: 14–15) briefly reviewed these descriptions, described the organs of *Dipsas nicholsi* and *D. andiana,* and corrected a few observations in previously published descriptions (see also Cadle, 2005). Hemipenes of Dipsadini include the following characters in addition to those considered synapomorphies of Dipsadinae: (1) calyces with well-developed papillae ornamenting the capitulum (the papillae on the proximal calyces are spinulate); (2) a well-developed capitular groove; (3) a battery of enlarged spines of varying width (generally three to four rows of spines across but varying from one to five) encircling the hemipenial body proximal to the capitulum; (4) an exceptionally long nude pocket extending from the base of the hemipenis to, or nearly to, the battery of spines around the midsection; and (5) usually two or more basal spines that are larger than, and separated from, spines in the midsection battery. Proximal to the battery of enlarged spines on the midsection, hemipenes of Dipsadini are ornamented with minute spines overall. A brief survey of published descriptions and unpublished data indicates that these characters commonly appear elsewhere among Dipsadinae (e.g., see illustrations of *Rhadinaea* in Myers, 1974), although comparative studies could reveal differences in their manifestation. In the following section, I briefly compare hemipenes of the northern species of *Sibynomorphus* and compare variation in these and other characters in *Sibynomorphus* vis-à-vis other Dipsadini and Dipsadinae.

Comparison of the Hemipenes of *Sibynomorphus*

Hemipenes of the five species of northern *Sibynomorphus* for which the organs are known (all except *S. oneilli*) are very similar to one another, but they seem to offer few characters that link two or more of the northern species of *Sibynomorphus* to the exclusion of others. References to *Sibynomorphus* in the following discussion refers explicitly to these five northern species only. No other hemipenes of *Sibynomorphus* have been described in sufficient detail to make meaningful comparisons. Cei (1993) and Scrocchi et al. (1993) briefly described organs of several southern species.

(1) Bilobation and Proportions of the Hemipenial Body. The organs are nonbilobed (*S. petersi*) or slightly bilobed. The bilobation is greatest in *S. williamsi* and *S. vagus* (approximately 12–13% bilobed compared with <7% in *S. vagrans* and *S. oligozonatus*). The degree of bilobation varies somewhat among species of Dipsadini, as seen from published illustrations of various species of *Dipsas, Sibon,* and *Tropidodipsas* (reviewed by Cadle and Myers, 2003). However, no species of Dipsadini seems to have more than slight bilobation, and that exhibited by *S. williamsi* and *S. vagus* is about as much as has been observed in any species; Porto and Fernandes (1996) illustrate the hemipenis of *D. neivai,* which shows a similar degree of bilobation.

The capitulum composes a large proportion of the hemipenial body in *Sibynomorphus.* In the species examined herein, the capitulum is approximately 50% or more of the body on the sulcate surface (see Figs. 32, 39). A review of notes and hemipenial illustrations in the literature suggests that this could be proportionally large compared with many other Dipsadinae. Further comparative studies are needed to determine whether useful systematic variation in this character exists.

(2) Orientation of the Sulcus Spermaticus. In hemipenes of all species of *Sibynomorphus* described herein, the orientation of branches of the sulcus spermaticus is centrolineal, but their distal tips pass somewhat to the outer edges of the lobes (Figs. 32, 39). In typical centrolineal sulci, the branches "diverge moderately and extend in relatively straight lines, to lie on the same side . . . as the forking point of the sulcus" (Myers and Campbell, 1981: 16). Thus, the condition in *Sibynomorphus* might be perceived as somewhat intermediate between centrolineal and centrifugal orientation (in which the branches diverge greatly, to lie ultimately on opposite, lateral sides of the organ; Myers and Campbell, 1981: 16). This somewhat intermediate condition has been noted in other Dipsadini, including *Dipsas andiana* and *D. nicholsi* (Cadle and Myers, 2003). However, Zaher et al. (2005: 22, fig. 3) described a seemingly very similar orientation of the sulcus spermaticus of *Atractus albuquerquei* as "centrifugal."

Published illustrations of hemipenes of other Dipsadini generally show more consistently centrolineal orientations of the sulcus (Kofron, 1982, 1985a,b), although the branches in *D. neivai* appear to pass somewhat lateral as well (Porto and Fernandes, 1996). The tips of the sulcus spermaticus in the five species of *Sibynomorphus* surveyed end at the lateral edges of the lobe(s) rather than passing to the apical surface of the organ, i.e., to the center of the lobe(s). This condition is similar to that in *D. andiana* and *D. nicholsi* (see Cadle and Myers, 2003: fig. 6, bottom).

(3) Spines Encircling the Hemipenial Body. A regular array of spines completely encircles the hemipenial body just proximal to the capitulum in *Sibynomorphus.* The array is consistently about three rows across, although in *S. vagrans* and *S. vagus* the array broadened to about four rows on the asulcate surface. This battery of spines appears to be a constant feature of hemipenes of Dipsadini, but its width varies from one to five rows in published descriptions (Cadle and Myers, 2003; Kofron, 1987). Observations of *Dipsas oreas* (Cadle, 2005: 108) suggest that this battery can vary in width intraspecifically so that too much should probably not be made of interspecific differences on the basis of ob-

servations of few organs. The size of the spines in the midsection battery varies within *Sibynomorphus* and in other Dipsadini (e.g., *Sibon*; Kofron, 1982, 1985b, 1987, 1988), but these are usually distinctly smaller than the enlarged basal spines characteristics of Dipsadini (character 7 below).

(4) Presence and Size of the Basal Nude Pocket. One unusual feature of hemipenes of Dipsadini seems to be the exceptional size of the basal nude pocket, which is commonly 30% or more of the overall length of everted organs. It extends from the base of the organ to, or almost to, the encircling battery of spines. The extremes as currently known are in species of *Sibynomorphus,* in which the pockets in everted organs of *S. vagus* and *S. vagrans* are 23% and 26% of the hemipenial length, respectively, whereas in *S. williamsi,* the pocket is 46% of the everted organ length. Too much should not be made of these quantitative comparisons until some potential sources of variation in relative pocket size are investigated more thoroughly, including the effects of preservation, overall size, and degree of inflation. Current data suggest that the size of the nude pocket relative to hemipenial size is greater in inverted organs than in everted ones. For example, the relative pocket size in inverted versus everted hemipenes of *S. vagrans* and *S. vagus,* as described herein, are 32% versus 26% and 30% versus 23%, respectively.

Some published descriptions of hemipenes of Dipsadini fail to mention a basal nude pocket but Cadle and Myers (2003: 15) pointed out that the pocket had probably been overlooked in several of these, as examination of additional specimens showed the pocket to be present. Peters (1960) did not mention the pocket at all in his brief characterizations of the hemipenes of *Dipsas, Sibon,* and *Sibynomorphus.* I now suspect that the pocket has been overlooked in all species of Dipsadini in which the pocket was not reported in published descriptions (e.g., MacCulloch and Lathrop, 2004; McCranie, 2006; Passos et al., 2005; Scrocchi et al., 1993; additional citations and observations in Cadle and Myers, 2003: 15) and that this character will prove universal in Dipsadini. Cadle and Myers (2003: footnote 7) pointed out that longitudinal folds on the base of the hemipenial body might need to be separated with fine forceps or needles to visualize the pocket and that the pocket is especially difficult to demonstrate if the organ is tied off with thread. I encourage workers to make efforts to verify the existence of the pocket during study of hemipenes. The exceptional size of the pocket in Dipsadini might prove to be another synapomorphy of the clade, although more extensive quantitative comparisons need to be made, as well as a broader survey to verify the presence or absence of a nude pocket in other Dipsadinae.

A basal nude pocket is present in some other Dipsadinae (and many other colubrids), including *Geophis* (Downs, 1967; Myers, 2003); *Imantodes* (Myers, 1982); the *Rhadinaea flavilata, R. godmani,* and *R. vermiculaticeps* groups (Myers, 1974); and *Atractus* (Hoogmoed, 1980; Myers and Schargel, 2006; Savage, 1960; Zaher et al., 2005). Moreover, judging from my experience with dipsadines, the failure to mention a nude pocket in published descriptions cannot be taken as definitive evidence of its absence. For example, photographs of hemipenes of three species of *Leptodeira* appear to show a basal nude pocket (Duellman, 1958: pls. 26, 27), even though pockets were not mentioned in any descriptions (the presence of pockets is indicated by what appears to be a deep furrow bordered by lobes such as commonly ornament the nude pockets in other snakes, as seen especially in Duellman's pl. 26, no. 1). Thus, the taxonomic distribution of basal nude pockets among Dipsadinae might be broader than indicated by a literature survey of hemipenial descriptions. The exceptional length of the nude pocket in Dipsadini is seemingly approached in some species of the genus

Atractus, in which the pocket in inverted organs of some species extends distally to the level of the division of the sulcus spermaticus (Hoogmoed, 1980; Savage, 1960). On the other hand, Zaher et al. (2005) described the nude pocket on the hemipenis of *A. albuquerquei* as "small."

(5) Position of the Basal Nude Pocket. The pocket is consistently on the lateral surface of the hemipenial body in *Sibynomorphus* (i.e., about midway between the sulcate and asulcate surfaces, as discussed in *Methods*), although in *S. williamsi* it seemed farther displaced toward the asulcate surface than in the other species. Cadle and Myers (2003) reported variation in the position of the basal nude pocket in different species of Dipsadini, with all species examined except two having the pocket positioned laterally as in *Sibynomorphus.* Cadle and Myers (2003) reported that in one specimen each of *Dipsas variegata* and *Sibon nebulatus,* the nude pocket was on the asulcate surface of the hemipenis. A review of my original notes suggests that this might have been overstated because the notes indicate that the pocket in these two specimens "is offset from the midpoint of the asulcate side"—a loose description that might be no different from the laterally positioned pockets observed in other Dipsadini. Cadle (2005) and Cadle and Myers (2003) reported a laterally positioned nude pocket in five other species of *Dipsas* and *Sibon.*

Nonetheless, Kofron (1982, 1985b, 1987, 1988) described the nude pocket in several species of *Sibon* and *Dipsas* as an "asulcate pocket" (species for which he used this descriptor include *S. annuliferus, S. carri, S. fasciatus fasciatus, S. fischeri fischeri, S. fischeri kidderi, S. sartorii, D. brevifacies,* and *D. gaigeae*). However, different observers could apply terminology differently, so this apparent variation should be verified before acceptance at face value. In addition, the manner of preparation or differential inflation of this pliant tissue could affect the position of the nude pocket, resulting in apparent intra- or interspecific variation.

(6) Lobes Associated with the Nude Pocket. The nude pockets in *Sibynomorphus oligozonatus* and *S. vagrans* are bordered on each side by a prominent lobe. The lobe on the asulcate edge of the pocket (i.e., toward the asulcate side of the organ) is larger than the lobe toward the sulcate side. The nude pockets in *S. petersi, S. vagus,* and *S. williamsi* are bordered only by a single lobe on the asulcate edge of the pocket. The lobes are usually near the midpoint of the pocket, but at least in *S. williamsi,* the single lobe was near the distal end. Other Dipsadini show variation in this feature as well: *Dipsas nicholsi* and *D. elegans* have a single lobe on the asulcate edge of the pocket; *D. andiana, D. oreas,* and *D. ellipsifera* have a lobe on each side of the pocket (Cadle, 2005; Cadle and Myers, 2003). In *D. ellipsifera,* the lobes are asymmetrical, with the asulcate lobe being larger than the lobe on the sulcate edge. In dipsadine species with two lobes, the lobe on the asulcate edge is often (? usually) larger than the sulcate lobe, and in species in which only one lobe is present, it consistently seems to be the lobe on the asulcate edge. One or more lobes are commonly associated with hemipenial nude pockets in diverse colubrids having a pocket, and the variation could merit further study.

(7) Enlarged Spines on the Hemipenial Body. In everted hemipenes of the species of *Sibynomorphus* described herein, usually two enlarged spines are present on the asulcate side of the organ below, or at the lower edge of, the encircling battery of spines (sometimes more closely associated with the nude pocket, as in *S. petersi*). In addition, another enlarged spine is present on the distal sulcate edge of the nude pocket. In everted organs, these enlarged spines are often, but not universally, clearly separated by a gap from spines in the midsection battery (in inverted hemipenes the enlarged basal spines are generally not clearly separated from spines in the mid-

section battery). Basal spines are generally notably enlarged compared with spines in the midsection battery, but because spines in the battery vary in size (see character 3 above), enlarged basal spines might not be clearly differentiated if there is not a distinct gap separating the basal spines from the battery (I recorded only a single asulcate spine in *S. vagus,* but that could reflect lesser size distinction in the specimen studied between the enlarged basal spines and those of the midsection).

Enlarged basal asulcate spines are frequently present in other Dipsadini judging from figures and descriptions in the literature (e.g., Kofron, 1982, 1985b, 1987; Porto and Fernandes, 1996), but their number varies. For example, Cadle and Myers (2003) reported 2–4 basal spines in *Dipsas nicholsi* (the number varied among specimens), and in a single organ of *D. andiana,* two enlarged basal spines were present in addition to two enlarged spines associated with the distal asulcate edge of the nude pocket (Cadle and Myers, 2003).

The position of the enlarged basal spines varies somewhat, sometimes being more closely associated with the asulcate edge of the nude pocket and in other cases deployed more clearly on the asulcate side of the organ. This variation could reflect differences in hemipenial preparations (e.g., degree of inflation) or their interpretation, but side-by-side comparisons are needed to verify the consistency of these placements. Moreover, Kofron (1985b) reported that the largest spines in the hemipenis of *Sibon carri* were on the sulcate side of the organ.

(8) Miscellaneous Variation. A few unique or unusual hemipenial characters seemingly pertain to individual species of *Sibynomorphus.* The proximal calyces on the hemipenis of *S. petersi* have weakly developed longitudinal walls, giving the appearance of weakly developed flounces on the proximal edge of the capitulum. This morphology is observed occasionally in colubrids, but I am unaware of other species of Dipsadini with incipient flounces. Species of *Sibynomorphus* (and other Dipsadini; see Cadle and Myers, 2003) vary in a few characters such as spine form (e.g., narrow, relatively straight, and hooked only at their tips in *S. vagrans,* compared with relatively robust and strongly hooked in the other species). The calycular papillae vary in length (e.g., longer in *S. vagrans* than in *S. vagus*), but I have been unable to compare organs of most species simultaneously to objectify these differences. Similarly, my notes indicate a distinct fringe of mineralized spinules or small spines on the proximal edge of the capitulum in *S. oligozonatus* and *S. vagrans.*

SIBYNOMORPHUS AND THE DIPSADINI: DIRECTIONS FOR FURTHER RESEARCH

In this paper, I lay some foundation for future work on *Sibynomorphus* by outlining patterns of variation in the Ecuadorian and Peruvian species, thus providing a framework for interpreting new specimens or data from northwestern South America. The systematic conclusions herein should facilitate a better understanding of the relationship (if any) between the *Sibynomorphus* species of Ecuador and Peru, and those of southern South America. Detailed comparisons of the two sets of species remain for future research.

Recent studies on the systematics and biology of Neotropical molluscivores (e.g., Cadle, 2005; Cadle and Myers, 2003; Fernandes, 1995; Fernandes et al., 2002; this paper) have already refined knowledge of the species-level taxonomy and distributions since the group was last reviewed (Peters, 1960). Nevertheless, much remains to be done. With over 60 species (including nominal taxa in the genera *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas,* as outlined by Peters and Orejas-Miranda, 1970, and subsequently described species), the Neotropical molluscivores comprise a highly diverse and tightly knit clade of Neotropical snakes (see ensuing discussion). More changes in the understanding of species limits can be expected. Moreover, the phylogenetic relationships among the species have been controversial (Fernandes, 1995; Kofron, 1985a; Wallach, 1995). Although this study does not attempt to address broader relationships among species of molluscivores (beyond comparisons among the species covered herein), the summaries of character variation contained herein should ultimately be useful to that end. In the following sections, I outline some of the problems as I see them and pose some questions for future research on this group.

The Systematics of Dipsadini—An Outline of Some Problems

The Content of Dipsadini. Within Dipsadinae, *Sibynomorphus* has long been considered closely related to the genera *Dipsas, Sibon,* and *Tropidodipsas* (e.g., Dunn, 1935, 1951), with the exception that Peters (1960) did not consider *Tropidodipsas* in his review of "Dipsadinae." Peters did not elaborate on his exclusion of *Tropidodipsas,* although he may have been following Boulenger (1894, 1896), who included *Tropidodipsas* as then known in the Colubrinae and recognized the Amblycephalidae for Asian molluscivorous colubrids and most species of *Dipsas, Sibynomorphus,* and *Sibon* then known. Zaher (1999) referred to the putative clade comprising *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas* as Dipsadini and I follow that usage here.

Underwood (1967) observed that *Dipsas, Sibon,* and *Sibynomorphus* have an extensive tracheal lung, which is lacking in *Tropidodipsas.* Wallach (1995) interpreted the presence of a tracheal lung as a derived character of *Dipsas, Sibon,* and *Sibynomorphus,* and explicitly excluded *Tropidodipsas* from the Dipsadini because it lacks this derived character.[17] However, that evidence could equally well be taken as a synapomorphy of *Dipsas, Sibon,* and *Sibynomorphus* within Dipsadini (including *Tropidodipsas*), rather than a reason for excluding *Tropidodipsas* from Dipsadini. At the least, *Tropidodipsas* shares with *Dipsas, Sibon,* and *Sibynomorphus* a behavioral propensity to consume gastropods as nearly the sole constituent of its diet (Cadle and Greene, 1993). Wallach (1995) viewed the dietary specialization as a derived feature linking *Tropidodipsas* with the other dipsadine genera but felt that, by extension, "a case could be made for the gastropod diet as a synapomorphy of the Dipsadini plus Pareatini [*Aplopeltura* and *Pareas*]" (Wallach, 1995: 479). However, the Pareatini lack the hemipenial and other synapomorphies of Dipsadinae (see Zaher, 1999), the broader clade to which the Dipsadini belongs, and moreover, some specializations for molluscivory in the two groups differ in details of anatomy (Brongersma, 1956, 1958; Zaher, 1999: 20). Those differences indicate that the dietary specializations of the Pareatini and Dipsadini are convergent in these groups.

Thus, there is no reason *not* to consider "molluscivory" a synapomorphy of *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas* within the Dipsadinae. The behavioral trait for dietary specialization can also be viewed as a proxy for an array of other traits associated with the physical ability to subdue these prey (head musculoskeletal system, head glands, dentition, head scalation; Peters, 1960) and, very likely, biochemical traits associated with the sensory apparatus involved in prey detection and recognition. For these reasons, I suggest that the Dipsadini be defined to include *Tropidodipsas* along with *Dipsas, Sibon,*

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[17] Wallach (1995: 479) also noted three characters of visceral topography that "separate the dipsadines from *Tropidodipsas,*" but it was not clear whether these were derived characters. One of these, the position of the posterior tip of the lung, does not seem to clearly differentiate *Tropidodipsas* from some species of each of the other three genera of Dipsadini (Wallach, 1995: table 1), contrary to the text discussion (Wallach, 1995: 479).

and *Sibynomorphus,* as already advocated by Zaher (1999). Although the morphological traits associated with molluscivory have been repeatedly described in general terms for the Dipsadini or portions thereof (e.g., Dunn, 1951; Peters, 1960: 15–19; Scott, 1967), a modern analytical study of their distribution across species is needed. When incorporated into a formal phylogenetic analysis of Dipsadini, this approach should yield valuable insights into the evolution of feeding specializations within a speciose clade.

Sibynomorphus *in the Context of Other Dipsadini: Is* Sibynomorphus *Monophyletic?* Species of Dipsadini have had an especially unsettled generic taxonomy, as examination of the synonymy of virtually any species will readily show (e.g., Cadle, 2005; Cadle and Myers, 2003). Useful reviews of the taxonomy are Peters (1960: 12–15 and, with special reference to *Sibynomorphus,* 142–144), Smith and Taylor (1945: 49), and Kofron (1985a: 85–86). The current generic taxonomy derives from Peters (1960), notwithstanding some disagreement about the recognition or composition of the included genera (e.g., Fernandes, 1995; Kofron, 1985a; Wallach, 1995). The generic taxonomy should be revised as understanding of relationships among species of Dipsadini improves, but that understanding is, as yet, elusive. Despite many suggested revisions of the generic taxonomy of Dipsadini, methodological or sampling problems pertain to many previous considerations of the issue. Here I outline some of the issues and point toward ways of possible resolution.

Kofron (1985a) synonymized *Tropidodipsas* with *Sibon* on the basis that species of both genera shared a "unique" posterolateral process on the maxilla (compared with its absence in three species of *Dipsas* he examined); the process was preceded by a notch on the dorsal surface of the bone. However, Scott (1967) had reported presence of the maxillary process in *D. gracilis,* and Boulenger's (1896: 461) illustration of the skull of *Dipsas indica* shows a maxillary notch similar to that portrayed by Kofron (1985a: figs. 1, 2). As discussed above, Wallach (1995) resurrected *Tropidodipsas* on the basis of tracheal lung and other visceral characteristics. These studies have contributed substantially to our knowledge of morphological characteristics in species of Dipsadini. However, the species and character sampling for a diverse clade such as Dipsadini has generally been less than desirable in previous broad taxonomic studies; they have essentially taken an "exemplar" approach, wherein a few species are taken to represent many others. For example, Kofron (1985a) used three species to represent *Dipsas* in his comparisons despite conflicting character data already reported for another (Scott, 1967). Despite the rarity of some dipsadines in collections, my impression is that there is much more material available than has yet been incorporated into broader phylogenetic studies. I encourage more comprehensive surveys of species and characters to flesh out the character distributions already noted in previous studies (Fernandes, 1995; Kofron, 1985a; Wallach, 1995).

Since Peters' (1960) review, *Sibynomorphus* has been understood to comprise more "generalized" or terrestrial members of the Dipsadini. Species of *Sibynomorphus* lack highly compressed bodies, enlarged heads and eyes, elongate bodies and tails, and enlarged vertebral scale rows (characters generally associated with arboreality in snakes). However, these characters also apply to most species of the related genus *Tropidodipsas* (sensu Wallach, 1995; see also Cadle, 1984a; Kofron, 1985a), a diverse assemblage of Mexican and Central American species that Peters (1960) did not consider in his revision of the Dipsadinae (= Dipsadini of present understanding, i.e., the genera *Dipsas, Sibon, Sibynomorphus,* and *Tropidodipsas*). Although *Sibynomorphus* are primarily terrestrial snakes, observations suggest that at least some species occasionally climb: *S. ventrimaculatus* climbs a meter or more (Cechin and Oliveira, 2003) and *S. neuwiedii* and *S. mikanii* have been described as "semi-arboreal" (Sazima, 1992) or "terrestrial/arboreal" (Rodrigues, 2003).

Furthermore, Peters (1960: 19) had pointed out that "one of the greatest obstructions to a satisfactory analysis of snakes of [the tribe Dipsadini] is that species with nearly every combination of . . . characters [associated with mollusc-feeding and arboreality] can be found." In view of this, Peters' (1960: 12–19, 141–145) discussion of generic delimitations within this group seems arbitrary. Cadle and Myers (2003) noted that most species of Dipsadini for which any data are available share some unusual characters of the hemipenes (e.g., very large basal nude pockets) and defensive behaviors, but none of these characters appeared to be restricted to particular genera of this group. The possibility should be addressed whether the species of *Sibynomorphus* are a phenotypically similar, but not monophyletic, set of species whose peculiar distribution is purely artifactual because of an erroneous understanding of relationships. Only a broader study of phylogeny at the species level among snakes of the tribe Dipsadini can resolve this issue.

Compared with *Sibon* and *Tropidodipsas, Sibynomorphus* shares with *Dipsas* some derived characters of the gular region: notably, the shape of the chin shields (squarish or polygonal rather than elongate and narrow), often more than two pairs of chin shields, and absence of the mental groove. *Sibon* and *Tropidodipsas* have corresponding character states that might be considered plesiomorphic because they are widespread among Dipsadinae and other colubrids: one or (usually) two pairs of narrow, elongate chin shields similar to those typically found in colubrids, and a mental groove (in *Sibon* often only the anterior chin shields are conspicuously elongate).

Sibynomorphus and *Dipsas* also are usually said to share a suite of musculoskeletal features of the head associated with molluscivory that are more derived than those of *Sibon* and *Tropidodipsas* (Kofron, 1985a; Peters, 1960; Savage, 2002), including an inward-turned maxilla with medially directed teeth, pterygoids that are parallel (as opposed to diverging), pterygoids with a flat ventral surface (as opposed to having a central fossa), mandibles bowed in a vertical plane, and a pivot joint between the dentary and compound bone of the lower jaw (Kofron, 1985a: 88; Peters, 1960). In reality, these characters have not been investigated in most species of either genus. For example, with the exception of a few skull characters described for *S. lavillai* (Scrocchi et al., 1993), the nature of these characters is unknown in the five species of *Sibynomorphus* described since 1970, and at least some of the characters have been reported in species of *Sibon* and *Tropidodipsas* (e.g., Fernandes, 1995; Scott, 1967). Newly described species of *Sibynomorphus* have been referred to the genus by a combination of "key" external and dentition characters usually used in generic recognition (e.g., Peters and Orejas-Miranda, 1970).

Over the years, several authors have recommended synonymizing *Sibynomorphus* with *Dipsas* (e.g., Brongersma, 1958; Kofron, 1990: 220; Parker, 1926: 206; Smith and Taylor, 1945: 49), a name that Boulenger (1896), among others, applied to a single species, *D. indica.* The two genera were traditionally distinguished by the presence (*Sibynomorphus*) or absence (*Dipsas*) of pterygoid teeth until Parker (1926) indicated that interspecific variation in this character was nearly continuous. Parker also reported intraspecific variation in the number of pterygoid teeth within "*Sibynomorphus oreas*" (= *Dipsas oreas*). That evidence is a red herring, however, inasmuch as the BMNH specimens Parker cited belong to two different species (Cadle, 2005: 114). Nonetheless, Peters' (1960) data show that absence of pterygoid teeth is approached in very few species of Dipsadini (e.g., *D. indica, D. variegata*) and that many species of *Dipsas* (sensu Peters, 1960) have as many, or more, pterygoid teeth as species of *Sibynomorphus.*

Peters' (1960: 144) justification for maintaining *Sibynomorphus* distinct from *Dipsas* seems particularly arbitrary: "I agree in part with Parker [1926]. I feel that the generic distinction between the many species formerly included in the genus *Sibynomorphus* and . . . the genus *Dipsas* is not valid, but I use the name *Sibynomorphus* in an extremely restricted sense, confining it to the stem forms found in southern Brazil and neighboring countries." It is unclear how the two species of *Sibynomorphus* from northern Peru known at the time, *S. vagrans* and *S. vagus,* fit into this concept. Peters (1960) provided little in the way of differential diagnoses for these two genera other than a few external characteristics in his "Key to the Genera" (Peters, 1960: 19), e.g., body form, head and eye size, relative enlargement of the vertebral scale row. Evidence for the monophyly of *Sibynomorphus* is thus particularly weak.

In an as yet unpublished doctoral dissertation dealing with a broad sampling of Dipsadinae, Fernandes (1995) argued that *Sibynomorphus* should be synonymized with *Dipsas* because his phylogenetic analysis recovered one character purportedly shared by two species of *Sibynomorphus* (*S. neuwiedii* and *S. ventrimaculatus*) and two species of the *Dipsas catesbyi* group (*D. catesbyi* and *D. pavonina*) to the exclusion of other *Dipsas* (seven additional species included in the analysis). It is beyond the scope of this report to present an extended critique of Fernandes' (1995) study, but taxon and character sampling issues alone suggest that synonymizing the two genera is premature. Only two of 12 species of *Sibynomorphus* (*S. neuwiedii* and *S. ventrimaculatus*) and nine of 30+ species of *Dipsas* were included in the taxon sampling for formal phylogenetic analysis (Fernandes, 1995: figs. 7, 8). None of the northern species of *Sibynomorphus* were investigated. The derived character linking the two species of *Sibynomorphus* and two members of the *D. catesbyi* group (*D. catesbyi* and *D. pavonina*) was an enlarged L-shaped Harderian gland. Although this character state was coded as present in *S. neuwiedii* (Fernandes, 1995: table 3), the list of material studied does not indicate that the head glands of this species were investigated (Fernandes, 1995: appendix B), and the character was scored as unknown in two of the nine species of *Dipsas* examined. Furthermore, the type species of *Sibynomorphus* is *S. mikanii* Schlegel, a species that Fernandes (1995) did not include in the formal phylogenetic analysis, so from a purely nomenclatural viewpoint, synonymizing *Sibynomorphus* with *Dipsas* on that basis entails some unwarranted assumptions about the phylogenetic unity of *Sibynomorphus.*

In addition to these issues, some analytical aspects of Fernandes' (1995) study need more careful consideration before making further changes in the generic taxonomy of these snakes. These include more thorough evaluation of intraspecific character variation, character scorings, and more robust tree searching and evaluation methods. For example, intraspecific variability (or error in character scoring) in the purported character linking *Sibynomorphus* with *Dipsas catesbyi* and *D. pavonina* is suggested by Brongersma's (1958: 11) observation that the Harderian gland is enlarged in *D. catesbyi* but "small" in *D. indica* and *D. pavonina,* contrary to Fernandes' (1995) finding.

Even as some authors have called for synonymizing *Sibynomorphus* with *Dipsas,* no one has specifically addressed whether *Sibynomorphus* itself (sensu Peters, 1960, and including subsequently described species) is monophyletic. Although quantification and comprehensive comparisons at the species level are needed, for present purposes, *Sibynomorphus* is distinguished from *Dipsas* by lacking physical characteristics associated with arboreality (highly compressed and attenuate body, prehensile tail, and different head, eye, and tail proportions; Peters, 1960). Many more characters should be investigated in a broad spectrum of species of *Sibynomorphus* and *Dipsas* from throughout their geographic ranges.

A search should also be made for new characters that could potentially inform phylogenetic studies of Dipsadini. Among these are perhaps patterns of sexual dimorphism. Cadle (2005: 77) noted that several species of *Dipsas* had unusual patterns of sexual dimorphism, including one species (*D. elegans*) in which males had greater numbers of ventral plates than females (i.e., the reverse of the common pattern in colubrids); two other species, *D. ellipsifera* and *D. oreas,* lacked sexual dimorphism in ventral plate numbers, which is also an uncommon pattern. A subsequent review of Peters' (1956: fig. 12) data for *D. catesbyi* suggested that the unusual pattern observed in *D. elegans* pertained to *D. catesbyi* as well, and perusal of several papers on other Dipsadini hinted at possible unusual patterns of sexual dimorphism in other species. These include considerable overlap in the ventral and subcaudal counts of male and female *Sibon annulifera, S. sartorii sartorii, S. dimidiata,* and *S. sanniola* (Kofron, 1988, 1990). Unfortunately, Kofron presented only ranges for most comparisons, and he combined male and female counts in other papers so that it is impossible to discern any trends (a practice followed also by Savage and McDiarmid, 1992). However, Kofron (1990) reported mean values for male and female ventrals in *S. s. sanniola* as 155 and 153, respectively. This suggests little or no sexual dimorphism in ventral counts for this species (the character ranges of males and females were nearly identical as well).

In contrast to these unusual patterns, the Ecuadorian and Peruvian species of *Sibynomorphus* are not unusual with respect to patterns of sexual dimorphism: they show the patterns most common in colubrids generally. Whether the southern species of *Sibynomorphus* show typical or unusual patterns of sexual dimorphism is not clear (e.g., data for *S. lavillai* from Scrocchi et al. [1993] showed little difference between males and females for ventral counts). Nonetheless, this character might provide an additional distinction between some species of *Sibynomorphus* and some *Dipsas.* Broader and more quantitative surveys could prove fruitful.

Sibynomorphus (or a part thereof) could thus be plesiomorphic relative to *Dipsas* in terms of ecomorphological characters associated with arboreality and with respect to patterns of sexual dimorphism. These plesiomorphic characters in *Sibynomorphus* do not support the monophyly of *Sibynomorphus* per se, but they do provide a differential diagnosis from *Dipsas* until more detailed studies are conducted. Further changes to the taxonomy of these snakes should be commensurate with an increase in understanding of a suite of characters and their variation across a broad sampling of nominal taxa of Dipsadini—something that has been lacking in previous examinations of the generic taxonomy.

The Peculiar Distribution of Sibynomorphus. Certainly one outstanding feature of *Sibynomorphus* as currently understood is its odd distribution, which is unlike most other Neotropical reptiles and amphibians (Fig. 44). Lest this peculiarity be construed as "evidence" for the nonmonophyly of *Sibynomorphus,* it is worth briefly comparing the distribution to other South American species. The six species of *Sibynomorphus* that form the focus of this report (the "northern species" in the following discussion) are distributed in southern Ecuador and the northern half of Peru, and these are species of the Pacific versant (coast, Andean slopes, and western inter-Andean valleys) or of the eastern inter-Andean valleys on the Amazonian versant (Río Marañón and its affluents, Río Huancabamba and Río Chotano). Then follows a broad geographic gap before the genus appears again in the dry woodlands of southern Bolivia (Fugler and Cabot, 1995; Fugler and De la Riva, 1990) and the Brazilian state of Mato Grosso, whence it is broadly distributed south of the main

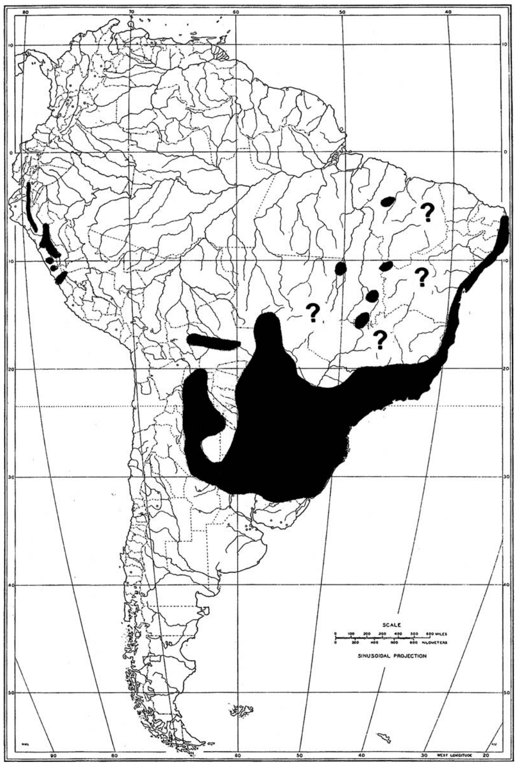

Figure 44. The widely disjunct distribution of species of *Sibynomorphus* in western Peru and Ecuador, and south of the Amazon basin. The distribution of the "northern" species is compiled from records herein. The distribution of the "southern" species is compiled from Peters (1960), Cei (1993), Leynaud and Bucher (1999), and various other faunal works. Question marks indicate my inability to find reliable records through a large part of the Brazilian cerrado. Similarly, the distribution might be more continuous in the borderlands between Bolivia, Paraguay, and Argentina.

course of the Amazon. About 1,500 km (straight line distance) separates the closest points in the two parts of the distribution, not to mention the rugged terrain of the Andes and parts of forested lowland Amazonia, where no species of *Sibynomorphus* seems to occur.

South of the Amazon, species of *Sibynomorphus* (the "southern species") occur in an extraordinary range of major habitats, including cerrado, caatinga, Atlantic forest, chaco, pantanal, and dry deciduous woodlands (Brites and Bauab, 1988; Cei, 1993; Leynaud and Bucher, 1999; Marques et al., 2000; Norman, 1994; Peters, 1960; Rodrigues, 2003; Vanzolini, 1948). There seem to be no definite records from within the Amazonian forest. The collective distributions of the southern species of *Sibynomorphus* are remarkably similar to that of the colubrid snake genus *Psomophis,* except that *Psomophis* is conspicuously absent from the Atlantic Forest and caatinga (Myers and Cadle, 1994) (Rodrigues [2003] described the presence of *S. mikanii* in caatinga as relictual). Apart from *S. vagrans* and coastal populations of *S. williamsi,* the northern species of *Sibynomorphus* are montane species and occur at higher elevations than are known for any of the southern species.

With the exception of *Sibynomorphus neuwiedii,* which is apparently restricted to forested regions of the Atlantic Forest biome (Hoge et al., "1978/1979" [1981]: 177), southern species of *Sibynomorphus* primarily occur in relatively open habitats, often with reduced rainfall. The ecological (particularly microhabitat) distribution of the northern species of *Sibynomorphus* is not well known, but subhumid to arid environments prevail in this region. Localities for most northern species, as documented in the natural history sections of the species accounts, are referred to frequently by descriptors such as arid habitats with cacti, semiarid brushland, dry deciduous forests, thorn scrub, arid rain shadow valleys, and montane steppe. Nonetheless, a few records for *S. petersi* (e.g., Río Zaña Study Site, Bosque Cachil, Canchaque, Río Chotano valley) suggest that this species, at least, occurs in the dry/humid forest ecotone, if not actually within humid montane forests (see species account), and other species might occur in more mesic areas, such as riparian habitats, than their general habitat associations might imply.

Species of *Sibynomorphus* are not unique among Dipsadini in their occurrence in subhumid to xeric habitats. A few species of the other genera occur in habitats such as dry deciduous forests, thorn forests, or deserts (e.g., *Dipsas brevifacies* and *D. gaigeae, Sibon sanniola, Tropido-*

dipsas annulifera). Nevertheless, species of *Dipsas, Sibon,* and *Tropidodipsas* overwhelmingly inhabit more mesic to humid environments than species of *Sibynomorphus.* In the case of broad macrosympatry between *D. oreas* and *S. petersi* (see its species account) in southern Ecuador and northern Peru, these two species might be segregated by habitat, with *S. petersi* occurring in more arid environments than *D. oreas* (see footnote 7).

The disjunct distribution of *Sibynomorphus* is unusual but not without parallels. The Pacific coastal and western Andean region of northern Peru and Ecuador (the generalized distribution of the northern species of *Sibynomorphus*) harbors a distinctive and largely endemic herpetofauna. Few components of this fauna have been subjected to phylogenetic studies, but three examples illustrate parallels with the distribution of *Sibynomorphus* (Fig. 45).

In the frog genus *Ceratophrys* ("Leptodactylidae" or Ceratophryidae), *C. stolzmanni* (southwestern Ecuador/northwestern Peru) is the sister taxon to *C. calcarata–C. cornuta* (Caribbean Colombia/Venezuela and the Amazon basin), and these three species, composing the subgenus *Stombus,* are the sister group to the subgenus *Ceratophrys* (Lynch, 1982), which occurs in forested and nonforested habitats from southern Bolivia and northern Argentina east throughout southern Brazil (Fig. 45B). Thus, apart from the existence of a widespread Amazonian species (*C. cornuta*) and a northern South American species (*C. calcarata*), the distributional relationships of the western South American species, *C. stolzmanni,* are similar to distribution patterns portrayed by species of *Sibynomorphus* as that genus is presently understood.

The lizard *Ctenoblepharys* (Liolaemidae; Fig. 45C) is endemic to loose sand habitats of coastal central Peru. It is the sister group to *Phymaturus* + *Liolaemus* of the southern Andes and Pacific coast (Argentina–Chile), and cis-Andean South America from Argentina to southern Brazil (Espinoza et al., 2004; Etheridge, 1995). Thus, an area cladogram for Liolaemidae is similar to that of *Sibynomorphus* (Fig. 45A), with the additional geographic components of the southern Andes and coast.

Finally, among tropidurid lizards, *Microlophus* (Fig. 45D), from western Ecuador and Peru (including inter-Andean Marañón valley of northern Peru and the Galapagos Islands), is the sister group to other tropidurid genera (*Tropidurus, Plica, Uracentron, Eurolophosaurus,* and *Strobilurus*) (Frost et al., 2001), whose geographic distribution encompasses Amazonia, the Guayanan region, and virtually all of austral South America (i.e., south of the Amazon basin). Again, Amazonian and Guayanan taxa represent geographic components not found in *Sibynomorphus.* Although the examples in Figure 45 seem most similar to the distribution of *Sibynomorphus,* other possible examples might be found in genera such as *Stenocercus* (Tropiduridae) and *Philodryas* (Colubridae), which have coastal/Andean components in Peru, Ecuador, or both and which are broadly distributed east of the Andes and in austral South America.

Each of these examples includes geographic components (Amazonia, southern Andes and southern Pacific coast, northern South America) not known in *Sibynomorphus.* Nonetheless, a complete phylogenetic analysis of Dipsadini at the species level might eventually show that these "missing" geographic components are represented by species whose relationship to *Sibynomorphus* is not yet demonstrated (i.e., species of *Dipsas*). This is especially true given that monophyly of *Sibynomorphus* is not yet demonstrated, and its relationship to other Dipsadini (particularly the diverse array of Amazonian and northern South American *Dipsas*) is presently murky.

Moreover, the cladograms in Figure 45 illustrate two alternative area relationships among species of western Ecuador/Peru, austral South America, and Amazonia. In *Ceratophrys* (Fig. 45B) the western Ec-

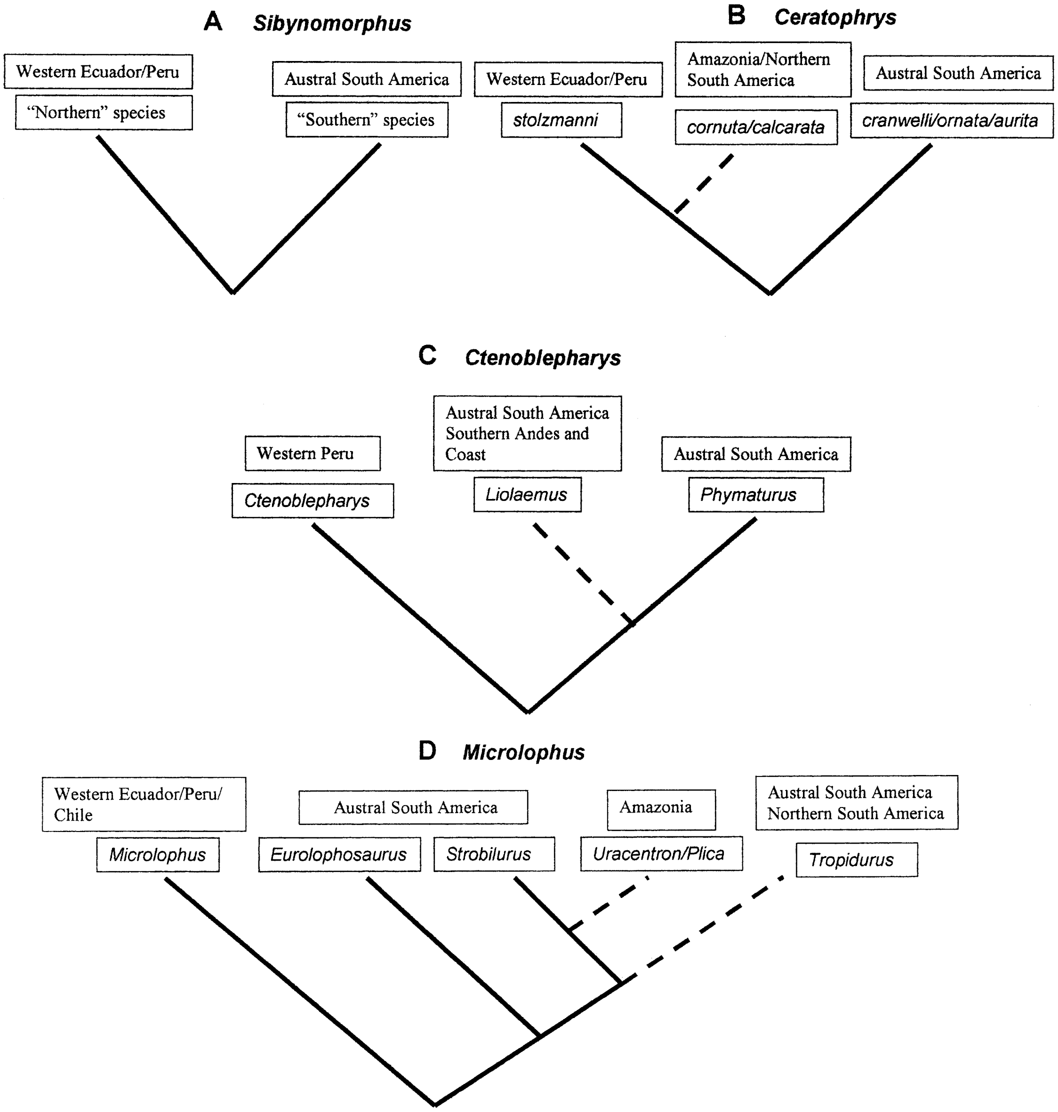

Figure 45. Area cladograms illustrating geographic components (areas of endemism) shared between *Sibynomorphus* and other taxa of western South America. "Austral South America" here refers to all of cis-Andean South America south of Amazonia; the exact area delimited varies somewhat in each case (see discussion and references in the text). Solid lines in the cladograms indicate shared geographic components. Dashed lines indicate one or more geographic components not present in *Sibynomorphus.* (A) Geographic components in *Sibynomorphus.* Neither the monophyly of the genus itself nor its geographic components ("northern" and "southern" species groups) is strongly supported (see text). (B) Geographic components in the frog *Ceratophrys* (Leptodactylidae or Ceratophryidae). (C) Geographic components in the lizard *Ctenoblepharys* (Liolaemidae). (D) Geographic components in the lizard *Microlophus* and related lizard genera (Tropiduridae).

uador/Peru taxon is most closely related to the Amazonian species, whereas in *Microlophus* (Fig. 45D), the Amazonian taxa are more closely related to the austral South American taxa. For *Ctenoblepharys* (Fig. 45C), the area cladogram is identical with that of *Sibynomorphus* (i.e., no Amazonian component is present) except that species of *Liolaemus* also occur in the southern Andes and the southern Chilean coast, geographic components also unknown in *Sibynomorphus.*

Depending on how the phylogenetic relationships among the northern and southern species of *Sibynomorphus* and the species of *Dipsas* are ultimately resolved, the area cladogram for *Sibynomorphus* could resemble any of the examples in Figure 45 or more complex geographic relationships. For example, three possible resolutions of the area cladogram for *Sibynomorphus* are shown in Figure 46, in which dashed lines to the geographic component "Amazonia" represent as yet undemonstrated relationships of the northern (western Ecuador/Peru; Fig. 46A) or southern (austral South America) species of *Sibynomorphus* (Fig. 46B). The former resolution is compatible with the area cladogram for *Ceratophrys* (Fig. 45B), and the latter is compatible with the area cladogram for *Microlophus* (Fig. 45D). Many more complex resolutions are possible, of which the example in Figure 46C is but one example (i.e., the northern and southern species of *Sibynomorphus* are each independently related to different species groups of Amazonian *Dipsas*). The example in Figure 46C would imply that *Sibynomorphus* as it is currently known is polyphyletic.

The possibilities outlined in Figure 46 are speculative, but they indicate ways in which some outstanding phylogenetic and biogeographic enigmas concerning *Sibynomorphus* might ultimately be resolved. Figure 46 also provides guidelines for constructing any rigorous test for relationships between *Sibynomorphus* or any of its geographic components and other Dipsadini. At the least, northern and southern species of *Sibynomorphus* must be included in analyses, preferably with a broad taxonomic and geographic representation of South American species of *Dipsas* as well. Unless tests are constructed such that these alternatives can potentially be discerned, we are left with more ambiguity than clarity.

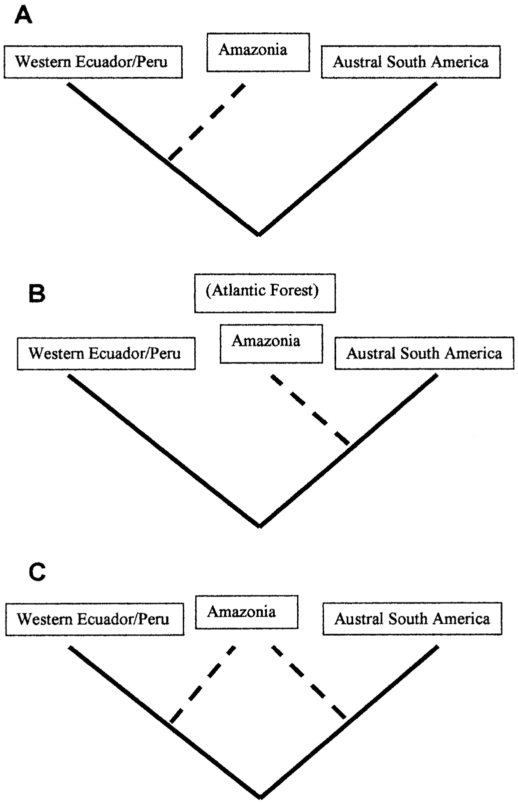

Figure 46. Examples of possible resolutions of "missing" geographic components in the area cladogram of *Sibynomorphus* (Fig. 45). These area cladograms assume a complex relationship between geographic components of *Sibynomorphus* and species of *Dipsas,* which currently is speculative (see text). (A) Resolution corresponding to the area cladogram of *Ceratophrys* (Fig. 45B). (B) Resolution corresponding to the area cladogram of *Microlophus* (Fig. 45D); a possible alternative is indicated by the additional geographic component "Atlantic Forest," which is a component of "Austral South America" used in Figures 45 and 46. (C) A more complex scenario in which the northern and southern species of *Sibynomorphus* are each related to different species of *Dipsas* in Amazonia, which implies polyphyly of *Sibynomorphus* as currently understood. Many more resolutions of these area cladograms are possible, but all depend on the precise relationship among the northern and southern species of *Sibynomorphus* and other species of South American Dipsadini. These relationships are largely unexplored.

Research Needs on the Northern Species of *Sibynomorphus*

More Field Work and Collections are Needed. Several topics addressed in this study need additional research based on more samples than currently exist. Systematic studies of some tropical snakes are hampered because few specimens from widely scattered localities are available, and species of *Sibynomorphus* in Ecuador and Peru are no exceptions. In extreme cases, species can be represented by unique or nearly unique specimens as, for example, in the species of "rare snakes" of the genera *Geophis* and *Atractus* studied by Myers (2003). None of the species of *Sibynomorphus* considered herein is as absolutely rare as the species considered by Myers (2003). However, interpreting patterns of variation and inferring species limits was difficult in several cases because of inferred intrapopulational or geographic variation combined with few specimens sampled across the complex terrain of the Andes. Even with the new material reported herein, one of the species is known from only four specimens, and three species are known from three or fewer localities. Great variability in systematic characters has been documented within species of *Sibynomorphus* (Rossman and Kizirian, 1993; this study) and related genera (e.g., *Dipsas*; Cadle, 2005; Cadle and Myers, 2003). The variation occurs at several levels (individual variation within populations, sexual dimorphism, and geographic variation among populations) and with respect to scutellation and color patterns. Teasing apart the sources of variation in taxa represented by few specimens is particularly difficult.

Because of the variability of informative systematic characters within and between population samples and few specimens spread over a topographically and environmentally diverse region of South America, the available material of Ecuadorian and Peruvian *Sibynomorphus* is insufficient to fully clarify their systematics. Thus, the identity of some populations proved difficult to resolve. Because of the extensive variation in characteristics such as color patterns and scutellation, the species limits recognized herein should be reviewed as more material and denser geographic sampling become available. In particular, the concepts of *Sibynomorphus oligozonatus, S. petersi,* and *S. oneilli* need reassessment. Full characterization of *S. oligozonatus* is hampered by few specimens and rather large disparity among specimens in a few characters, such as ventral counts within males and between males and females.

For *Sibynomorphus petersi* and *S. oneilli,* the problems of species limits have more to do with character variation among localities. The Peruvian samples of *S. petersi* are heterogeneous in color patterns among themselves and compared with Ecuadorian samples. Ecuadorian specimens tend to be more homogeneous in color patterns, but they also form a more cohesive geographical unit than Peruvian samples, which are spread in a linear array along the western Andean front (Fig. 25). For *S. oneilli,* the problem is that the type specimen differs in several characters from virtually all other specimens referred to this species, and it is the only specimen currently known from the Cordillera Oriental. Efforts should be made to obtain additional specimens (particularly adults) from the vicinity of the type locality to verify whether the unusual characters of the holotype pertain to this individual or reflect population or regional characteristics.

Additional field work is needed to flesh out the distributions of *Sibynomorphus* in Peru in more detail. In particular, field work at the northern end of the Cordillera Oriental in Peru (east of the Río Marañón in La Libertad, San Martín, and Amazonas Departments) should be undertaken to understand more fully the distribution of *S. oneilli* in this region (currently known only from a single specimen, the holotype, from east of the Río Marañón). Similarly, *S. petersi* is known from a single specimen on the Amazonian versant, and the extent of its distribution east of the continental divide should be established. There is also a broad geographic gap in the distribution of *S. petersi* on the Pacific versant between southern Ancash Department and the next locality to the north, San Pablo (Cajamarca Department) (Fig. 25). *Sibynomorphus vagus* and *S. vagrans* are known only from single locations, and the latter species has apparently not been collected since Noble collected the type series in 1916, even though it seemed to be common at that time (see species account).

As currently known, the distribution of *Sibynomorphus williamsi* along the Peruvian coast is peculiarly circumscribed. Specimens have been recovered from several localities in the immediate vicinity of Lima and from the relatively well-studied Lomas de Lachay just north of Lima (Fig. 43). The lomas formations extend from northern Chile to northern Peru and, although their general aspect becomes drier from the vicinity of Lima southward, the climate in general for this region is relatively homogeneous (Rundel et al., 1991). Comprehensive field surveys of the lomas formations should reveal whether *S. williamsi* is more broadly distributed in this habitat along the Peruvian coast. These environments have rarely been given attention by zoologists, and new discoveries are likely. (Pearson and Ralph [1978] studied bird, mammal, and lizard communities of a loma in southern Peru, but their sampling protocol was unlikely to reliably sample secretive or highly seasonal snakes.)

A further paradox concerning the distribution of *S. williamsi* concerns its elevational distribution. All initially reported localities were from coastal lomas formations less than 1,000 m in elevation (and all, except the Lomas de Lachay, <300 m) (Carrillo de Espinoza, 1974). The localities in Ancash Department differ in elevation (>1,800 m) and environment (more xeric) from these coastal formations. The breadth of the elevational distribution of *S. williamsi* (10 to perhaps 3,600 m) is extraordinary for a species of snake and invites more detailed distributional studies and population comparisons to determine whether all are, in fact, the same species.[18] In particular, field studies of coastal areas in southern Ancash Department could determine whether the upland populations are linked to any at lower elevations in this region. Similarly, additional study of the Andean foothills east of Lima should determine whether *S. williamsi* occurs more generally in this area (the species is currently known only from one inland locality in Lima Department, Santa Eulalia).

Currently, the only known case of sympatry among any of the northern species of *Sibynomorphus* is the presence of *S. petersi* and *S. oligozonatus* at their type locality in Azuay Province, Ecuador. It seems likely that these two species are broadly sympatric throughout the highland areas of southern Ecuador and (possibly) northern Peru (Figs. 7, 25). Potential areas of sympatry for species of *Sibynomorphus* in Peru include southern Ancash Department, where three species (*S. oneilli, S. petersi,* and *S. williamsi*) occur in close proximity (Fig. 43). Further field work is needed to determine whether there is microsympatry among these species and, if so, to what extent their resource use patterns are similar.

Systematic and Phylogenetic Issues. Much work remains to be done on the systematics of *Sibynomorphus* in the broad sense and achieving a well-supported phylogenetic hypothesis for its relationships within Dipsadini. Chief among the outstanding questions is whether *Sibynomorphus,* as it has been understood since Peters (1960) (i.e., the northern + southern species), is monophyletic. Fernandes (1995) formalized the suggestion raised many times previously that *Sibynomorphus* stemmed from within *Dipsas,* but the possibility also exists that *Sibynomorphus*

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[18] Two other snakes of the Pacific versant also have huge elevational ranges. *Mastigodryas heathii* and *Philodryas simonsii* are known from near sea level. The former ranges to at least 2,500 m and the latter to over 3,000 m in the Andes of northern Peru (Cadle, unpublished data).

is polyphyletic with respect to *Dipsas.* For example, the two geographic units (northern and southern) could be independently related to different clades within *Dipsas* or there could be an even more complex relationship among species of the two genera (see above discussion and Figs. 45 and 46). These are unexplored questions.

This study yielded few clues as to relationships among any of the species reviewed. Three species, *Sibynomorphus oligozonatus, S. williamsi,* and *S. vagrans,* resemble one another in several characters. Their color patterns are less variable intraspecifically, and they are more similar to one another than any of the other three northern species, which are quite variable in color pattern. *Sibynomorphus oligozonatus, S. williamsi,* and *S. vagrans* all have highly contrasting dorsal patterns (bold crossbands on relatively pale ground colors) and relatively unmarked venters compared with *S. oneilli, S. petersi,* and *S. vagus. Sibynomorphus oligozonatus* and *S. williamsi* share some characters that are rare or absent in other species of the genus: (1) They share the uncommon characteristic of having six supralabials with the third and fourth bordering the eye—a characteristic seen elsewhere in some specimens of *S. lavillai* and *S. ventrimaculatus* (Scrocchi et al., 1993), but not among other northern species of *Sibynomorphus* (Table 1). (2) They consistently lack separate preoculars (i.e., the preocular is always fused with the prefrontals in the specimens examined) and have elongate loreal scales. Among the northern species of *Sibynomorphus,* lack of a separate preocular was observed elsewhere only in some specimens of *S. oneilli* but was reported as a consistent feature of *S. mikanii* and the usual condition in *S. ventrimaculatus* (Cei, 1993). (3) They tend to have fewer maxillary teeth than the other northern species. The color patterns of *S. oligozonatus* and *S. williamsi* are similar except for the less distinct bands/blotches on the posterior body of *S. oligozonatus* and its broader anterior crossbands compared with *S. williamsi.*

On the other hand, *Sibynomorphus oligozonatus* shares with *S. vagrans* the presence of two lobes associated with the nude pocket on the hemipenial body (one asulcate lobe in the other northern species). The color patterns of these two species are also very similar, including broad anterior crossbands, less distinct posterior crossbands, and relatively unmarked venters (Figs. 1, 3–6, 28, 29). It is unclear whether any of these similarities among *S. oligozonatus, S. vagrans,* and *S. williamsi* are indicative of close phylogenetic relationships in the absence of broader comparisons. Also, as perceived by Dunn (1923), *S. vagrans* is similar to *S. vagus* in having low ventral counts compared with the other species.

Further comparative studies of all species referred to *Sibynomorphus* are needed, particularly in the context of other Dipsadini. Three of the northern species, *Sibynomorphus oneilli, S. petersi,* and *S. williamsi* attain larger sizes (males, 563–763 mm total length; females, 718–790 mm total length; Table 1) than any of the southern species (generally <500 mm total length in males and females; Cei, 1993; Scrocchi et al., 1993). Intraspecific variation in scutellation is generally much less in *Sibynomorphus* than in *Dipsas* (Peters, 1960; this study; cf. Cadle, 2005; Cadle and Myers, 2003). Such comparative studies should yield insights not only into the systematics of this group, but into aspects of their natural history.

Natural History Studies. The paucity of data on the natural history of all northern species of *Sibynomorphus* is evident from the species accounts contained herein. Microhabitat and behavioral data are almost completely lacking for all species, and only a single dietary record (a gastropod) is available (see *S. oligozonatus*). Two records document predation on *S. petersi* and *S.* cf. *oneilli* by coral snakes (*Micrurus*). Three records document clutch sizes for *S. petersi* (two clutches of five eggs each) and *S. williamsi* (six eggs), but dates of collection are not available for these specimens, and nothing concerning reproduction is known for the other northern species of *Sibynomorphus.* Most specimens with recorded dates of collection have been obtained in the austral summer (i.e., generally between October and April), although *S. petersi* has also been obtained during the austral winter (June–August) in southern Ecuador. Seasonal activity and reproductive patterns for these species need to be documented with greater precision. The proximity of two species, *S. williamsi* and *S. oneilli,* to major population centers (Lima vs. Huaráz and Cajamarca, respectively), offers significant opportunities for detailed local natural history studies.

Finally, two aspects of variation within *Sibynomorphus* and the Dipsadini deserve further study relative to the natural history of these snakes: color and scales. A puzzling aspect of variation in several species of northern *Sibynomorphus* (*S. oneilli, S. petersi, S. vagus*) is considerable intra- and interpopulational variation in color pattern. Each of these species varies in pattern from relatively unicolor (or finely reticulated or flecked) to strongly banded (see species accounts and illustrations herein). This variation poses a systematic question: Are species limits correctly inferred, and do the color patterns thus truly represent intraspecific variation? Assuming that the answer to the first question is "yes," how is the color pattern variation related to the natural history of the snakes?

Species of Dipsadini are widely suspected to mimic pit vipers in color patterns and behaviors (Greene and McDiarmid, 2005). Such mimicry has been specifically suggested for *Sibynomorphus neuwiedii* (Sazima, 1992), and defensive behaviors similar to that of *S. neuwiedii* have been reported for *S. mikanii* (Cadle and Myers, 2003). Perhaps the extreme pattern polymorphism in several northern species of *Sibynomorphus* is associated with specific and, as yet unknown, defensive behaviors or mimicry systems.

Some northern species of *Sibynomorphus* are known to be regionally sympatric with species of *Bothrops*: *S. oligozonatus* and *S. petersi* with *B. lojanus* and *B. osbornei* in southern Ecuador (Campbell and Lamar, 2004; Parker, 1930, 1932, 1938); *S. oneilli* and *S. williamsi* with *B. pictus, B. roedingeri,* or both in northern and central Peru (inferred from distributions in Campbell and Lamar, 2004). In addition, some of these species of *Bothrops* are highly polymorphic in color and pattern (e.g., *B. pictus*; Campbell and Lamar, 2004). Parallel studies of geographic color pattern variation could shed light on potential mimicry systems in these snakes, as could a study of populations at localities in which high intrapopulational pattern variation has been documented (e.g., *S. oneilli* in the Río Santa valley of Ancash Department, Peru; *S. vagus* from the vicinity of Huancabamba, Piura Department, Peru). Although current evidence suggests that little or no ontogenetic change in color pattern occurs in *Sibynomorphus,* more detailed investigations of this phenomenon should be conducted. Do potential models (*Bothrops*) and mimics (*Sibynomorphus*) undergo parallel ontogenetic color changes, as is known in some other snake mimicry systems (Greene and McDiarmid, 2005)?

A second intriguing aspect of the biology of *Sibynomorphus* and other Dipsadini (particularly *Dipsas*) is the extreme variation in external scalation (Cadle, 2005; Cadle and Myers, 2003; Peters, 1960). The variation in standard scutellation characters, particularly of the head, seems greater than occurs in many other colubrid groups. It calls for study in mechanistic terms (What developmental processes result in the variation?); in functional biology terms (What is the functional significance of the variation?); and in evolutionary terms (What is the phylogenetic distribution and origin of the variation?).

It is tempting to link variability in scutellation to the molluscivorous diet of Dipsadini (and perhaps some correlated changes such as the musculature underlying the temporal scales; see Dunn, 1951). Indeed, the absence of a mental groove and the peculiar form of the chin shields have been linked specifically with the ability to consume gastropods (Gans, 1952: footnote 5; Peters, 1960: 17–18). But that can be only part of the story because *Sibynomorphus* and *Dipsas* are more derived in these two characters than are *Sibon* and *Tropidodipsas* (see above discussion). *Sibynomorphus* itself is less variable in some head scale characters than are at least some *Dipsas* (e.g., scales in the loreal and temporal regions). The variation among species could be related to different functional requirements for different prey, and different species of Dipsadini are already known to have different prey preferences and correlated morphology (e.g., in *Sibynomorphus*; LaPorta-Ferreira et al., 1986; Sazima, 1989). Functional and comparative studies of head scale variation in snakes could shed light on this phenomenon in Dipsadini. A fruitful avenue of research also includes a variational study of the Asian molluscivores (Pareatini). Do their patterns of variation entail the same scales and to the same degree of variation as in Dipsadini? This could suggest insights into how the variation might be related, if at all, to molluscivory in colubrids.

Species of *Sibynomorphus* in Ecuador and Peru offer many opportunities for deepening our understanding of the biology of the South American radiation of Dipsadini. Hopefully, the analyses presented here will stimulate further studies of these snakes to resolve outstanding systematic and phylogenetic questions and will serve as a point of departure for improving knowledge of their natural history.

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SPECIMENS EXAMINED AND LOCALITY RECORDS

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	The Natural History Museum, London
EPN	Escuela Politécnica Nacional, Quito, Ecuador
FMNH	Field Museum of Natural History, Chicago
KU	Museum of Natural History, University of Kansas, Lawrence
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
MUSM	Museo de Historia Natural de San Marcos, Lima, Peru
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Sibynomorphus oligozonatus

ECUADOR: Azuay: Zhila, Parroquia Oña, Cantón Girón, 2,250 m [03°30′S, 79°12′W],[19] EPN 3612 (holotype). About 6 km airline W Santa Isabel, 1,440 m, Río Jubones drainage [03°16′S, 79°19′W], AMNH 110587. **Loja:** Catamayo Valley, 30 km W Loja [approximately 04°01′S, 79°20′W], BMNH 1935.11.3.108.

PERU: Piura: No specific locality, MUSM 2192, 2248.

Sibynomorphus oneilli

PERU: Ancash: Provincia Antonio Raimondi: Yuracyacu, 3,500 m [09°15′S, 77°01′W[20]], MUSM 3211, 3296, 3303, 3334, 3392, 3448. Huaráz [3,060 m; 09°32′S, 77°32′W], MUSM 3395, 2660. Provincia Huaylas: Huaylas [2,721 m; 08°52′S, 77°54′W], MUSM 2662, 2687, 3089. Provincia Huaylas: Hacienda Santa Rosa, 1,800 m [now Provincia Santa: approximately 08°46′S, 78°08′W [21]], MUSM 2390. **Amazonas:** 5,400 ft. (1,646 m) on road between Balsas and Abra Chanchillo [06°49′S, 77°59′W], LSUMZ 33736 (ho-

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[19] Coordinates for this locality given by the GeoNet Names Server (03°30′S, 79°12′W) differ from those given in the original description (03°39′45″S, 79°17′26″W). Consultation with several maps suggests that the former are more accurate. The Global Gazetteer gives the elevation of Zhila as 2,818 m.

[20] Instituto Geográfico Militar, Departamento de Ancash, 1:400,000, 1979.

[21] Stiglich (1922) indexes two haciendas in Ancash Department with the name "Santa Rosa": one in the District of Mácate, the other in the District of Pueblo Libre. All of the territory of Pueblo Libre is ≥2,000 m, whereas Mácate has significant area <2,000 m, and I infer this is the Santa Rosa referred to. Mácate has subsequently been incorporated into Santa Province (IGM Departamento de Ancash, 1:400,000, 1979). The coordinates are an approximation on the basis of the closest territory to Mácate that is <2,000 m. MUSM 2390 was collected by Roberto Donoso-Barros, but no date was recorded.

lotype). **Cajamarca:** Abra Gelic, 13 km E Celendín, 3,080 m [06°51′S, 78°08′W], KU 212599. Provincia Cajabamba, 10 km SSE Cajabamba, 2, 900 m [approximately 07°37′S, 78°03′W], KU 212600. Provincia Cajabamba: Cajabamba [2,654 m; 07°37′S, 78°03′W], MUSM 3103. **La Libertab:** Provincia Santiago de Chuco: Hacienda Ticapampa [= Hacienda Ticabamba, Distrito de Mollepata; Stiglich, 1922; approximately 08°11′S, 77°57′W, the coordinates of Mollepata], MUSM 2770.

Sibynomorphus cf. *oneilli*

PERU: "Bellavista," MUSM 2258 (see text discussion at end of species account for *S. vagrans*).

Sibynomorphus petersi

ECUADOR: Azuay: Zhila, Parroquia Oña, Cantón Girón, 2,250 m [03°30′S, 79°12′W; see footnote 19], EPN 2659 (holotype; not seen), 2660 (paratype). **Loja:** Loja City, 2,200 m [04°00′S, 79°13′W], BMNH 1924.6.24.110–111, 1930.1.30.7, 1930.10.12.24–25, 1931.2.12.30–31, BMNH 1933.6.24.110–111. Vicinity of Loja City, 7,280 ft. [2,219 m; 04°00′S, 79°13′W], BMNH 1935.11.3.111. 0.5 km E Loja City on road to Zamora, 6,765 feet [2,063 m; 04°00′S, 79°13′W], USNM 237040. 2 km E Loja, 2,200 m [04°00′S, 79°13′W], KU 121309. 10 km E Loja City [04°00′S, 79°11′W], EPN 4737. Catamayo Valley, 30 km W Loja, 4,780 ft. [1,457 m; 04°01′S, 79°20′W], BMNH 1935.11.3.109–10. 7.3 km N Loja, 2,080 m [03°58′S, 79°13′W], KU 142804. Cantón Saraguro, El Tablón, 03°28′42″S, 79°10′30″W, EPN 1847 (not seen; Orcés and Almendáriz, 1989).

PERU: Ancash: Malvas, 3,120 m [09°55′S, 77°39′W], SMF 80048. Cajacay, 2,599 m [10°09′S, 77°26′W], MUSM 20583 (not seen; Lehr et al., 2002).[22] **Cajamarca:** 3–4 km N Paraguay (along road from Querocoto to Hacienda La Granja), 2,420 m [06°21′S, 79°05′W],[23] MUSM-JEC 12884. Approximately 1 km NE (airline) of Monte Seco on trail between Monte Seco and Chorro Blanco, Río Zaña, 1,250 m [06°51′S, 79°06′W], FMNH 232569. El Chorro, 1 km N (airline) Monte Seco, 1,400 m, Río Zaña, ANSP 31806 (= stomach contents, not separately catalogued, associated with a *Micrurus mertensi* (see Fig. 26). San Pablo [2,400 m; see Cadle, 1998: footnote 6; 07°07′S, 78°50′W], BMNH 1900.3.30.19. Bosque de Cachil, 3 km (airline) SW Contumazá, 2,200–2,400 m [07°23′S, 78°47′W], MCZ 178047. **Piura:** 33 km SW Huancabamba, below (west) crest of the Cordillera Huancabamba ["below camp, ca. 6800 ft" (2,073 m) fide field notes of Richard Thomas; approximately 05°21′S, 79°34′W],[24] LSUMZ 27374.

Sibynomorphus vagrans

PERU: Cajamarca: Bellavista [421 m; 05°37′S, 78°39′W], MCZ 17284 (holotype), 17428, 17436–52 (paratypes).[25]

Sibynomorphus vagus

PERU: [Piura]: Huancabamba [1,929 m; 05°14′S, 79°28′W], MCZ 17420–23,

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[22] I assume that the identity of MUSM 20583 is the same as SMF 80048, which I examined. Both specimens are from the same collection and from geographically close localities (see Lehr et al., 2002).

[23] Coordinates derived from 1: 100,000 Carta Nacional Incahuasi, Departamento Cajamarca (IGM, 1965, reprinted 1973).

[24] This locality is roughly equivalent to "Canchaque" or "Cruz Blanca" in some literature on this locality. See footnote 13.

[25] Paratypes of *Sibynomorphus vagrans* comprised 26 specimens (Dunn, 1923), but Barbour and Loveridge (1929) indicated only 23 [*sic*] at that time: MCZ 17430–53 [= 24 specimens]. Several paratypes were exchanged to other collections: Instituto Butantan (17429–30, 17435), University of Illinois Museum of Natural History (17431), Hebrew University of Jerusalem (17432), AMNH (17433, 17453), and the Naturhistorischen Museums in Wien, Austria (17434). These exchanged specimens were not examined for this study.

17425–26[26]; Huancabamba (1,900 m), KU 135180; Huancabamba (1,820 m), KU 219121–22. 5.7 km N Huancabamba on road to Salala, 1,920 m, KU 219123; MUSM 15464–65 (not seen; Rossman and Kizirian, 1993).

Sibynomorphus williamsi

PERU: ANCASH: Huayllacayán [3,626 m (?)[27]; 10°15′S, 77°26′W; also spelled Huayacayán], MUSM 2665. Provincia Bolognesi: Huanchay [1,857 m; 10°31′S, 77°25′W ; on the Quebrada Huanchay, a tributary of the Río Pativilca], MUSM 3025. Provincia Bolognesi, Distrito Huayllacayán: Yumpe [2,989 m; 10°15′S, 77°29′W], MUSM 3378, 3412–14, 3475. **LIMA:** Distrito San Juan de Lurigancho: Canto Grande [311 m; 11°59′S, 77°01′W], MUSM 10034. Lomas de Atocongo [to 540 m; 12°08′S, 76°54′W], MUSM 19236. Lomas de Lachay [300–900 m; 11°21′S, 77°23′W], MUSM 2668 (paratype), 3400. Lomas de Lurín [10 m; 12°17′S, 76°52′W], MUSM 2171 (paratype). Radio Observatorio de Jicamarca [approximately 300–400 m; 11°57′S, 76°52′W], MUSM 2170 (holotype), 2173–74, 2867 (paratypes). Lomas de Pachacamac [75 m; 12°14′S, 76°53′W] (Carrillo de Espinoza, 1974). Provincia Huarochirí: Santa Eulalia [1,036 m; 11°51′S, 76°40′W], MUSM 3137.

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[26] MCZ 17424 and 17427 were exchanged to the Instituto Butantan.

[27] According to the IGM 1:400,000 Ancash Department map, Huayllacayán is between 3,000 and 4,000 m. According to the Global Gazetteer, its elevation is 11,899 ft. (= 3,626 m), which is much higher than the next lower recorded elevation for *S. williamsi* (2,989 m). Another specimen, MUSM 3376, is listed from the same locality in the MUSM catalogues but explicitly notes the elevation as “2,700 m.” The latter specimen is a juvenile with no discernible dorsal pattern, but all scutellation features are similar to *S. williamsi* except for 8 supralabials (4–5 touching the eye); in addition, the venter appeared to have large bold spots, which is uncharacteristic of most specimens of *S. williamsi.* For these reasons, I excluded MUSM 3376 from the study, but it indicates that specimens from this locality could come from lower elevations near Huayallcayán, in which case the upper elevational extent of *S. williamsi* is not known with precision. Another interpretation is that the catalogue entry “Huayllacayán” refers to the political unit district (Distrito) and not to the town of the same name.

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