An Enigmatic New Snake from Cloud Forest of the Península de Paria, Venezuela (Colubridae: Genus Taeniophallus?)

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An Enigmatic New Snake from Cloud Forest of the Península de Paria, Venezuela (Colubridae: Genus *Taeniophallus*?)

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ABSTRACT

The snake *Taeniophallus nebularis*, new species, is known from a single specimen collected in montane cloud forest, 800 m above sea level, Península de Paria, northeastern Venezuela. It is a small ''xenodontine'' colubrid (adult male, 492 mm total length); dorsal scales in 19-19-17 rows, smooth, with paired apical pits anteriorly; brown dorsally and grayish laterally, with ill-defined pattern; white postocular stripe; and bright yellow midventrally between serrated black edges.

The species is easily diagnosed, although assignment to *Taeniophallus* is problematic. However, a few suggestive characters are shared with *T. brevirostris* and *T. nicagus*. These species, presumably the closest geographic relatives of *T. nebularis*, occur in the Amazon basin and the Guianas, indicative of a biogeographic parallel with certain plants. *Taeniophallus occipitalis*, with extreme scale-row reduction and a distinctive color pattern possibly derived from a *brevirostris*-like precursor, is widely distributed south of the Amazon. Four additional species of *Taeniophallus* s.l. comprise the monophyletic *affinis* species group centered in southeastern Brazil.

The genus *Echinanthera* (also centered in southeastern Brazil) is sometimes expanded to include all of *Taeniophallus*. *Echinanthera* s.s. is viewed as a demonstrably monophyletic group of six named species, whereas relationships of the subgroups of *Taeniophallus* s.l. among themselves and to *Echinanthera* remain uncertain.

Evolutionary divergence in copulatory organs of the otherwise similar *Taeniophallus nicagus* and *T. brevirostris* is extraordinary, suggesting that uncritical weight cannot safely be assigned to hemipenial characters of presumptive relatives. The hemipenis of *Taeniophallus nebularis* differs from those of other taxa discussed in being conspicuously bilobed for nearly a third of its length. However, some degree of bilobation is symplesiomorphic for these snakes, as evidenced by presence or absence of weak bilobation in a few species and divided insertions of retractor muscles in all. The penial asulcate interspinal gap in *T. nebularis* also might be symplesiomorphic for *Taeniophallus* s.l. and *Echinanthera* s.s., but homologies and level of generality for this character are not yet clear.

RESUMEN

La serpiente *Taeniophallus nebularis*, especie nueva, se conoce de un solo ejemplar colectado en bosque nublado montano, 800 m sobre el nivel del mar, en la Península de Paria, en el noreste de Venezuela. Se trata de un colúbrido ''xenodontino'' de pequeño tamaño (macho adulto con un largo total de 492 mm); escamas dorsales en 19-19-17 hileras, lisas, con fosas apicales en pares en la parte anterior; marrón dorsalmente y grisáceo lateralmente, con patrón poco definido; banda postocular blanca; amarillo brillante en región media del vientre con bordes laterales negros en patrón aserrado.

La especie es fácilmente diagnosticable, aunque su colocación en el genero *Taeniophallus* es problemática. Algunos caracteres sugestivos son compartidos con *T. brevirostris* y *T. nicagus*. Estas dos últimas, presumiblemente las especies relacionadas más cercanas geográficamente a *T. nebularis*, se encuentran en la cuenca Amazónica y en las Guayanas, indicando un paralelismo biogeográfico con ciertas plantas. *Taeniophallus occipitalis*, especie con extrema reducción de hileras de escamas dorsales y un patrón de color distintivo posiblemente derivado de un precursor similar a *T. brevirostris*, está ampliamente distribuida al sur del Amazonas. Cuatro especies adicionales de *Taeniophallus* sensu lato constituyen el grupo monofilético *affinis* con centro de distribución en el sureste de Brasil.

El genero *Echinantera* (también con un centro de distribución en el sureste de Brasil) es algunas veces expandido a incluir todo las especies en *Taeniophallus*. *Echinantera* s.s. es visto como un grupo demostrablemente monofilético que contiene seis especies, mientras que las relaciones entre los subgrupos de *Taeniophallus* s.l. y con respecto a *Echinantera* permanecen inciertas.

La divergencia evolutiva en los órganos copulativos es extraordinaria en las especies otrora similares *Taeniophallus nicagus* y *T. brevirostris*, lo cual sugiere que no se puede asignar de forma segura peso a los caracteres del hemipene en especies presumiblemente cercanas. El hemipenes de *T. nebularis* difiere de los de los otros taxa estudiados en ser conspicuamente

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bilobado en casi un tercio de su longitud. Sin embargo, cierto grado de bilobación es simplesiomórfico para estas serpientes, como se evidencia por la presencia o ausencia de bilobación débil en algunas especies y división de la inserción del músculo retractor en todas. La región desnuda en el lado asulcado del hemipenes en *T. nebularis* también pudiera ser simplesiomórfico para *Taeniophallus* s.l. y *Echinantera* s.s., pero la homología y nivel de generalidad de este carácter no es claro todavía.

INTRODUCTION

The Península de Paria marks the eastern end of the Cordillera de la Costa, a low mountain range that stretches brokenly along the north coast of Venezuela (map 1). This relatively small peninsula juts eastward for some 100 km, pointing to the disjunct Northern Range less than 40 km away on the island of Trinidad. The mountainous backbone of the Península de Paria attains a maximum elevation of 1370 m at Cerro Humo, but for the most part rarely exceeds 1000 m. The higher elevations in this region are protected by the National Park System of Venezuela (Península de Paria National Park) and support a lush cloud forest vegetation (Steyermark, 1973). The herpetofauna of the Península de Paria remains poorly studied, but recent work has resulted in the discovery of new species of frogs and lizards presumed to be endemic to the peninsula (Ayarzagüena and Señaris, ''1996'' [1997]; Rivas et al., 1999; Mijares-Urrutia et al., 2000).

The first two authors conducted fieldwork in the region of Cerro Humo in June 2002 and collected a single specimen of a distinctive new snake that we tentatively assign to the genus *Taeniophallus*, a genus previously unknown in Venezuela (reports of *T. brevirostris* in Venezuela were based on misidentifications; see Rivas et al., 2000; Rivas, 2001). The genus as presently constituted otherwise occurs from Guyana and Colombia south to Argentina, with seven recognized species (Myers and Cadle, 1994). The new snake from the Península de Paria has features of color pattern and morphology that readily distinguish it from other species of *Taeniophallus* s.l. and the possibly allied *Echinanthera* s.s.

MATERIALS AND METHODS: The specimen described is in the collection of the Museo de Historia Natural La Salle (MHNLS) in Caracas. Some comparative materials were used from the collections of the American Museum of Natural History (AMNH), the Museu de Zoologia da Universidade de São Paulo (MZUSP), and the University of Michigan Museum of Zoology (UMMZ).

Total length and tail length were determined to the nearest millimeter by straightening the preserved specimen along a metric rule. All other measurements were taken to the nearest 0.1 mm under a dissecting microscope, with dial caliper or ocular micrometer. Ventral scales were counted by the Dowling method with the number of preventrals noted (Myers, 2003: 6–7). Bilateral counts are separated by a solidus as left/right.

One hemipenis, half everted in the field, was removed from the snake and softened for 4 hours in a 3% solution of potassium hydroxide (KOH). The organ was checked at half-hour intervals until it had become flexible enough for the retractor muscle to be pulled back far enough to see (under a dissecting microscope) the 3-mm-long division of the muscle prior to its insertions on the hemipenial lobes; the muscle was severed across the insertion slips. The bilobed organ then was manually everted with the round head of a number 7 insect pin and inflated with carmine-dyed petroleum jelly for study and illustration. The other hemipenis was opened along the midventral surface and pinned flat for complementary comparison of the retracted condition (Myers and Cadle, 2003: 297–298).

Comparisons were made with everted hemipenes from representative *Echinanthera* and *Taeniophallus*; poorly resolved structures in the photographs are subtly emphasized by brush. Organs were removed for photography from the specimens below:

Echinanthera amoena, Brazil: Rio de Janeiro: near SE edge Teresópolis, 950 m (AMNH 119761)

Echinanthera sp., cf. *E. amoena*, Brazil: São Paulo: Boracéia, 850 m (AMNH 119763)

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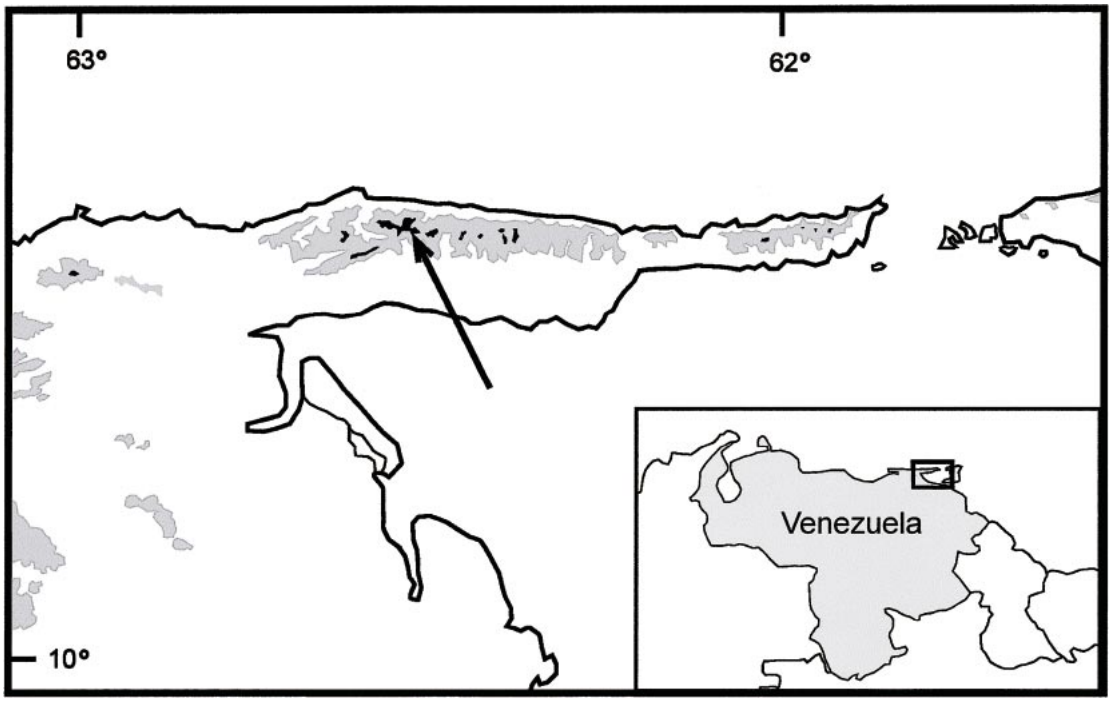

Map 1. Eastern end of the Cordillera de la Costa in the Península de Paria, which points east toward the island of Trinidad. Areas in gray are above 300 m, in black above 1000 m. Arrow denotes the type locality (800 m) of *Taeniophallus nebularis*, new species.

Echinanthera melanostigma, Brazil: São Paulo: Boracéia, 850 m (AMNH 119766)
Echinanthera undulata, Brazil: São Paulo: Boracéia, 850 m (AMNH 119767)
Taeniophallus affinis, Brazil: Espírito Santo: Santa Tereza (MZUSP 5032)
Taeniophallus bilineatus, Brazil: São Paulo: Campos do Jorão (MZUSP 1902)
Taeniophallus brevirostris, Ecuador: Pastaza: Sarayacu (AMNH 28799)
Taeniophallus nicagus, Brazil: Amazonas: Reserva INPA-WWF (MZUSP 7608)
Taeniophallus occipitalis, Brazil: São Paulo: São Paulo (MZUSP 2002)
Taeniophallus persimilis, Brazil: São Paulo: Boracéia (MZUSP 4108)

Taeniophallus nebularis, new species
Figures 1–6; map 1

HOLOTYPE: MHNLS 15743, an adult male from trail between Las Melenas and Cerro Humo, 800 m elevation (10°39′N, 62°34′W), Península de Paria, Estado Sucre, Venezuela. Collected by G. Rivas, C. Barrio, and W. Schargel on June 2, 2002.

ETYMOLOGY: The species name *nebularis*, ''belonging to the mist'', is derived from the stem of the Latin noun *nebula* (mist, fog) + the adjective-forming suffix *-aris* (belonging or pertaining to). The suffix (a variant of *-alis*), for stems ending in *l*, is declined *-aris* (masculine and feminine), *-are* (neuter).

DEFINITION AND DIAGNOSIS: Distinguished from all other species of New World ''xenodontine'' colubrids by the following combination of characters (based on the one known specimen, a male). *Size and proportions:* Small terrestrial colubrid more or less 500 mm in total length, with tail comprising about a third of total. Head distinct from neck, body slightly higher than wide, ventrolaterally rounded, with 19-19-17 rows of smooth dorsal scales; paired apical pits anteriorly. *Color pattern:* Dorsally brown with dark vertebral line from anterior body onto tail, sides gray; white postocular stripe to corner of mouth and lower neck. Midventer yellow between serrated edges of two parallel rows of triangular dark markings. *Scu-*

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Fig. 1. *Taeniophallus nebularis*, a new species of snake from Venezuelan cloud forest (MHNLS 15743, the adult male holtype), shown 3.2 times life size.

tellation: Ventrals 156, subcaudals 92 pairs, anal plate divided. Normal complement of colubrid head plates. Supralabials 8, with labials 2–3 touching loreal, 3–5 touching eye; one preocular, no small subpreocular. *Dentition:* Moderately high number (20) of maxillary teeth followed by diastema and two enlarged, offset, ungrooved fangs. *Hemipenis:* Noncapitate, approximately distal 30% bilobed. Sulcus spermaticus dividing about halfway up the organ, with centrolineal branches. Sulcate side calyculate to flounced above sulcus fork and on lateral sides of lobes, with large papillae tending to have spinulate tips. Lobes tipped with one or more enlarged apical calyces. Asulcate side of hemipenis with wide interspinal gap that becomes a broad nude area on eversion, extending distally from a transverse pair of large spines onto medial sides of lobes, flanked by dense clusters of small spines. Basal nude pocket present.

Readily distinguished from all other named *Taeniophallus* and also from species of *Echinanthera* s.s. by the presence of 19 rows of dorsal scales at midbody (vs. 17 or 15 rows) and unique hemipenis.

Description of the Holotype

The holotype is a male, shown to be sexually mature by strongly convoluted vasa deferentia, visibly convoluted kidney tubules, and hardened hemipenial spines. It is in good condition except that the posterior 13 mm of the intestinal/urogenital tract has been removed, and the left maxilla and both hemipenes were dissected out for study and illustration.

Proportions and Scutellation: A small snake, 492 mm in total length, with a moderately long tail comprising 32.7% of total length (tail length, 161 mm). Body higher than wide (midbody height 8.3 mm, midbody width 7.6 mm). Head wider than neck, 1.5 times longer than wide (head length 12.1 mm from tip of snout to corner of mouth; greatest head width about 8.0 mm). Snout truncated in dorsal view, rounded in profile; length from tip of snout to eye 3.8 mm (sagittal plane). Eyes somewhat protuberant, corneal outline visible in ventral view. Diameter of right eye 2.7 mm, left eye 2.6 mm, eye slightly greater than distance from its anterior edge to edge of naris. Pupil of eye round in preservative and in life (figs. 1, 2).

Rostral plate barely visible in dorsal view, 1.8 times wider than high. Internasals paired, each slightly wider than long. Prefrontals paired, each slightly longer than wide, 1.8 times longer than internasals, each in contact with its mate and with frontal, supraocular, preocular, loreal, posterior nasal, and internasal. Frontal roughly pentagonal, 1.7 times longer than wide, 1.4 times longer than distance from its anterior edge to tip of snout. Supraoculars twice as long as wide, 0.9 times frontal length. Parietals 1.4 times longer than wide; interparietal suture 0.8 times frontal plate length.

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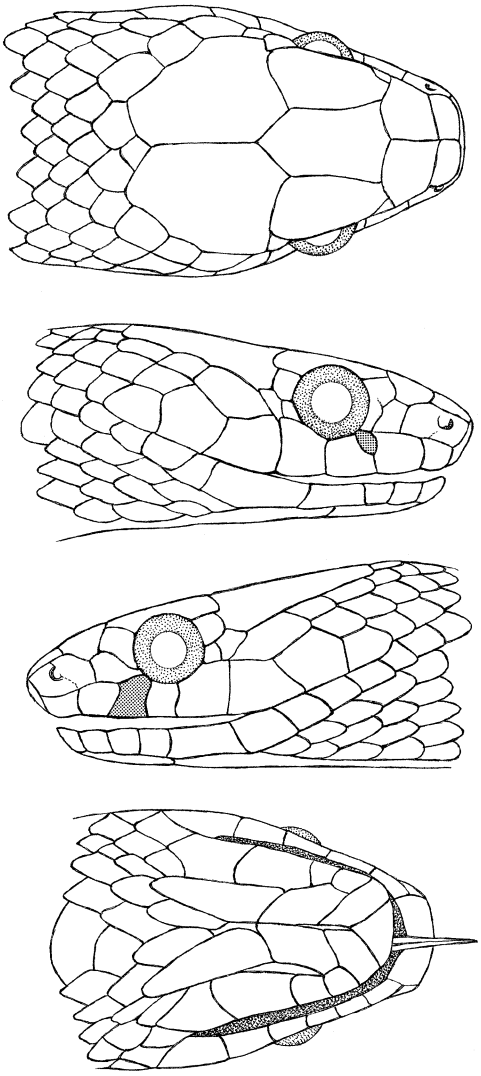

Fig. 2. Head scutellation of *Taeniophallus nebularis*, new species (holotype), approximately ×4. Note bilateral variation in third supralabial (shown in gray) and in loreal-preocular region.

Nasal plate divided, forming two subequal plates. Loreal higher than long, narrowly touching the eye below preocular on left side of head, but excluded from eye on right side (fig. 2). Single preocular. Two postoculars, upper about three times larger than lower. Temporals 1 + 1 + 2, the primary temporal small (perhaps aberrantly so), about same size as upper postocular. Supralabials 8/8—but third labial on right aberrantly small, not reaching lip (fig. 2); labials 2–3 in contact with loreal, 3–5 touching eye. Infralabials 8/8, 1–4 touching anterior genial, 4–5 touching posterior genial. Two pairs of genials, posterior pair 1.5 times longer than anterior genials and strongly diverging posteriorly. Minute sensory tubercles are present on all head plates. Relatively large, unpigmented circumocular scale organs (''pits'') absent on supraoculars but present on loreal and preocular, and present but inconspicuous on supralabials 2–5, upper postocular, and (on right side of head) on lower postocular and the small primary temporal.

Ventrals 156 + 1 preventral; subcaudals in 92 pairs. Anal plate divided. Dorsal scales smooth, lacking anal ridges, disposed in 19-19-17 rows. There are 19 rows one head length behind the head; reduction to 17 rows occurs by fusion of rows 3 + 4 at level of ventral 10, but 19 rows appear again by division of row 4 at ventrals 25/20; final reduction to 17 rows occurs by fusion of rows 3 + 4 at ventral 80. Small apical pits, usually paired (positioned off-center if single), discernible on most dorsal scales on neck—inconspicuous and easily overlooked (pits best seen under magnification while specimen is immersed in alcohol).

COLORATION (fig. 3): In life, dorsum brown on median 7–9 scale rows. Sides below brown middorsum dark grayish brown, gradually fading ventrad and turning pale gray on tips of ventral plates, forming a diffuse, indistinct ventrolateral stripe; this ventrolateral stripe wider on anterior fourth of body, extending up to second scale row. A dark grayish brown vertebral line extending from neck onto posterior half of tail, fading out toward the tip. The vertebral line on anterior third of body edged by small yellow dashes situated on adjacent basal edges of scales between vertebral and paravertebral scale rows; a few pale yellow dashes also present posterior to neck on basal scale edges between rows 4 and 5.

Brown atop head and on rostral and loreal regions; distinct small black blotches on prefrontals, internasals, nasals, rostral and postoculars; pair of pale parietal dots (color not noted in life). Supralabials white with some brown suffusion and black markings. A distinct, black-edged white postocular stripe extending from below lower postocular scale to

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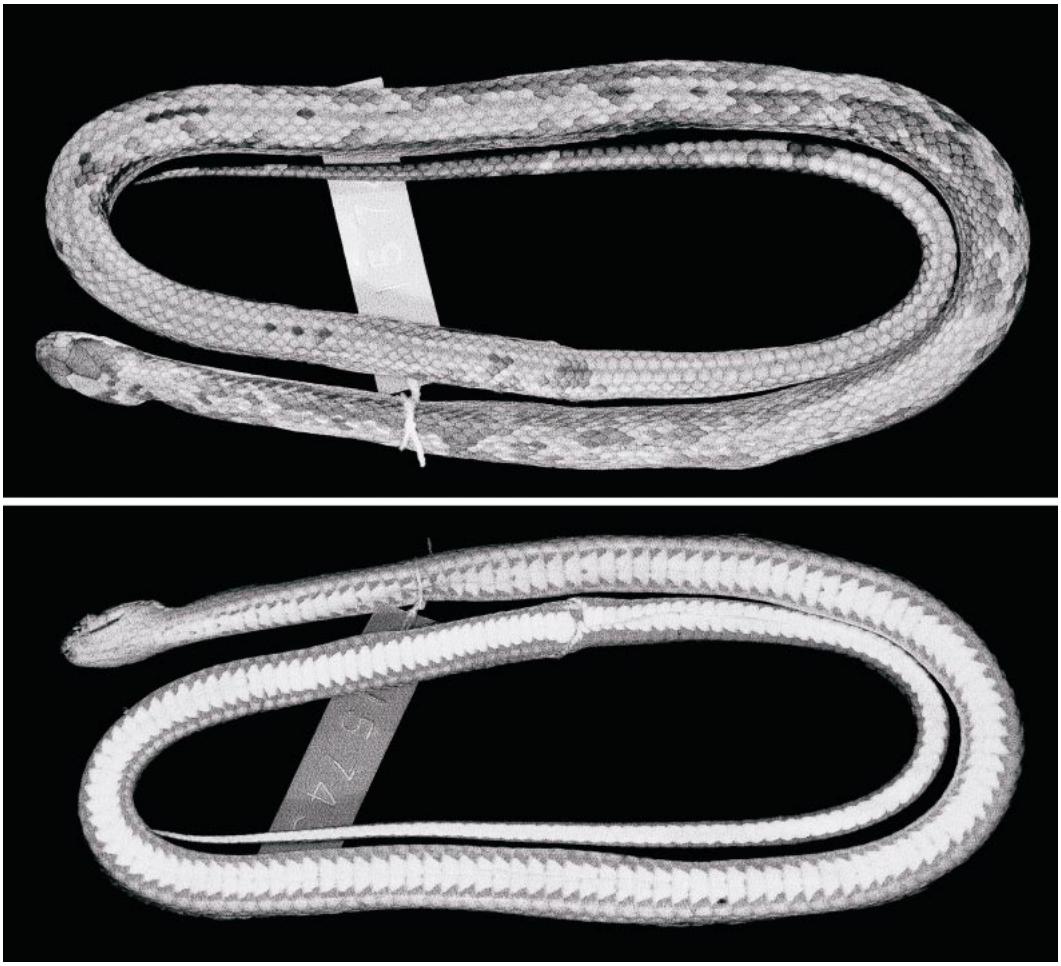

Fig. 3. *Taeniophallus nebularis*, new species. Dorsal and ventral views of the holotype and only known specimen (MHNLS 15743♂), shown about life size (×1.02).

corner of the mouth, then slanting posteroventrad and fading out on the neck at dorsal scale row 3. Iris pale on upper quarter sector, dark reddish brown below (fig. 1).

Underside of head white with some brown suffusion. Ventral surfaces of body and tail mostly bright yellow. The yellow coloration, which occupies about the median 55% of the venter, is in the shape of a trapezoid on each ventral plate, delimited on each side by a triangular blackish gray spot. The triangular dark spots, which are situated well away from the tips of the ventral plates, form parallel sawtoothed lines separating the bright yellow color from the gray ventrolateral stripe on each side.

After two years in 70% ethanol, most scales have lost the stratum corneum, with the dorsal ground color now appearing gray, with dark gray sides. The yellow anterior dorsal dashes have faded to white, and the yellow ventral color to cream. On the posterior part of the body, an ill-defined black lateral stripe can be seen on scale row 4 and the adjacent part of row 5, along the upper edge of the dark sides.

MAXILLARY DENTITION: In lateral view the maxillary bone (fig. 4) is slightly curved ventrad anteriorly and dorsad posteriorly. There are 20 relatively small, recurved maxillary teeth followed by a moderate-sized diastema and two enlarged, ungrooved fangs.

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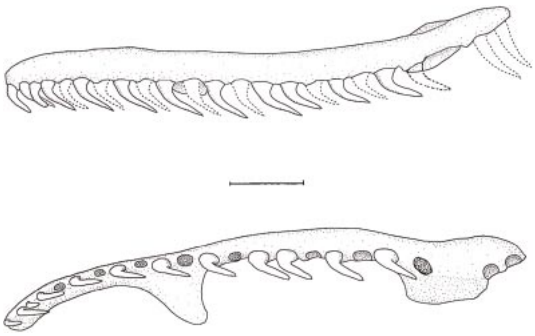

Fig. 4. Left maxilla of *Taeniophallus nebularis*, new species, shown in lateral and ventral view. Scale line = 1 mm.

The diastema is about equal to the space occupied by two prediastemal teeth. The posterior fang is offset laterad. The largest prediastemal teeth are those along the middle part of the maxilla. The last prediastemal tooth is situated posterior to the anterior edge of the ectopterygoid process. In ventral view, the maxilla anteriorly is slightly curved toward the medial plane of the mouth. The palatine process is blunt and slightly curved posteriorly.

Hemipenis

The left hemipenis, partially everted in the field, was removed from the snake and fully everted as explained in Materials and Methods. The right uneverted organ was also removed from the snake, for complementary description of the retracted morphology. The degree and manner in which parts of a hemipenis expand differentially cannot be determined by initial inspection of the retracted organ—nor can one easily retrieve the inverted morphology from the everted condition. Complementary comparisons provide better understanding of the hemipenis and potentially increase the number of taxonomic characters (Myers and Cadle, 2003: 297–298).

Retracted Hemipenis: The right uneverted hemipenis (figs. 5, 6A) extended to the level of subcaudal 7, with its retractor muscle originating posteriorly at the level of subcaudal 23. The following measurements (by ocular micrometer) were obtained after removing the organ from the snake, opening it along the midventral surface, and pinning it flat: total length, 11.5 mm; length of distal lobes 3.3 mm; length of insertion slips of the retractor muscle also 3.3 mm. The demarcation between muscle insertions and hemipenial lobes is unusually vague, since there is no abrupt change in circumference or any sharply defined juncture of the different tissues at insertion.

The distal lobes comprise 29% of the organ's total length. The sulcus spermaticus lies high along the lateral wall and forks a little more than halfway (52%) from the base—well below the start of bilobation—with one branch seen extending not quite to the end of the ventral lobe and the other branch disappearing into the dorsal lobe. The visible branch terminates about 0.8 mm from the apex of the lobe, just below the cluster of apical papillae.

The hemipenis is calyculate on its sulcate side; the calyces are flimsy and easily distorted, as emphasized in the caption to figure 5. Calyces originate slightly above the sulcus fork and extend distad between the sulcus branches and to either side (continuous into the dorsal lobe) as a distinct patch of papillate calyces. The outer calyces along the lateral edge of the patch are remarkably large and visually set off the patch from adjacent spines. The calyces bear large papillae that are compressed and pointed; although some of the papillae seem to have soft tips, most are seen under high magnification to be minutely spinulate. The calyces continue onto the apex of the lobe with larger, spinulate papillae and one terminal calyx that is exceptionally large and deep.

On the asulcate side of the hemipenis, a transverse pair of large, slightly recurved spines arise about 4.5 mm (39%) above the base. Above and slightly to the outside of these, two parallel rows of tightly packed and progressively smaller spines extend distad; one row (incised down its middle and shown along each edge of the opened organ in fig. 5) is seen extending nearly to the apex of the ventral lobe, whereas the other row of clustered spines disappears into the unopened dorsal lobe. The area between the two rows of clustered spines—the asulcate interspinal gap—is completely nude, extending from the enlarged spines nearly to the apex of the

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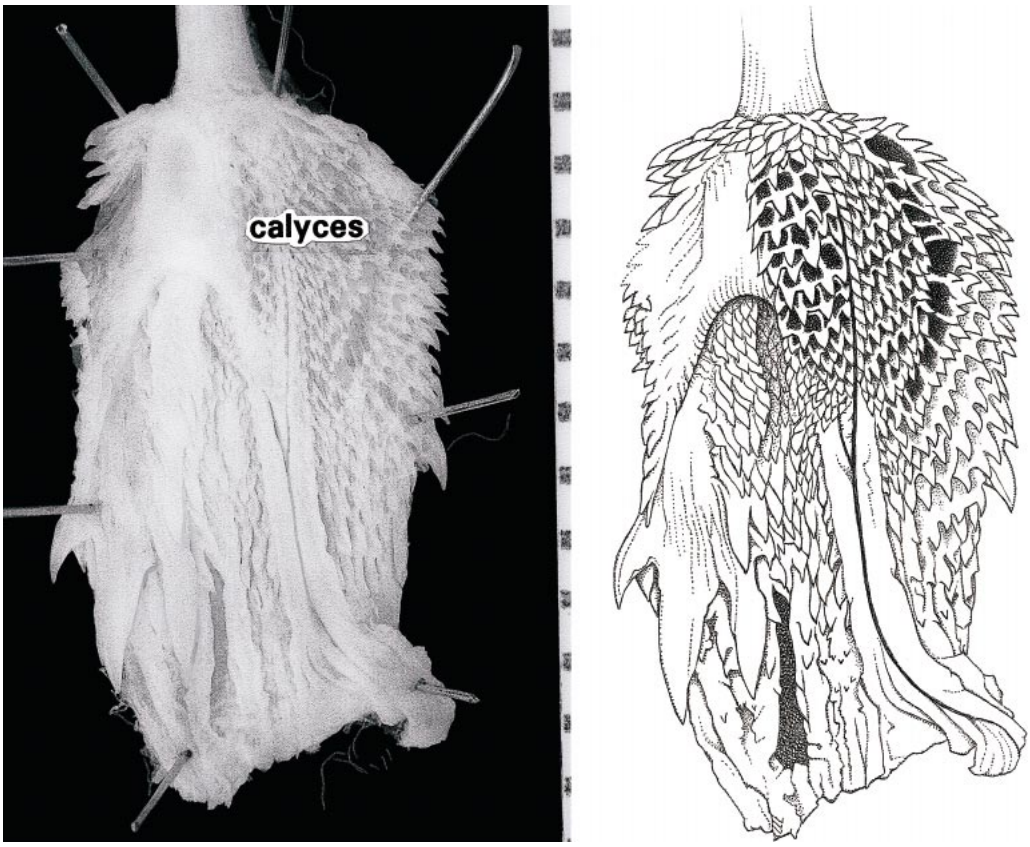

Fig. 5. Retracted hemipenis *Taeniophallus nebularis*, new species (right organ of holotype). **Left.** Enlarged photographic view of hemipenis opened midventrally and pinned flat. The walls of the different sized calyces are all thin and weak, leading to distortion at the slightest manipulation. **Right.** Scale drawing of same organ, showing diagrammatic rendition of the calyces. About ×8 (vertical scale divisions = mm).

lobe, terminating below the enlarged apical papillae. There is no indication anywhere of a groove or overhang that would convey capitation or semicapitation upon eversion.

A zone of small recurved spines extends across the organ below the calyculate area, becoming smaller on approaching the sulcus spermaticus. The lower edge of this zone is about at the level of the pair of enlarged spines, although there also are a few small spines just below the large pair. A long (2.8 mm), well-defined basal nude pocket extends up to the zone of small spines. Otherwise, the basal 22% of the organ is nude except for small, scattered spinules.

EVERTED HEMIPENIS: The everted organ (fig. 6B–D) is about 10 mm along its longest axis, and rather abruptly reclined at midorgan.[4] The lobes (including the apical ornamentation) comprise the distal 30% of the hemipenis. The sulcus spermaticus divides 5.5 mm (48%) from the base, with the branches extending in centrolineal orientation and terminating on the lobes short of the apices.

The distal part of the organ—from the division of the sulcus spermaticus—is both calyculate and flounced between the sulcus branches and on the sides of the lobes. The basal part of this area has fairly evident ca-

[4] It is not determinable whether this shape is inherent or a result of the hemipenis having been fixed in a half-everted condition.

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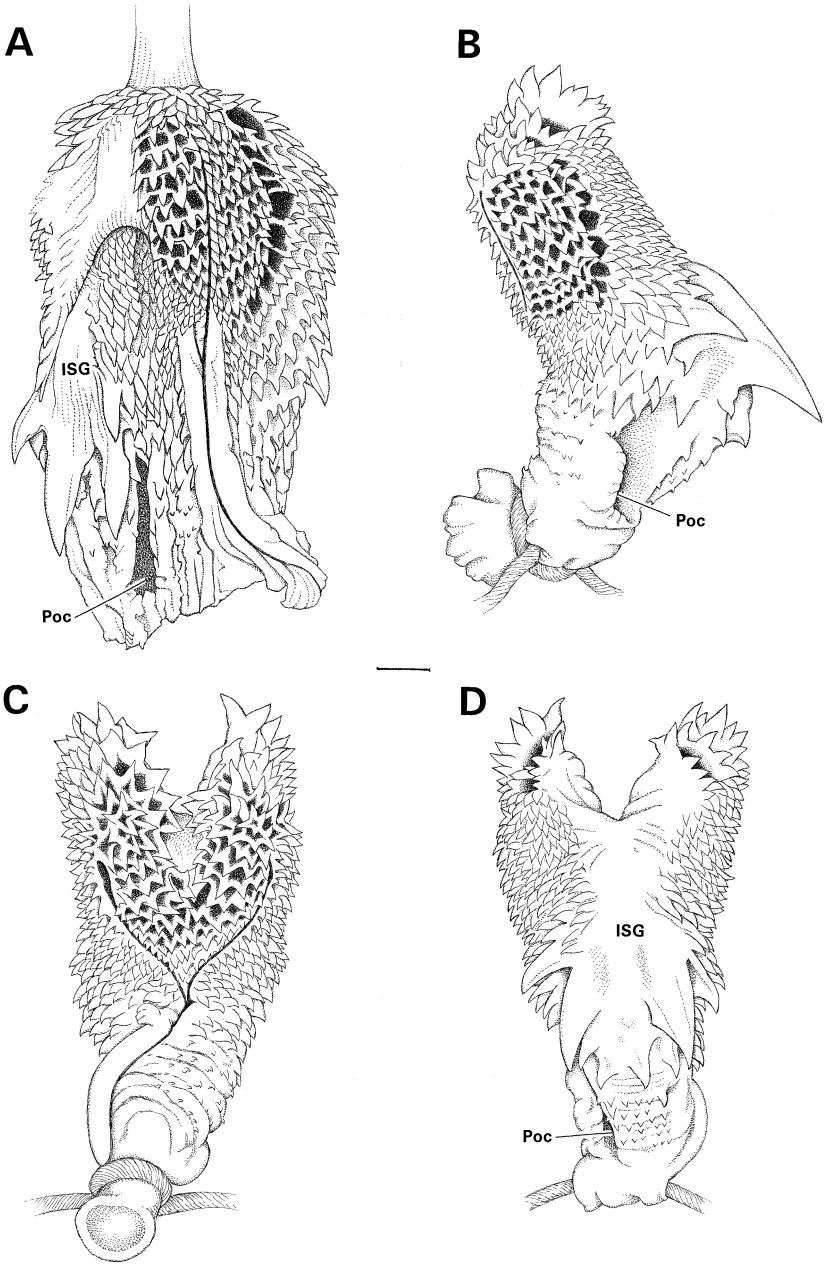

Fig. 6. Hemipenes of *Taeniophallus nebularis*, new species, left and right organs removed from holotype, all ×7. **A.** Retracted right hemipenis opened midventrally and pinned flat (see also fig. 5). **B–D.** Fully everted left hemipenis in lateral (B), sulcate (C), and asulcate (D) views. *Abbreviations:* Poc, basal naked pocket; ISG, interspinal nude gap on asulcate side. Scale line = 1 mm.

lyces, but distally on the lobes some of the vertical (longitudinal) calycular walls have so stretched on eversion that they have disappeared, leaving much of the area more flounced than calyculate. Both calyces and flounces bear large compressed pointed papillae, many of which can be seen on high magnification (e.g., ×30) to terminate in a

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minute hardened spinule. Laterally, the calyculate/flounced area ends as a longitudinal row of 5–6 greatly enlarged calyces with stretched and inconspicuous transverse walls. The calyces do not extend onto the medial walls of the lobes or into the lobular crotch, which are nude.

The apical ornamentation at the tips of the lobes is noteworthy. One lobe terminates in several enlarged, rather irregularly arranged calyces bearing large spinulate papillae. In contrast, the other lobe terminates in a single deep, relatively gigantic calyx, which bears a circle of a dozen large spinulate papillae.

The basal 20% of the hemipenis is nude except for a scattering of spinules and a long nude basal pocket. The asulcate side above the nude base bears several small spines, above which is a transverse pair of conspicuous and very large spines. The asulcate side of the organ is completely nude from the pair of large spines to the crotch and thence along the medial sides of the lobes to the apical calyces. The asulcate nude area is bordered along each side by a dense cluster of mostly small spines; each cluster begins with a medium-size spine above and to each side of the large pair, followed distally by numerous, tightly packed smaller spines of decreasing size. The basal section of each longitudinal spine cluster is confluent with an area of small spines that continues around to the sulcus spermaticus below the calyculate area.

Hemipenial Changes from Retracted to Everted: Considering measuring and other problems of comparing a straight flat object with an inflated one, basic proportions seem to be similar in these organs (retracted to everted): nude base 22–20% of organ's total length; lobes 28–30% of total length; division of sulcus spermaticus 52–48% from base. Also, there is good correspondence in the termini of the sulcus branches, which fail to reach the apices of the lobes in both retracted and everted states.

Aside from eversional acquisition of an inflated shape that cannot be precisely predicted from the retracted condition, the most striking difference is the change from a calyculate to a partially flounced ornamentation distally on the lobes. The calycular walls are fragile, quite unlike the relatively sturdy structures of many snakes. Some of the longitudinal calycular walls in the distal part of the calyculate patch have disappeared during tissue expansion, leaving a few distinct lines of papillate flounces.

Distribution, Habitat, and Associates

Taeniophallus nebularis is known only from the type locality, at an elevation of 800 m in the region of Cerro Humo (map 1, fig. 7). The vegetation at this locality falls within the category of ''Coastal Cloud Forest'' according to the classification of Huber and Alarcón (1988). Cloud forests in Paria extend from just below 800 m up to the highest elevation in this region (Steyermark, 1973). These forests were described by Steyermark (1973) as having trees reaching 20–25 m in height, with an abundance of epiphytic plants that include bromeliads, ferns, and orchids among others. A diversified lower stratum is composed mainly of palms, such as *Prestoea pubigera* and *Bactris* spp., and small trees and bushes in the families Lauraceae, Rubiaceae, Melastomataceae, and Meliaceae.

The only known specimen of *Taeniophallus nebularis* was active during daylight hours on the forest floor when first seen. It retreated under a rock when approached. Other species of reptiles known to occur in the Paria cloud forests are: *Anadia pariaensis*, *Bothrops venezuelensis**, *Euspondylus monsfumus*, *Gonatodes ceciliae**, *Liophis reginae**, *Mabuya* sp.*, *Plica plica**, and *Proctoporus* sp.* (an asterisk denotes species collected by Rivas and Schargel in June 2002). Several unidentified species of frogs in the genera *Colostethus* and *Eleutherodactylus* were common in the leaf litter where the specimen of *Taeniophallus nebularis* was collected. Other frogs collected by Rivas and Schargel on Cerro Humo were *Cochranella castroviejoi* and *Mannoprhyne riveroi*, which were always associated with streams, and *Flectonotus fitzgeraldi*, found sitting on leaves inside the forest. Additionally, on repeated occasions at night, an unidentified *Gastrotheca* was heard calling from high in the trees.

GENERIC COMPARISONS AND PLACEMENT

Historical Perspective

At one time, the new snake named above would have been assigned to the old Copeian

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Fig. 7. Montane cloud forest at the type locality of *Taeniophallus nebularis*, new species.

genus *Rhadinaea*. In the loosest sense, this was an artificial (nonmonophyletic) assemblage of small serpents widely distributed on the New World mainland from North Carolina to east-central Argentina. The *Rhadinaea*-like snakes are mainly tropical species of similar habits and habitus—terrestrial in forest, usually diurnal (always with round pupils), small and slender, often striped, and with a generalized colubrid morphology.

Although still not yet strictly monophyletic, *Rhadinaea* currently is recognized as a primarily Middle American genus belonging to the colubrid subfamily Dipsadinae. *Taeniophallus nebularis*, on the other hand, is to be compared with two groups of South American snakes formerly associated with *Rhadinaea*: (1) the *R. brevirostris* group sensu Myers (now = *Taeniophallus* s.l.), and (2) a cluster of species allied with "*Rhadinaea*"

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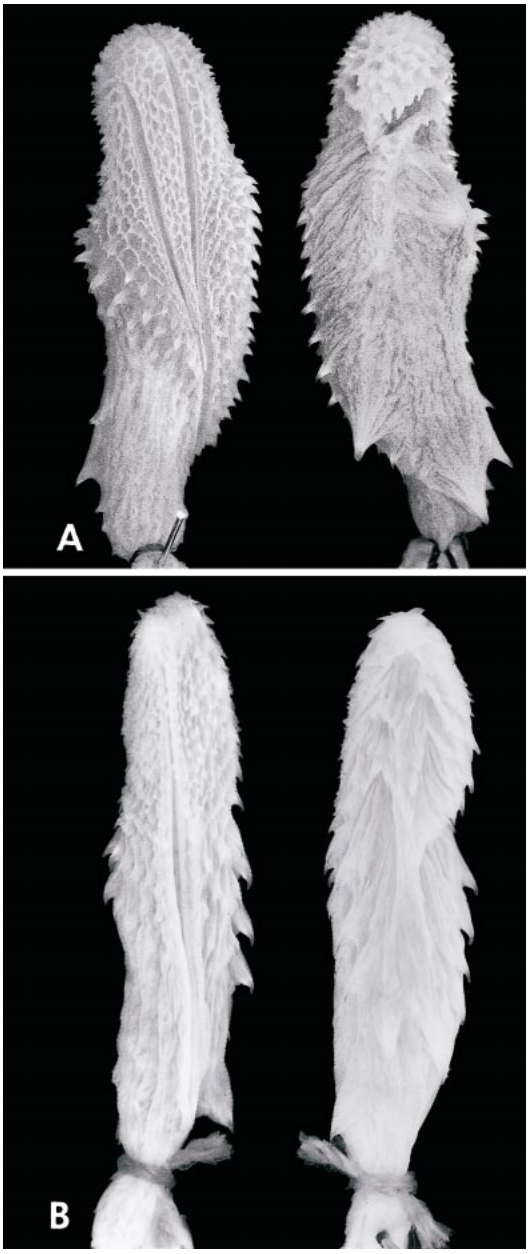

Fig. 8. Everted hemipenes of *Taeniophallus* s.s., in sulcate and asulcate view. **A.** *T. brevirostris*, AMNH 28799, right organ ×3.4. **B.** *T. nicagus*, MZUSP 7608, right ×5.8. (Laboratory preparations from preserved retracted hemipenes, fully everted but incompletely expanded.) Notice the unequal branch lengths of the sulcus spermaticus in *T. brevirostris*, and the *single*, undivided sulcus spermaticus in *T. nicagus*. These derived-conditions are rare among New World ''xenodontine'' snakes and suggest caution in the uncritical acceptance of hemipenial characters in generic diagnoses.

undulata sensu Boulenger, later known as the ''*Liophis undulatus* group'' (now = *Echinanthera* s.s.).

The subfamilial status of the South American genera *Echinanthera* and *Taeniophallus* is not settled, as indicated by Zaher (1999: 4), who placed them as ''Xenodontinae and Dipsadinae Incertae Sedis''. Biochemical and molecular data indicate that *Taeniophallus* (*T. brevirostris*, *T. occipitalis*) is allied with Xenodontinae s.s. (Cadle, 1984; Vidal et al., 2000).

Also unsettled is the relationship between *Taeniophallus* and *Echinanthera*. Di-Bernardo (1992) resurrected the name *Echinanthera* Cope, for which he included the closely related species *amoena*, *cyanopleura* (type species), *melanostigma*, and *undulata*, and also the six species that had been earlier placed by Myers in the ''*Rhadinaea*'' *brevirostris* group (*affinis*, *bilineatus*, *brevirostris*, *occipitalis*, *persimilis*, and *poecilopogon*). Myers and Cadle (1994: 4–5) commented on two reasons given by Di-Bernardo's (1992: 227) rationale for including the *brevirostris* group, stating that Di-Bernardo had misinterpreted Cadle's previously published immunological data, and disputing the presence of ''enlarged asulcate papillae'' (sensu Myers) on the hemipenis as a shared character.

Myers and Cadle (1994: 4–6) reported the discovery that *Taeniophallus nicagus* (type locality unknown) is a South American snake. Although *nicagus* is highly unusual among Neotropical ''xenodontines'' in having a simple sulcus spermaticus (fig. 8B), in other features it is remarkably similar to *Rhadinaea brevirostris*, which is itself unusual in having one of the sulcus branches shorter than the other (fig. 8A). The relationship between *nicagus* and *brevirostris* seemed as unmistakable as accumulating evidence that the *brevirostris* group should not be kept in *Rhadinaea* (see Myers and Cadle, 1994: 3–4). For those reasons, *Taeniophallus* was resurrected as a convenient depository for the entire *brevirostris* group.

Cacivio et al. (1999: 81) and Giraudo and

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Scrocchi (2002: 15) stated that Di-Bernardo and Di-Bernardo had conducted a new study and had demonstrated that there are more synapomorphies between *Echinanthera* and the species of the *R. brevirostris* group than between these and *Taeniophallus* sensu stricto (i.e., *T. nicagus* only). The study cited was a partial-page meeting abstract in which the authors were bothered by the simple sulcus spermaticus of *Taeniophallus nicagus*, and so they suggested the following ''synapomorphies'' shared by *Echinanthera* and the *brevirostris* group minus *T. nicagus*:

> These possible synapomorphies are represented by the (1) lack of dorsal scale-row reduction except in *occipitalis* and *brevirostris*, (2) semicapitation of the hemipenes except perhaps in *brevirostris*, (3) asulcate side of hemipenis with a distinct longitudinal nude strip devoid of ornamentation, and (4) bifurcation of the sulcus spermaticus. (Translated from Di-Bernardo and Di-Bernardo, 1996)

There seems to be some confusion in the paragraph above about what a synapomorphy is. A bifurcated sulcus spermaticus, for example, is shared with few exceptions by nearly *all* dipsadine and xenodontine colubrids and is therefore plesiomorphic in *Echinanthera* and *Taeniophallus*. The undivided sulcus of *Taeniophallus nicagus* simply is a single-species apomorphy whose polarity seems to be clearly established by the shortening of one sulcus branch in the related *T. brevirostris*. Character 3 above—the interspinal asulcate gap (not always nude)—certainly is informative at some level to be explored, but Cadle and Myers (1994: 5) had already commented on aspects of its taxonomic distribution in ''*Rhadinaea*'' s.l., including the fact that it is *not* shared by *T. brevirostris*, nor is it present in *nicagus*.

Myers and Cadle (1994: 5) stated that ''possible relationships between the *brevirostris* group (in whole *or in part*) and *Echinanthera* have not been demonstrated and remain to be investigated'' (emphasis added). Zaher (1999: 78–79, 81–82, figs. 85–86, 92–93) contributed to the process, with new descriptions of the everted hemipenial morphology of three species of *Echinanthera* (*amoena*, *melanostigma*, *undulata*) and four species of *Taeniophallus* (*affinis*, *bilineatus*, *occipitalis*, *persimilis*). Zaher agreed with Di-Bernardo's earlier observations of hemipenial similarity among the species that he studied. However, Zaher noted Myers and Cadle's earlier comments on the differing hemipenial morphology of *T. brevirostris* and *T. nicagus*, and concluded that,

> Although it is suggested that the nude areas present in some species of *Rhadinaea* and *Echinanthera*/*Taeniophallus* may not be homologous, evidence supporting this view is tenuous and a more thorough review of the hemipenial morphology of these genera is needed before the nude area edged by rows of spines can be interpreted as a synapomorphy of an *Echinanthera*/*Taeniophallus* clade (the hemipenial morphology of *T. occipitalis* being especially puzzling). (Zaher, 1990: 79)

The new snake ''*Taeniophallus*'' *nebularis* will be compared with *Taeniophallus* s.l. and *Echinanthera* s.s. after a few preliminary background observations on each.

Taeniophallus Cope

This genus may not be monophyletic, but data are insufficient for firm conclusions. Three species groups can be recognized for discussion.

1. *Taeniophallus brevirostris* and *Taeniophallus nicagus*: Cope's description of the then monotypic *Taeniophallus* (type species *Lygophis nicagus*, type locality unknown) was based partly on material of ''*Rhadinaea*'' *brevirostris* (fide Myers, 1974: 208); these two snakes were long confused until the rediscovery of *T. nicagus* as a South American snake (Myers and Cadle, 1994: 4). Sufficient material has been accumulated for more detailed comparisons and elucidation of geographic ranges of *T. brevirostris* and *T. nicagus* (Myers and Cadle, in prep.).

They are small snakes, less than 500 mm in total length, usually with a broad middorsal stripe having undulating or serrated edges. Dorsal scale formula 17-17-15; apical pits often present. There are consistently 8 supralabials (variation is rare), with the 2nd touching the loreal and the 3rd–5th touching the eye. There are about 12–16 prediastemal maxillary teeth. Striking similarity in color pattern and morphology is suggestive of close relationship. Hemipenial differences, although remarkable, do not necessarily contradict such a relationship.

Taeniophallus nicagus is characterized by an undivided sulcus spermaticus (fig. 8B).

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Taeniophallus brevirostris has a bifurcated sulcus, but one branch is shorter than the other (fig. 8A). These conditions are rare or unique among Neotropical dipsadine and xenodontine colubrids. Shortening and eventual loss of one branch seems the likely explanation for the simple sulcus in *T. nicagus*. Neither *brevirostris* nor *nicagus* has an interspinal nude area on the asulcate side of the hemipenis.

2. *TAENIOPHALLUS OCCIPITALIS*: This is a distinctive species that is set off by a low number of scale rows (15-15-15 or 15-15-13, apical pits not detected) and an unusual anteriorly blotched to posteriorly spotted color pattern (Myers, 1974: 209, figs. 46E, 48). It is a small snake, with total length approaching (and probably exceeding) 500 mm. There are consistently 8 supralabials, with the 2nd touching the loreal and the 3rd–5th touching the eye. There are 13–15 prediastemal maxillary teeth ($N = 12$ specimens).

There is a distal interspinal nude area on the asulcate side of the single or slightly bilobed hemipenis, but it is quite short, being set off proximally by a very large spine at midorgan (fig. 9D) and ending distally deep under the overhanging edge of the capitulum. The papillae on the calyces gradually become thick and spinulate over the asulcate side of the capitulum, becoming largest near the edge of the capitulum, where a horizontal row of large soft spinules overhangs the distal end of the short interspinal nude gap.

Taeniophallus occipitalis resembles *T. poecilopogon* (see below) in having a conspicuous pale canthal line, but its closest relationships may well be with *T. brevirostris* and *T. nicagus*. The everted hemipenes of *T. brevirostris* and *T. occipitalis* are more different than had been suspected from study of retracted organs, but similar ''thick, knoblike spinules'' were noted on the asulcate side of the capitulum of some retracted organs of both species (Myers, 1974: 205, 211), and the ''gigantic calyx'' or pocket in the lower edge of the capitulum of *T. brevirostris* may well be a homolog of the very deep but proximally open capitulate overhang in *T. occipitalis*. Aspects of the dorsal color pattern in some specimens of *T. occipitalis* suggest the possibility of derivation from a *brevirostris*-*nicagus*-like ancestor (Myers and Cadle, unpubl.).

3. *TAENIOPHALLUS AFFINIS* GROUP: This comprises the four southernmost species of the old *Rhadinaea brevirostris* group, namely *Taeniophallus affinis*, *T. bilineatus*, *T. persimilis*, and *T. poecilopogon*. Myers (1974) had available fewer than 20 specimens of these (1–8 specimens per species), but, in a series of papers, Di-Bernardo and Lema (1986–1991) subsequently presented data on some 200 specimens (9–110 per species), extending the known variation and geographic ranges, and confirming Myers' placement of two older names (*Liophis insignissimus*, *Rhadinaea beui*) in the synonymy of ''*Rhadinaea*'' *persimilis*.

These are rather small snakes, seldom exceeding 500 mm in total length, except for the medium-sized *Taeniophallus affinis*, in which males exceed 600 mm and females 700 mm in total length. There are 17 dorsal scale rows without reduction; apical pits appear to be absent in the *affinis* group.[5]

There are 7 supralabials, with the 2nd in contact with the loreal and with the 3rd–4th *consistently* touching the eye. Deviation from this pattern is rare (one specimen of *T. bilineatus*, MZUSP 4500, has 8 supralabials on one side only, with the 2nd–3rd touching the loreal but with the 3rd–4th in the orbit as normal).

A vertebral dark line or a wider *nonundulatory* middorsal stripe present or absent; a tendency for a thin pale line or row of pale spots along row 4, above a narrow dark stripe or dark sides; a tendency for a line of dark dots on each side of the venter (or ventrals dark-edged in *poecilopogon*), with venters otherwise immaculate or nearly so.

There are usually fewer than 20 prediastemal maxillary teeth except in *bilineatus*, which has a maximum of 23, with species differences as follows[6]:

[5] Myers (1974: 40) failed to find apical pits in these four species, and Di-Bernardo and Lema (1987: 212) specifically mentioned their absence in *T. poecilopogon*.

[6] The ranges in numbers of prediastemal teeth are derived from Myers (1974: 197, and subsequent unpubl. data), combined with the larger samples in Di-Bernardo and Lema (1986: 117–118; 1987: 213; 1988: 232, 234; ''1990'' [1991]: 372, 390).

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T. affinis 8–18 (N = 54)[7]
T. bilineatus 18–23 (N = 28)
T. persimilis 15–18 (N = 18)
T. poecilopogon 13–18 (N = 17)

The hemipenis is single, with an asulcate interspinal gap that becomes conspicuous on eversion. This gap is not nude, but bears a medial line of at least several spinules or papillae. The interspinal gap, open proximally, extends distally nearly to the calyculate tip of the hemipenis, where it terminates at an asulcate cluster of several enlarged papillae that are further differentiated in being flap-like or spinelike. Figure 9 shows these differentiated asulcate papillae on everted hemipenes of three of the four species in the group—*T. affinis* (fig. 9A), *T. bilineatus* (fig. 9B), and *T. persimilis* (fig. 9C). A retracted organ of the fourth species, *T. poecilopogon*, was said to have ''relatively large'' papillae on the asulcate side of the tip, and to be similar to that of *T. affinis* (Myers, 1974: 217).

The differentiated asulcate papillae appear to be a hemipenial synapomorphy supporting the monophyly of the *Taeniophallus affinis* group. Also synapomorphic is the supralabial pattern (7 labials, 2nd in loreal, 3rd–4th in orbit), which is practically invariant. These snakes otherwise are generalized small terrestrial colubrids that are ''*Rhadinaea*-like'' in most external features.

The hemipenial interspinal asulcate gap is similar to that in *Echinanthera* s.s., the species of which differ in most other features.

Echinanthera Cope

This is a well-defined genus, at least in the strict sense when considering the closest relatives of the type species. In this context, six species seem assignable: *Echinanthera amoena*, *E. cephalomaculata*, *E. cephalostriata*, *E. cyanopleura* (type species), *E. melanostigma*, and *E. undulata*. Two of these were recently described by Marcos Di-Bernardo, the principal authority on the genus: he named the outlying *E. cephalomaculata* based on two specimens from Estado Alagoas in northeastern Brazil (Di-Bernardo, 1994), and he teased out the new *E. cephalostriata* from *E. cyanopleura*, with which it had been confused (Di-Bernardo, 1996).

These are medium-sized terrestrial snakes, all probably exceeding 600 mm total length.[8] Based on relatively few measurements (Myers, unpubl.; Di-Bernardo, 1996: 123), maximum total lengths reach or exceed 700 mm in *amoena*, *cephalostriata*, and *undulata* and exceed 800 mm in *cyanopleura* and *melanostigma*. A female *melanostigma* (UMMZ 63030) was measured at 882 mm total length, and meter-long *Echinanthera* seem likely.

There are 17 dorsal scale rows without reduction. Apical scale ''pits'' are present on some specimens of at least five species.[9] These scale organs are either paired or single (if single, the pit is an apparent remnant of a pair, being offset from the median). There normally are 8 supralabials (rarely 7 or 9), usually with 2nd–3rd or 2nd only touching the loreal and 3rd–5th (less commonly 4th–5th) in the orbit. This differs significantly from the *Taeniophallus affinis* group (7 supralabials, 3rd–4th in orbit).

The color pattern includes a strongly undulating middorsal stripe in *cephalomaculata* and *undulata* and in at least some specimens of *cyanopleura* (e.g., the syntypes), but this stripe seems to have been degraded to some

[7] There is variation in numbers of prediastemal teeth in most snakes, with the difference between extreme counts usually seeming to be in the range of perhaps 2–5 teeth for many South American colubrids (e.g., Myers, 1974: 29, table 1). The large variation in *Taeniophallus affinis* is therefore noteworthy.

Myers (1974: 29, 199) noted that two *affinis* specimens with the maxillary formula 10 + 2 had all the teeth short and thick, compared with relatively longer, more slender teeth in four snakes with the formulae 14 + 2–18 + 2. Since then, however, an additional specimen with the formula 10 + 2 was coded with seemingly normal teeth. This variation is not explained, although Di-Bernardo and Lema (1988: 232) showed that geographic variation is involved in total counts. Assuming that sibling species are not being confused, one might expect the existence of geographic shifts in availability of major prey types.

[8] The female holotype of *Echinanthera cephalomaculata* measured 561 mm total length, but only two specimens of this species are known (Di-Bernardo, 1994).

[9] Apical pits were not mentioned in Di-Bernardo's (1994) description of *Echinanthera cephalomaculata*. Myers has coded presence of these scale organs in specimens of *E. amoena*, *E. cyanopleura*, *E. melanostigma*, and *E. undulata*, and Di-Bernardo (1996: 123) reported small paired (rarely single) apical pits in *E. cephalostriata*. Some specimens seem to lack these structures completely. They are constant and easily seen in some genera, but a difficult character in such groups as *Echinanthera*. See Myers (1974: 40–41) for discussion.

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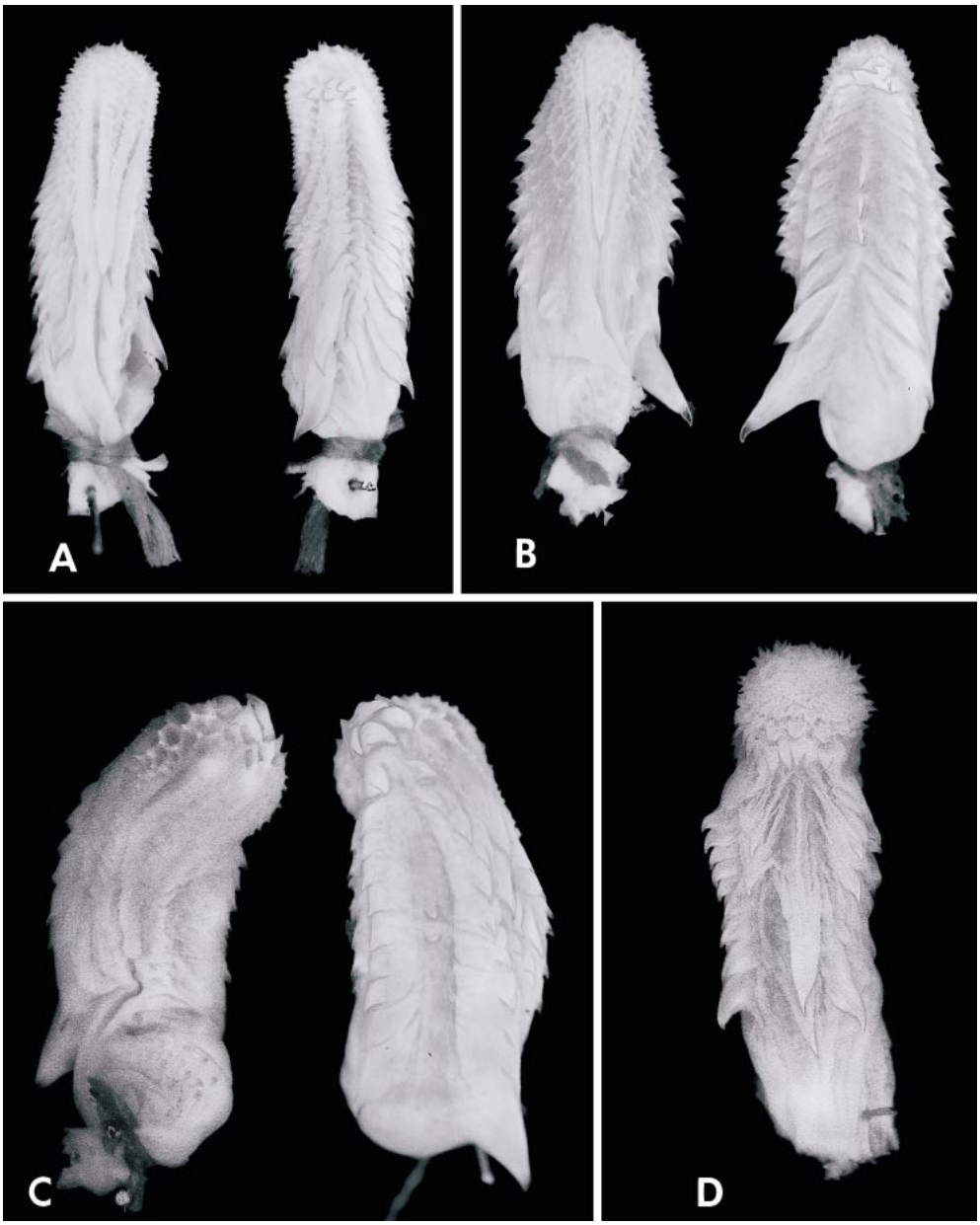

Fig. 9. Everted hemipenes of *Taeniophallus* s.l., in sulcate and asulcate view. **A.** *T. affinis*, MZUSP 5032, right organ ×6.9. **B.** *T. bilineatus*, MZUSP 1902, left ×6.3. **C.** *T. persimilis*, MZUSP 4108, left ×6.7. **D.** *T. occipitalis*, MZUSP 2002, right organ in asulcate view, ×7.1. (Laboratory preparations from hemipenes preserved in retracted or partially everted condition; fully everted but not necessarily completely expanded.)

isolated spots in *cephalostriata* (Di-Bernardo, 1996: fig. 1) and *melanostigma*, and it is essentially lost in *amoena*. A line of whitish dashes or small spots along rows 3 and/or 4. Normally dark dots on the ends of the ventrals. Specimens of all species except *amoena* and *cephalomaculata* have conspicuous gray or blackish crossbanding over much of the

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belly; variation in the ventral crossbands includes their ontogenetic development, at least in *undulata*; a few traces of crossbanding are retained in some specimens of *amoena*.

There normally are more than 25 prediastemal maxillary teeth, with variation as follows[10]:

E. amoena 25–28 ($N = 4$)
E. cephalomaculata 27–28 ($N = 2$)
E. cephalostriata 24–32 ($\bar{x} = 27.8$, $N = 35$)
E. cyanopleura 27–29 ($N = 2$)
E. melanostigma 27–32 ($N = 6$)
E. undulata 29–32 ($N = 12$)

The strongly calyculate hemipenis has an interspinal asulcate gap that becomes pronounced upon eversion. This gap is not necessarily nude as sometimes stated, but usually contains a median line of tiny spines or spinelike papillae along part of its length (fig. 10). The calyces are papillate, with the papillae becoming either slightly or markedly larger, even spinulate on the asulcate side above the upper end of the interspinal gap—but they do not form a differentiated cluster. There is no small asulcate cluster of *abruptly* enlarged, strongly differentiated papillae such as in the *affinis* group of *Taeniophallus* (compare fig. 10 with fig. 9A–C).[11]

The monophyly of *Echinanthera* s.s. is supported by the derived condition of a large number of prediastemal maxillary teeth (25–32)—an unusually high number among most dipsadine and xenodontine colubrids. An undulating middorsal stripe and ventral crossbanding also may be synapomorphic for *Echinanthera*, with apomorphic degradation in a few species. Other characters that distinguish *Echinanthera* s.s from the *Taeniophallus affinis* group include scale pits and generally larger size of the former, and the apomorphic supralabial pattern in the latter.

Systematic Conclusions

Echinanthera sensu stricto comprises a demonstrably monophyletic group, compared with *Taeniophallus* sensu lato, which is comprised of two or three definable groups whose relationships among themselves and with *Echinanthera* remain to be demonstrated.

The new snake named herein as *Taeniophallus nebularis* does not fit easily into either genus, differing notably in dorsal scale formula and especially in the hemipenis. Clearly, however, it does not fall within *Echinanthera* s.s. It is a smaller snake, lacking a high number of prediastemal maxillary teeth, and it has none of the dorsal or ventral pattern elements that characterize species of *Echinanthera*.

The unique hemipenis of the new snake might justify separate generic status. However, as emphasized by a few students of the subject (especially Zaher and Prudente, 2003; see also Myers, 1974: 30), hemipenial characters are not necessarily as conservative as often thought. Caution is especially warranted when dealing with possible relatives of *Taeniophallus brevirostris* and *T. nicagus*, in which hemipenial evolution seems to have outpaced that of other standard characters.

The pronounced bilobation of the hemipenis of *Taeniophallus nebularis* is judged primitive relative to the condition in other *Taeniophallus* and *Echinanthera*. These mostly have single organs, but a slight division in the insertion of the retractor muscle of all species points to bilobed precursors, which is further indicated in two species of *Taeniophallus*—the hemipenes of both *T. brevirostris* and *T. occipitalis* vary intraspecifically from single to slightly bilobed. The pronounced (wide) asulcate interspinal gap on the *T. nebularis* hemipenis also might be a plesiomorphy broadly shared with *Echinanthera* and the *affinis* and *occipitalis* groups of *Taeniophallus*, but the homologies and level of generality assignable to this character are not yet clear.

Accepting that hemipenial morphology provides insufficient support for establishing a new genus in this case, the allocation of

[10] The ranges in numbers of prediastemal teeth are from Myers (unpubl. data) for all species except *E. cephalomaculata* and *E. cephalostriata*, which are based on the original descriptions by Di-Bernardo (1994, 1996: 123). It would be interesting to know if there is a geographic component in the extensive variation of *E. cephalostriata*.

[11] For species of both *Taeniophallus* and *Echinanthera*, Zaher (1999: 78–79, 81–82) mentioned "enlarged flaplike papillae" around the edge of the asulcate interspinal area, apparently not distinguishing the *abruptly differentiated cluster* of enlarged papillae that characterizes *T. affinis* group species. This character is visible in figure 9A–C. The *Echinanthera* organs in figure 10 show nothing comparable on close examination.

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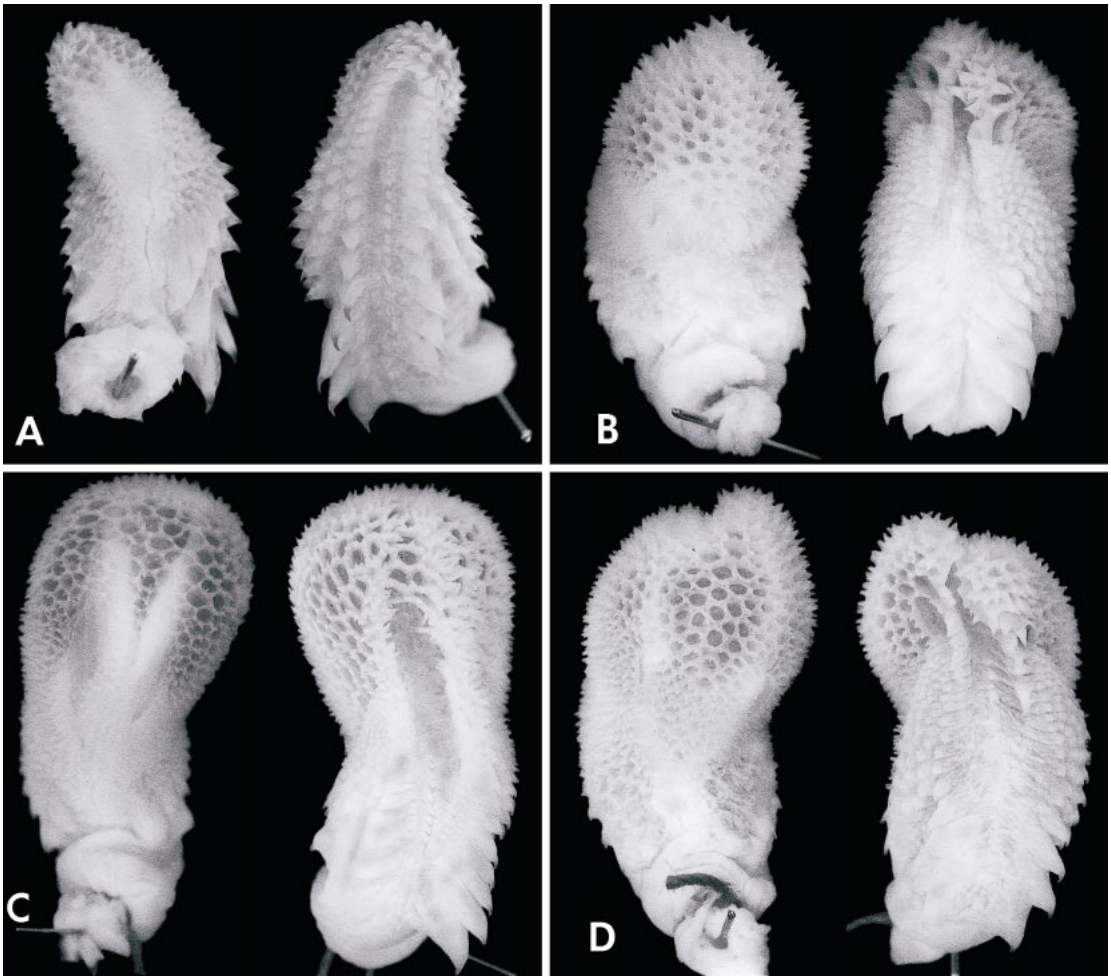

Fig. 10. Everted hemipenes of *Echinanthera* s.s., in sulcate and asulcate view. **A.** *E. undulata*, AMNH 119767, right organ ×6.4. **B.** *E. amoena*, AMNH 119761, left ×5.5. **C.** *E. melanostigma*, AMNH 119766, left ×4.3. **D.** *E.* species, cf. *E. amoena*, AMNH 119763, left ×4.7. (Field eversions made before preservation.)

the new snake to *Taeniophallus* s.l. seems the most reasonable alternative. One derived character points to possible alliance with *Taeniophallus* s.s. (i.e., *T. nicagus* + *T. brevirostris*): *T. nebularis* resembles these species in possessing unusually large scale organs (''pits'') that involve all circumocular scales except the supraocular.[12]

[12] See Myers (1974: 40, 203) for discussion of this character in *Taeniophallus brevirostris*. Smaller pits (coded as ''small'' or ''moderate'') can be seen mainly on the preoculars and postoculars of some specimens of *Taeniophallus occipitalis* and species of *Echinanthera*. All seem likely to be homologous, but their development is striking in *T. nebularis* and especially *T. brevirostris*.

The ventrolateral triangular black markings of *T. nebularis* (fig. 3) seem novel at first blush, but variation in *T. brevirostris* provides a parallel and possible homology. *Taeniophallus brevirostris* normally has on each side a fairly straight-edged ventrolateral dark line or stripe, but sometimes the inner sides of this narrow stripe are strongly serrated. In *T. nebularis*, the serration is strong and extensive, appearing on each side as a contiguous series of dark triangles, which confine the bright midventral color to trapezoidal shape on the individual ventral plates. Essentially the same pattern, albeit less pro-

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nounced, occurs in occasional specimens of *brevirostris* (e.g., Myers, 1974: 199, fig. 46D).

The above resemblances suggest that *Taeniophallus nebularis* may be correctly placed generically. The allocation seems at least consistent with current knowledge, although the taxonomy of these snakes is far from settled.

BIOGEOGRAPHY

Taeniophallus nebularis is the northernmost species assigned to the genus. Its geographically closest congeners are *T. brevirostris*, a widespread species in the Amazon basin, and *T. nicagus*, from the lower Amazon and the Guianas. The remaining named species of *Taeniophallus* are distributed south of the Amazon River, with the greatest diversity centered in southeastern Brazil.

There is slender speculative evidence that, among known snakes, *Taeniophallus nebularis* might be most closely related with *T. brevirostris* and *T. nicagus*. If so, the presence of a species of *Taeniophallus* in cloud forests of the Península de Paria might not be as biogeographically puzzling as it first appears. Rather, it would be consistent with Steyermark's (1974, 1979, 1982) observations on the phytogeography of the Coastal mountain range of Venezuela.

During botanical exploration, Steyermark (1966) discovered a significant relationship between the floras of the Península de Paria and the nearby island of Trinidad. Subsequently, Steyermark (1974) noted that cloud forests in Venezuela's Cordillera de la Costa generally, including the Paria highlands, also contain significant elements that show close relationships with Amazonian/Guayanan species. In Paria, species of plants in the genera *Cespedezia*, *Elvasia*, *Passiflora*, *Platycentrum*, and *Stephanopodium* were mentioned by Steyermark (1974, 1979, 1982) as examples of either endemic elements closely related to Amazonian/Guianan elements, or as species with disjunct distributions between the cloud forests of Paria and Amazonian/Guayanan humid forests.

Steyermark's scenario for explaining this biogeographic pattern invoked a past connection, probably during one of the humid phases of the Pleistocene, between the flora of the Cordillera de la Costa and that of the humid forests to the south. During a warmer period this connection was broken and some of the lowland flora migrated upward with the vertical shift of climate, adapting to cooler but similarly humid environments in montane cloud forests of the coastal range (Steyermark, 1979).

If hypothesized relationships are correct, *Taeniophallus nebularis* would seem to fit in with the above scenario. However, its distinctiveness and uncertain affinities also are consistent with the possibility of an older isolation and subsequent extinction of all close relatives, in which case separate generic status might be warranted for this enigmatic little snake.

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Myers gained background field experience with southeastern Brazilian species of *Echinanthera* and *Taeniophallus* in 1979, owing to the kind offices of Paulo E. Vanzolini. Dr. Vanzolini promoted the work in every way and provided the loan of specimens from the collections of the Museu de Zoologia da Universidade de São Paulo (MZUSP). The pen-and-ink and photographic illustrations of hemipenes were prepared by Patricia J. Wynne

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