

Taxonomic revision and comments on two groups of the genus *Coniophanes* (Squamata: Dipsadidae)

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Abstract

A revision of the *Coniophanes lateritius* and *C. piceivittis* groups was conducted to evaluate the taxonomic status of their members. The supraspecific groups of *Coniophanes* can be easily distinguished from each other, but the species within them exhibit wide overlap in scutellation. Apparently, these taxa can be differentiated by color pattern and geographic distribution. However, we report polymorphism in the color pattern of the *lateritius* group. Maxillary and hemipenial morphology can be useful and informative in the groups studied. The revision of these characters (scutellation, color pattern, maxillary and hemipenial morphology, and geographic distribution) led us to conclude that *C. sarae* is a junior synonym of *C. lateritius*, and to resurrect the name *C. taeniatus* **new comb.**, for the Atlantic versant populations of Mexico previously assigned to *C. piceivittis*.

Key words

Dipsadidae, hemipenial morphology, maxillary morphology, Mexico, nomenclature.

Resumen

Se llevó a cabo la revisión de los grupos *Coniophanes lateritius* y *C. piceivittis* para evaluar el status taxonómico de sus integrantes. Los grupos supraespecíficos en *Coniophanes* pueden ser fácilmente diagnosticables entre sí, pero las especies que los conforman muestran amplio solapamiento de caracteres de escutelación y parecen ser diferenciables sólo por patrones de coloración y distribución geográfica. Sin embargo, registramos polimorfismos en el patrón de coloración en el grupo *lateritius*. La morfología maxilar y hemipenial puede ser informativa y útil en los grupos abordados en este trabajo. La revisión de estos atributos (escutelación, morfología maxilar, hemipenial y distribución geográfica) nos lleva a considerar a *C. sarae* un sinónimo de *C. lateritius* y a resucitar el nombre *C. taeniatus* **nueva comb.**, para las poblaciones de la vertiente del Atlántico de México previamente asignadas a *C. piceivittis*.

Palabras clave

Dipsadidae, México, morfología hemipeneal, morfología maxilar, nomenclatura.

Introduction

Dipsadid snakes are one of the most diverse groups of Colubroids, with more than 800 described species to date (UETZ *et al.*, 2019). Their taxonomic story has been long, and there have been many taxonomic changes at the generic and specific level. The group contains three of the most speciose genera of the Western Hemisphere (*Atrac-*

tus with 143 species, *Dipsas* with 52, and *Geophis* with 50 according to UETZ *et al.*, 2019), and with the use of novel taxonomic approaches it is highly probable that the family will include more species in years to come (e.g. ARTEAGA *et al.*, 2018).

Within dipsadids, the genus *Coniophanes* Hallowell is a group of opisthoglyph snakes of Neotropical distribution with its greatest diversity in southern Mexico and northern Central America (BAILEY, 1939). The genus *Coniophanes* has received very little attention from researchers since the last generic revision by BAILEY (1939) in which the species groups were defined; the remainder of the literature concerning the systematics of the genus focused on species descriptions (CADLE, 1989; CAMPBELL, 1989; FLORES-VILLELA & SMITH, 2009; PONCE-CAMPOS & SMITH, 2001) with scattered comments on its phylogenetic relationships with other dipsadid genera (MYERS, 1974; MYERS & CAMPBELL, 1981; CADLE, 1984a, b).

Here, we conducted a revisionary study of the *C. lateritius* and *C. piceivittis* species groups, *sensu* BAILEY (1939), in order to ascertain the taxonomic validity of its members. Although these groups do not seem to be closely related, their taxonomic history and taxonomic decisions have been based mainly on coloration traits (stripes, collars, dorsal coloration) and the assumed allopatri of their members.

Historical Resumé

Coniophanes lateritius group

COPE (1862) described *Coniophanes lateritius* from a specimen collected near Guadalajara, Mexico sent to the U. S. National Museum by J. J. Majors (ZWEIFEL, 1959). PETERS (1869 [1870]) described *Tachymenis melanocephala* from a series of specimens collected by Louis Berkenbusch, noticing that most of the specimens lacked precise locality data; these came from Puebla and Matamoros, Mexico (u. a. O. [= und anderen Orten]). *Tachymenis melanocephala* was considered a synonym of *C. lateritius* by BAILEY (1939) and TAYLOR (1941), until SMITH & GRANT (1958), based on color pattern and distribution, considered it a subspecies of *C. lateritius*. The type specimen of *C. lateritius* was presumed to be lost by BAILEY (1939), which led TANNER & ROBINSON (1960) to designate BYU 13793 (not BYU 12795, as stated on top of page 60, a lapsus), from 7.5 miles north of Magdalena, Jalisco, Mexico (approximately 70 km directly NW of Guadalajara), as the neotype for this species. WELLMAN (1959) reported on the first specimens of *Coniophanes lateritius* collected from the states of Nayarit and Michoacán in Mexico, observing that specimens from the latter (UMMZ 118954) had an unusual orange dorsal coloration and suggesting that, though there is much agreement with the species, it might represent “a distinct race living on the Pacific slopes of the Sierra de Coalcomán”. About forty years later, PONCE-CAMPOS & SMITH (2001) reviewed the status of *Coniophanes lateritius*, after acquiring an additional specimen from Michoacán (MZFC 13030) that exhibited the same orange dorsal coloration as the specimen from Michoacán reported by WELLMAN (1959). They described a new taxon, *Coniophanes sarae*,

based on these two specimens. These authors also elevated *C. melanocephalus* to species rank. The description of *C. sarae* is rather brief and focused on the differences of between this taxon and *C. melanocephalus*, but the differences of the former with *C. lateritius* (condition in parenthesis) are few, namely: 1) orange dorsal coloration of the body (bright red), 2) lack of a dark border posterior to the narrow light ring following the black head and neck (present), and 3) melanophores evenly distributed on back and sides (denser towards the mid-dorsum and tail).

Coniophanes piceivittis group

COPE (February 1870) described *Coniophanes piceivittis* from near Tehuantepec, Oaxaca, Mexico, but in January 1870 PETERS described *Tachymenis taeniata* and *T. melanocephala*. Since BAILEY'S (1939) revision of the genus *Coniophanes*, the name has been credited to COPE (1870). Nonetheless, OSBORN (1930) gives a publication date for COPE'S description as February 18, 1870. This date is few weeks after PETERS (1869 [1870]) published the name *Tachymenis taeniata* (BAUER *et al.*, 1995), a fact overlooked by BAILEY (1939), SMITH & TAYLOR (1945) and subsequent researchers.

BAILEY (1937) described *Coniophanes schmidtii* from Chichen Itzá, Yucatán, Mexico noticing that the main difference between *C. schmidtii* and *C. piceivittis* was the first having narrower lateral lines which gradually became lighter towards the ventrals. In the same paper BAILEY also mentioned that the holotype of *Tachymenis taeniata* should be reexamined but it was included under the synonymy of *Coniophanes piceivittis* by SMITH & TAYLOR (1945: p. 42). The type locality of *T. taeniata* (Peters) was restricted to Puebla and its taxonomic status was not discussed further (SMITH & TAYLOR, 1945). JAMES A. PETERS (1950) described *Coniophanes frangivirgatus* from a single specimen obtained “1/2 mile east of Plan del Río, Veracruz”, he distinguished it from other members of the *piceivittis* group by the presence of distinctive light spots on the nape; seven supralabials and nine infralabials. PETERS (1950) suggested that *C. frangivirgatus* was part of the *C. piceivittis* group on the Gulf Coast of Mexico north of the Isthmus of Tehuantepec, and relegated *C. piceivittis* to the Pacific Coast of Mexico and Central America. The other taxon in the *C. piceivittis* group, *C. schmidtii*, was considered to be restricted to the Atlantic lowlands of the Yucatán Peninsula. Finally, HALL (1951) described *C. p. taylori* from Agua de Obispo, Chilpancingo and the coastal plain of Guerrero. Several authors suggested that all the taxa in the *C. piceivittis* group be considered subspecies of *C. piceivittis* (PETERS, 1950; WERLER & SMITH, 1952; MARTIN, 1955; NEILL & ALLEN, 1960). Based on all of the above authors and HALL (1951), SMITH & TAYLOR (1966) placed all taxa in this group as subspecies of the group nominal species.

WILSON & MEYER (1985) discussed the subspecies of *C. piceivittis* and concluded that the characters formerly used by other researchers to differentiate them were not

Table 1. Morphological variation in the *C. lateritius* group. The legend “Striped” refers to the population from Ixtlahuacán, Colima (see text).

Taxon	Sex	n	SVL	Supra-labials	Infra-labials	Dorsals	Ventrals	Subcaudals	Segmental counts
<i>C. lateritius</i>	♂	6	221–301	7(8)/7(8)	9/9	19-19-17	141–147	86–97	234–244
	♀	8	126–365	7/7	9(8)/9	19-19-17	145–164	84–96	229–245
<i>C. lateritius</i> Striped	♀	3	289–350	7/7	9(8)/9	19-19(16)-17	146–156	93–102	245–249
<i>C. “sarae”</i>	♂	1	214	7/7	9/9	19-19-17	156	85	241
	♀	1	125	7/7	9/9	19-19-17	151	92	243
<i>C. melanocephalus</i>	♂	4	164–335	7(8)/7(8)	9(8)/9(8)	19-19-17	145–149	92–96	240–242
	♀	2	171–303	7/7	9(8)/9(8)	19(20)-19-17	154–158	88	242–246

diagnostic. Based on their own revision of specimens, they relegated all subspecies to the synonymy of *C. piceivittis*.

HARRISON (1992), in an unpublished Master of Science thesis, evaluated the taxonomic status of the taxa described in the *C. piceivittis* group based on a phenetic approach and concluded that only *C. piceivittis* and *C. schmidtii* were valid species within the group. However, FLORES-VILLELA & SMITH (2009), based on a revision of the color pattern and alleged geographic isolation, stated that most of the taxa formerly described within the group were valid species (*C. piceivittis*, *C. schmidtii*, *C. taylori*) and described *C. michoacanensis*, as part of the *C. piceivittis* group.

Materials & Methods

We examined a selection of comparative material of the genus *Coniophanes*, especially that of the *lateritius* and *piceivittis* species groups. Specimens are housed in the herpetological collections of the American Museum of Natural History (AMNH), Brigham Young University (BYU), Colección Nacional de Anfibios y Reptiles, Instituto de Biología, Universidad Nacional Autónoma de México (CNAR), Field Museum of Natural History (FMNH), Instituto de Investigación sobre Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo (INIRENA), Louisiana State University Museum of Zoology (LSUMZ), Museo de Zoología “Alfonso L. Herrera”, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC), Universidad Autónoma de Aguascalientes (UAA), University of Florida (UF), University of Michigan, Museum of Zoology (UMMZ), University of Texas at Arlington (UTA), and Zoologisches Museum, Berlin (ZMB). The type specimens of *Tachymenis taeniata* (ZMB 6672), *C. frangivirgatus* (UMMZ 101160), *C. michoacanensis* (MZFC 10393), *C. sarae* (MZFC 13030, holotype, and UMMZ 118954, paratype), and the neotype of *C. lateritius* (BYU 13793) were also examined. Specimens examined are listed in Appendix 1.

All measurements were taken with dial calipers and rounded to the nearest 0.1 mm, except for the snout-vent

length (SVL) and tail length, which were measured with a metal ruler and rounded to the nearest millimeter. Ventral scales were counted according to DOWLING (1951), segmental counts are as defined by SAVAGE & LAHANAS (1991). Scale counts and measurements were made separately for males and females. Hemipenial preparations were made following the procedures of MYERS & CADLE (2003) and ZAHER & PRUDENTE (2003), as modified by SMITH & FERRARI-CASTRO (2008). Hemipenial terminology follows DOWLING & SAVAGE (1960) and MYERS & CAMPBELL (1981). Maxillary dentition was observed *in situ* by making a lateral incision between the supralabials and the maxillary arch, removing tissues and counting teeth and empty sockets. In some specimens, the maxilla was removed and cleaned with a diluted solution of Proteinase K for about an hour until most of the soft tissues had been removed. We use the term fangs, as proposed by MYERS (1974), referring to the enlarged grooved teeth posterior to the diastema.

Results

The examination of many specimens in the genus, led us to recognize a trend in which most of the proposed groups can be easily differentiated from each other by a combination of morphological characters (i.e. scutellation, color pattern, maxillary and hemipenial morphology), but species within these groups are more difficult to diagnose, since scutellation characters overlap to a large extent (Tables 1, 2). The main differences are: color pattern and geographic distribution (see BAILEY, 1939; FLORES-VILLELA & SMITH, 2009).

Variation and distribution in the *lateritius* group

BAILEY (1939) said that this group only contained the nominal species, and that it was poorly defined due to its rarity in museum collections during the first part of the 20th century. It currently comprises three species, namely: *C. lateritius*, *C. melanocephalus* and *C. sarae*.

Table 2. Morphological variation in the *Coniophanes piceivittis* group.

Taxon	Sex	n	SVL	Supra-labials	Infra-labials	Dorsals	Ventrals	Subcaudals	Segmental counts
<i>C. taeniatus</i>	♂	9	167–451	8/8	9(11)/9(11)	23-25(27)-19	154–164	83–91	241–246
	♀	6	251–387	8(7)/8(7)	10(9)/10(9)	23-25(23)-19	165–168	78-89	244–246
<i>C. michoacanensis</i>	♀	2	391–406	8/8	9/9	23-25-19	159–164	87	246–251
<i>C. piceivittis</i>	♂	8	149–334	8/8	10/10	23-25-19(21)	158–171	85–94	243–265
	♀	11	217–379	8/8	10(9)/10(99)	23-25-19(21)	161–172	76–87	242–253
<i>C. schmidtii</i>	♂	21	200–584	8(9)/8(9)	10/10	23(22)-25-19	154–159	84–100	239–266
	♀	17	168–594	8/8	10/10	23(21)-25(27)-19	154–174	79–97	236–273
<i>C. taylori</i>	♂	6	144–384	8/8	10/10	23(23)-25(23)-19	161–169	83–89	250–258
	♀	6	137–403	8/8	10/10	23-25-19	167–175	82–90	249–261

They are small to medium-sized snakes (up to 365 mm SVL), slender, with heads distinct from neck; 7/7 supralabials; 9/9 infralabials; loreal scale about as wide as tall; one preocular; 19–19–17 dorsal scale rows; 141–158 ventrals; 84–102 subcaudals; 229–249 segmental counts (Table 1). Dorsal coloration is red or orange, generally smooth throughout, but also might have densely aggregated melanophores towards the mid-dorsum and the posterior (Fig. 1B), or have fine light-colored stripes (Fig. 1D; HEIMES, 2016: Fig. 263); venter immaculate, white or yellowish; distinctive light collars, from 1 (*C. lateritius*, *C. sarae*) to 4 scales wide (*C. melanocephalus*); black heads, with scattered, tiny white spots either present (*C. lateritius*, *C. sarae*) or absent (*C. melanocephalus*); white markings on the labial scales; and bold mottling of the chin. The hemipenes are simple, unicapitate and spinose, with a centrolineal sulcus spermaticus dividing just below the capitulum. The retracted organs range from 8 to 11 subcaudals long and the retractor muscle inserts at the level of the 28–31 subcaudal. The hemipenis of *C. lateritius* (Fig. 2) has minute spinules at the base on the sulcate view, has spines on the second third of the organ body, and has papillate calyces on the capitulum; on the asulcate side spinules are absent at the base and the capitulum has paired cup-shaped depressions at the base of the capitulum. The maxillae have 10–12+2 teeth, fangs grooved and offset laterad; maxillary arch slightly curved, almost straight; teeth slender, progressively increasing in size towards the diastema; diastema very wide, almost three teeth long. Two morphotypes are diagnosable based on the maxillary anterior process direction, one in which it is directed towards the front and the other in which the process is directed backwards (Fig. 3i–l).

Members of the *C. lateritius* group are endemic to the lowlands of the Pacific versant of Mexico from sea level to 1,600 m a.s.l., including the Balsas River Basin, collectively ranging from Sonora, southwards to central Guerrero on the windward slope and to Puebla in the inner slope of the Balsas River Basin. *Coniophanes lateritius* and *C. sarae* are distributed on the windward side on the Pacific versant mountain ranges and *C. melanocephalus* is restricted to the dry lowlands of the leeward side of the Sierra Madre del Sur mountain range, on the Balsas River Basin (Fig. 4).

Variation and distribution in the *piceivittis* group

When defined, BAILEY (1939) thought that this group was probably the closest to the ancestral condition of the genus, probably because of the higher number of dorsal scale rows and ventral scales. It currently comprises four valid species: *C. michoacanensis*, *C. piceivittis*, *C. schmidtii*, and *C. taylori*. They are medium-sized snakes (up to 584 mm SVL), with a somewhat stout body, and heads distinct from the neck; 8/8 supralabials; 10/10 infralabials; loreal scale slightly wider than tall; one large preocular and a small subpreocular always present; 23–25–19 dorsal scale rows; anal ridges prominent in males; 154–175 ventral scales; 75–115 subcaudals; 236–273 segmental counts (Table 2). Dorsal coloration in this group is very distinctive, with wide dark vertebral lines, in most species associated lateral dark lines are present, but in *C. schmidtii* these lines fade progressively towards the ventrals; venter immaculate creamy white; white postocular lines always present, these can be continuous with the lateral light lines of the body or interrupted by light spots at the nape in the case of Atlantic populations of *C. piceivittis* (see below); supralabials mostly light colored with dark spots and scattered tiny dark spots; gular region with numerous stippled dark markings. The hemipenes of the group (Fig. 5) are bilobed, unicapitate, calyculate and spinose, with a centrolineal sulcus spermaticus that bifurcates in the middle of the capitulum. On the sulcate view the hemipenial body has many spinules covering the basal third, but some organs have naked bases (*C. schmidtii*); the medial third has large hook-shaped spines, and the capitulum has numerous papillate calyces (these papillae can be very long in the Atlantic populations of *C. piceivittis*). On the asulcate view the ornamentation is essentially the same, except that on the spinose region of the body a nude region is present at the middle; and there are paired cup-shaped depressions at the base of every lobe. The retracted organs are 10–14 subcaudal scales long and the retractor muscle inserts at the level of the 26–36 subcaudal. The maxillae (Fig. 3a–h) have 10–13+2 teeth (BAILEY, 1939: 31 reports 8 maxillary teeth as a minimum), the first fang can be offset internally; maxillary arch very curved and dorso-laterally compressed; two lateral pro-



Fig. 1. Color pattern variation in *Coniophanes lateritius*. Specimens from San Antonio-Ciudad Altamirano highway, Guerrero (1A; MZFC 32626); Rancho San Pablo, Sonora (1B, not collected); Cerro La Imagen, Guerrero (1C, MZFC 31980); and Ixtlahuacán, Colima (1D, specimen not located in any collection).



Fig. 2. Hemipenis of *Coniophanes lateritius* from Coahuayana-Palos Marias road, Michoacán (INIRENA 1069). Sulcate, lateral, and asulcate views. Scale bar = 1 mm.

cesses on the maxillary arch are present, the anteriormost being noticeably larger; teeth slender and subequal in size, increasing in length towards the rear; diastema very wide.

Members of the *C. piceivittis* species group collectively range from Tamaulipas on the Atlantic versant, and from Michoacán in the Pacific of Mexico southward to northern Costa Rica, on the Atlantic versant *C. schmidt*

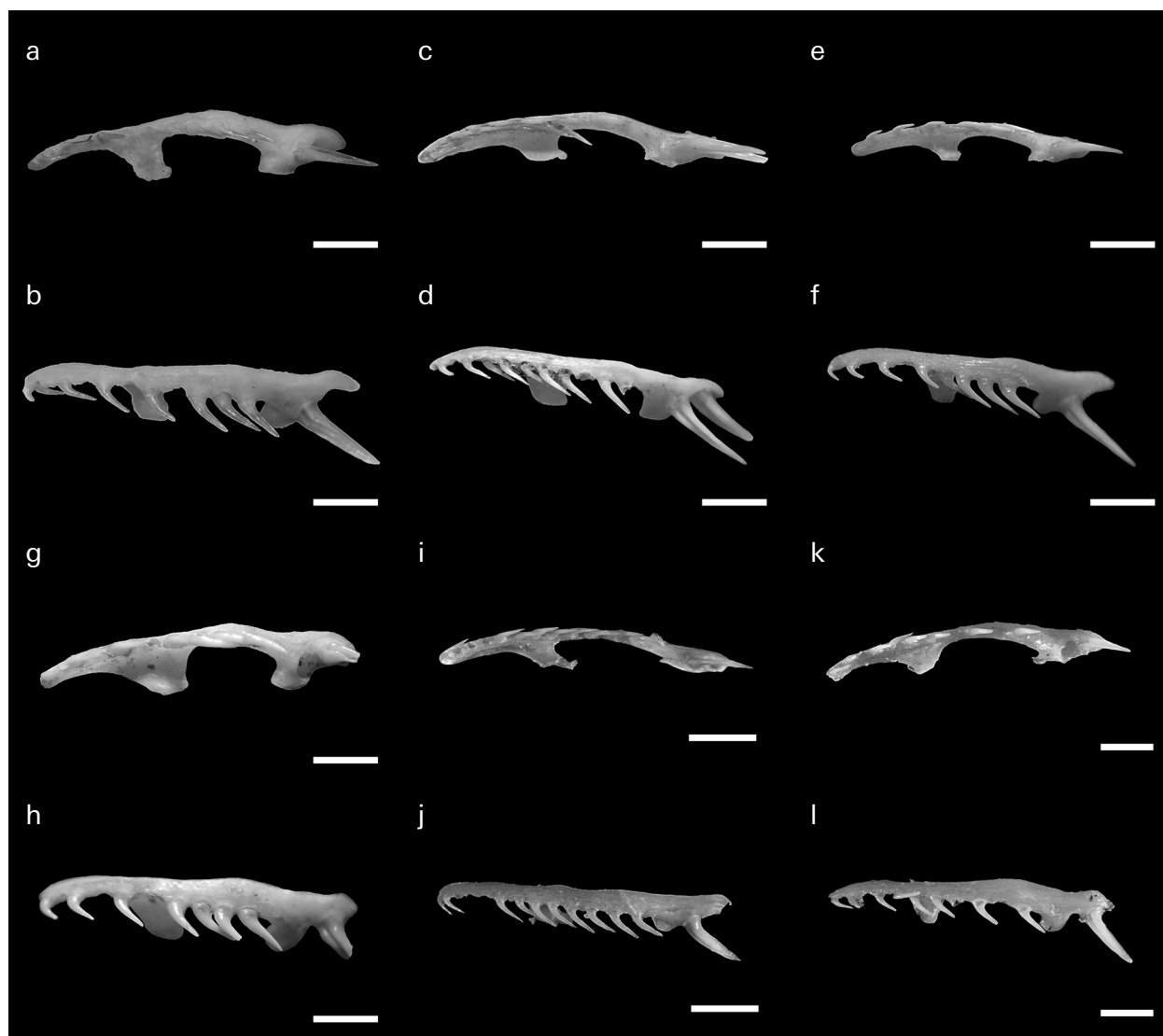


Fig. 3. Maxillary morphology in the *Coniophanes lateritius* and *C. piceivittis* groups. Figures a–b: *C. piceivittis* (MZFC 25265); c–d: *C. taylori* (MZFC 34556); e–f: *C. schmidtii* (MZFC 22080); g–h: *C. taeniatus* (MZFC 34557); i–j: *C. melanocephalus* (INIRENA 1760); k–l: *C. laeritius* (INIRENA 1069). Ventral (a, c, e, g, i, k) and lateral (b, d, f, h, j, l) views. Scale bar = 1 mm.

reaches Belize (Fig. 6). All members of this group are associated with tropical subhumid forests from sea level to about 1500 m a.s.l. Currently, no case of sympatry is known in the group but contact zones are likely, since there are no important barriers throughout their range. Here we report the first verified record of *C. schmidtii* from the state of Tabasco (MZFC 14885, Piscifactoría José Narciso Roviroso, Teapa), which represents the westernmost locality of this species.

When examining species of the group we noticed that the Atlantic populations assigned to *C. piceivittis* exhibited several morphological characters that allowed them to be differentiated from the Pacific populations (condition in parentheses): 1) an acuminate snout in dorsal view (vs rounded), 2) an upturned rostral scale (vs truncate snout on lateral view [Fig. 7]), 3) presence of light spots on the nape (vs no light spots, temporal light line in contact with lateral light line), 4) lack of a definite dark bar from the anterior margin of the eye to the posterior margin of

the naris (present), 5) a robust maxillary bone, with an anterior maxillary process very wide towards the base (vs slender maxillary bone and anterior maxillary process), and 6) long papillae around the calycular region of the hemipenis (short papillae). Differences based on coloration are: the presence of light spots on the nape; several authors from the mid-20th century have referred to these populations as *C. frangivirgatus* Peters, 1950. This character is almost invariable, but occasionally the light spot can be in contact with the light lines on body. Only one specimen from the Pacific versant of Mexico examined by us exhibited light spots on the nape (AMNH R 68029), but it is easily differentiable by snout and head shape. On examination, the holotype of *C. frangivirgatus* exhibits all the diagnostic features observed; however, a formerly described taxon, *Tachymenis taeniatus* Peters, 1869 [1870], has not been properly evaluated in the past. WILHELM PETERS described this taxon in a footnote: “Wir haben neuerdings eine Schlange, *T. taeniata* n. sp?,”

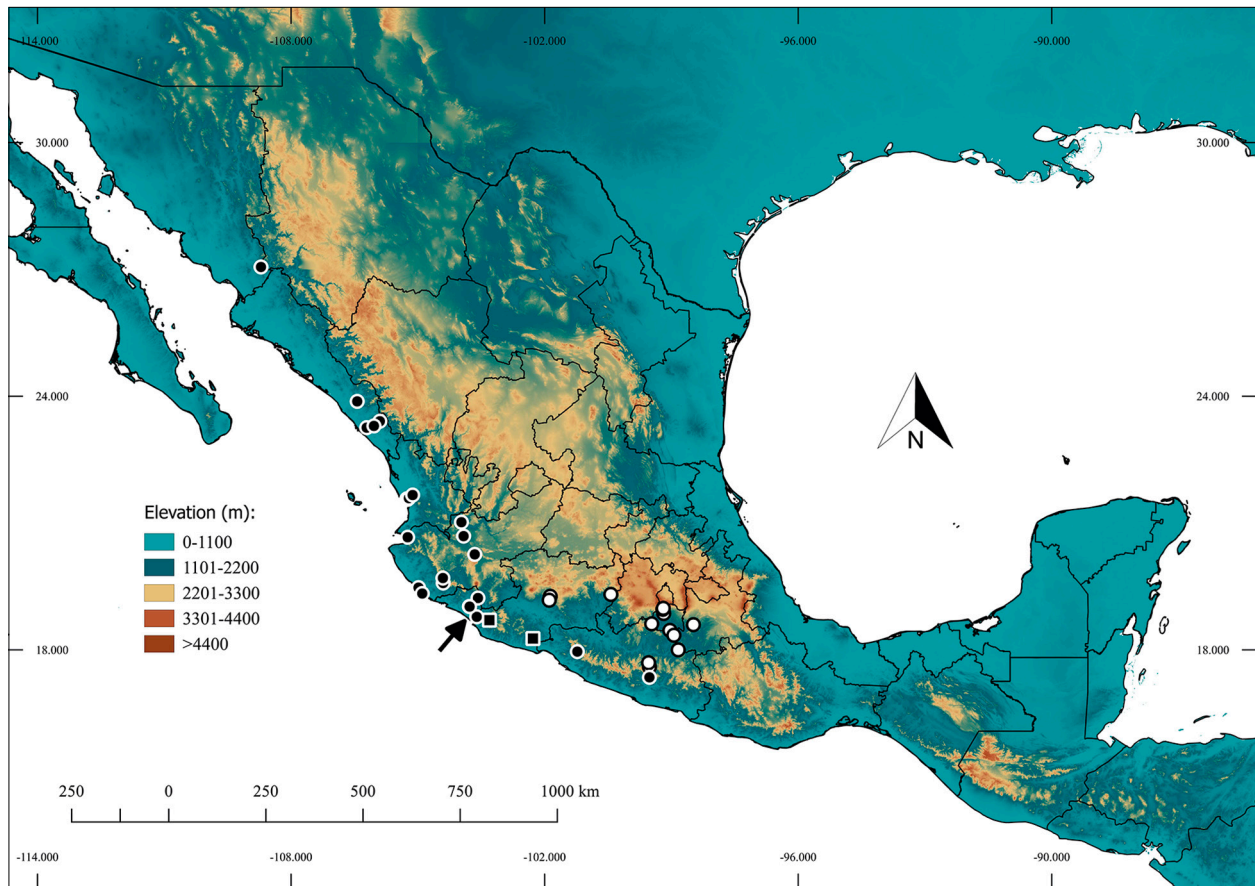


Fig. 4. Geographic distribution of the *Coniophanes lateritius* group. *Coniophanes lateritius* (closed circles), *C. melanocephalus* (open circles), *C. "sarae"* (closed squares). The arrow indicates the region of Ixtlahuacán, Colima where the striped morph has been observed.

ebenfalls aus Mexico erhalten, welche ganz ähnlich gezeichnet ist, wie die im Jan'schen Werke abgebildete Varietät von *T. fissidens* Gthr. (18. Livr. Taf. 5 Fig. 3b.), welche aber zwei Anteorbitalia und fünfundzwanzig Schuppenreihen hat (We have recently received a snake, *T. taeniata* n. sp?, also from Mexico, which is drawn very similar to the variety of *T. fissidens* Gthr depicted in Jan's work (18. Livr. Plate 5 Fig. 3b.), but which has two anteorbitalia and twenty-five rows of scales)". Though brief, the description gives us some clues on the relationships of the specimen such as a) two preoculars, a character rare in most *Coniophanes* exclusive to the *piceivittis* group (FLORES-VILLELA & SMITH, 2009), and b) twenty-five scale rows at midbody.

We examined the holotype of *Tachymenis taeniata* deposited in the Zoologisches Museum Berlin (ZMB 6672; Fig. 8). It is a mature male with 387 mm TL, 105 mm tail length; a robust snake, rounded body. The specimen is well preserved and has been cut open ventrally, exhibiting a voluminous prey item that according to a note made by W. C. Peters is a *Sceloporus variabilis* (Franck Tillack, pers. comm). Head wider than the neck, acuminate in dorsal and lateral view. Rostral scale enlarged and visible from above between the frontals. Supralabials 8 on both sides of the head, 1–2 contacting the divided nasal, 2–3 in contact with a loreal wider than high, 4–5 entering the

orbit. Infralabials 9, 1–4 (right side) and 1–5 (left side) in contact with the anterior pair of genials. Preoculars 2 on both sides, a small subpreocular present. Eye small with a round pupil. Postoculars 2 on both sides. Temporal scales 1+2. Dorsal scale rows in 23–25–19 rows, smooth thorough. Ventrals 159, with 2 preventrals; cloacal plate divided; paired subcaudals 83 + terminal spine. The head is light brown on the dorsal surfaces up to the parietals; light postocular marks encompass the upper postoculars, outer sides of the parietals and secondary temporals, a dark contour borders these marks; scattered light, ill-defined markings are in the snout; on lateral view a dark band is clearly defined posterior to the eye, encompassing the temporals and upper parts of the 6–7th labials; a light nape spot is one scale below the rear of the postocular markings, on the left side it is three scales long and is separated by one scale from the lateral light stripe of the body, that of the right side is fused with the line; labials are white with scattered brown spots; ventral surfaces of the head and gular region are white with brown stippling. Dorsal coloration consists of black and creamy white stripes, lateral dark stripes at midbody are three and two half scales, and are separated from ventrals by two light scales and one-half of a light scale; vertebral dark stripe at midbody is seven and two half scales wide and is separated from the dark lateral stripes by one light

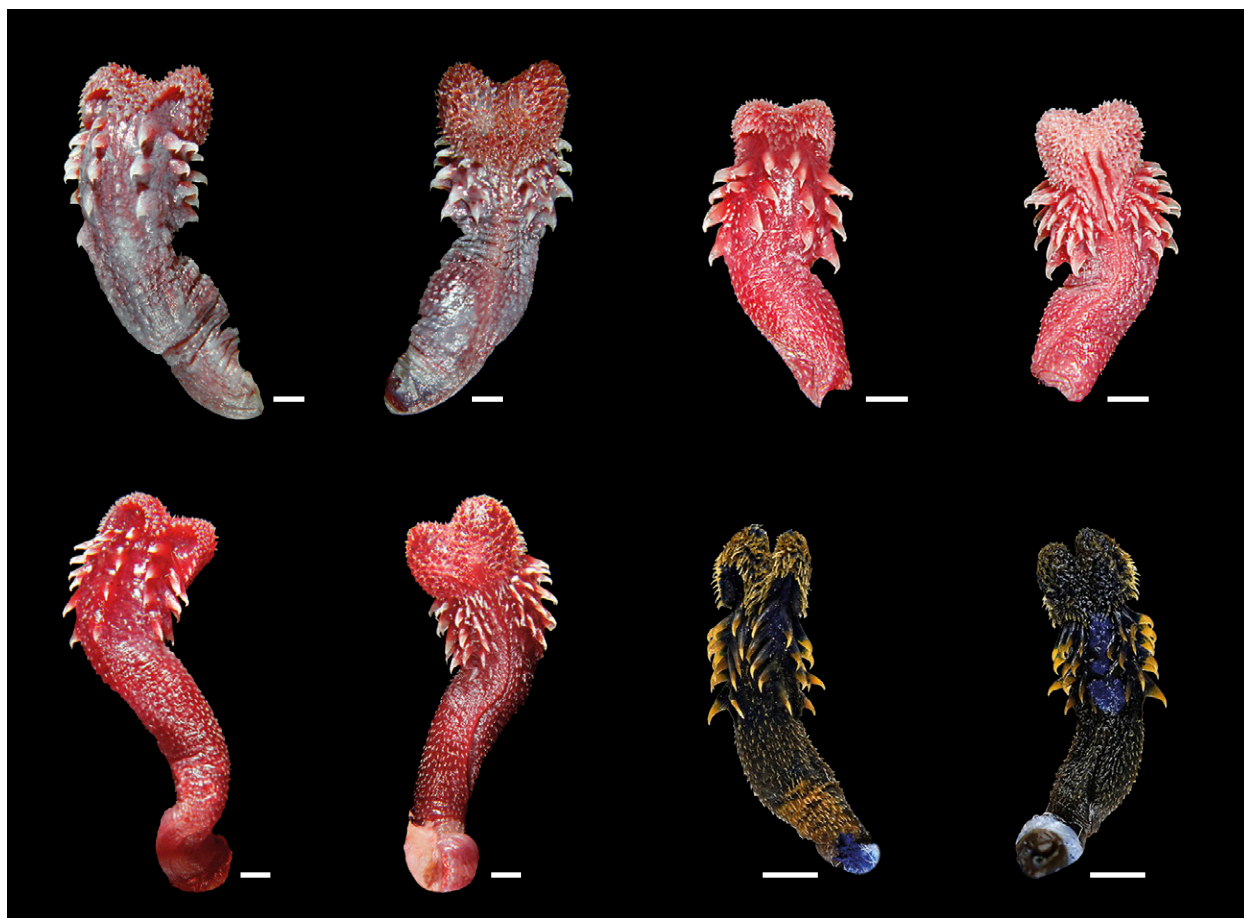


Fig. 5. Hemipenial morphology of the *Coniophanes piceivittis* group. *Coniophanes taylori* (MZFC 34558, upper left), *C. piceivittis* (MZFC 17292, upper right), *C. schmidtii* (MZFC 22080, lower left), and *C. taeniatus* (UMMZ 114533, lower right). Asulcate views on the left, sulcate views on the right. Scale bar = 2 mm.

scale and two half, light scales. Ventral surfaces of body and tail are immaculate white.

Based on external, hemipenial, and maxillary morphology, color pattern and distribution as stated above, it is clear that different species are under the name *C. piceivittis* and we suggest that those from the Atlantic versant of Mexico be known as: *Coniophanes taeniatus* (Peters, 1869 [1870]) **new comb.**

Discussion

The *lateritius* group

Although it has been suggested that color pattern is of taxonomic importance in other groups of the genus, such as the *C. imperialis* and the *C. piceivittis* groups (BAILEY, 1939; FLORES-VILLELA & SMITH, 2009), the *lateritius* group seems to be polymorphic in this trait, at least in the nominal species. There are specimens from the region of Ixtlahuacán, Colima that exhibit a striped dorsal pattern (Fig. 1; HEIMES, 2016: Fig. 263), and according to our observations there are additional variants such as the intensity of dorsal coloration ranging from orange to bright

red (Fig. 1). Also, the aggregation of melanophores on the dorsum and tail seems to be quite variable and, thus to be of no taxonomic value. As for the former case, two alternatives could explain this variation: a) these striped specimens are representatives of an undescribed taxon restricted to the Sierra de Manantlán mountains, or b) this color polymorphism has not been reported previously due to the imperfect sampling of the coastal lowlands of western Mexico. The latter is likely since collections from the Coalcomán and Manantlán mountain ranges have been scarce and color polymorphism has been previously recorded in other Mexican snakes such as *Geophis* (PAVÓN-VÁZQUEZ *et al.*, 2011), *Loxocemus* (RAMÍREZ-BAUTISTA & SMITH, 1992), *Stenorrhina* (DAVIS & DIXON, 1959), and *Thamnophis* (HEIMES, 2016). The former explanation, however, cannot be deemed impossible considering that in recent decades many novel reptile species have been described from the Pacific lowlands of western Mexico such as *C. michoacanensis* (FLORES-VILLELA & SMITH, 2009), *Lepidophyma tarascae* (BEZY *et al.*, 1982), *Leptodeira uribei* (RAMÍREZ-BAUTISTA & SMITH, 1992), *Phyllodactylus benedetti* (RAMÍREZ-REYES & FLORES-VILLELA, 2018), and *Porthidium hespere* (CAMPBELL, 1976). We think that the second explanation is the most conservative and the best option, at least until more ma-

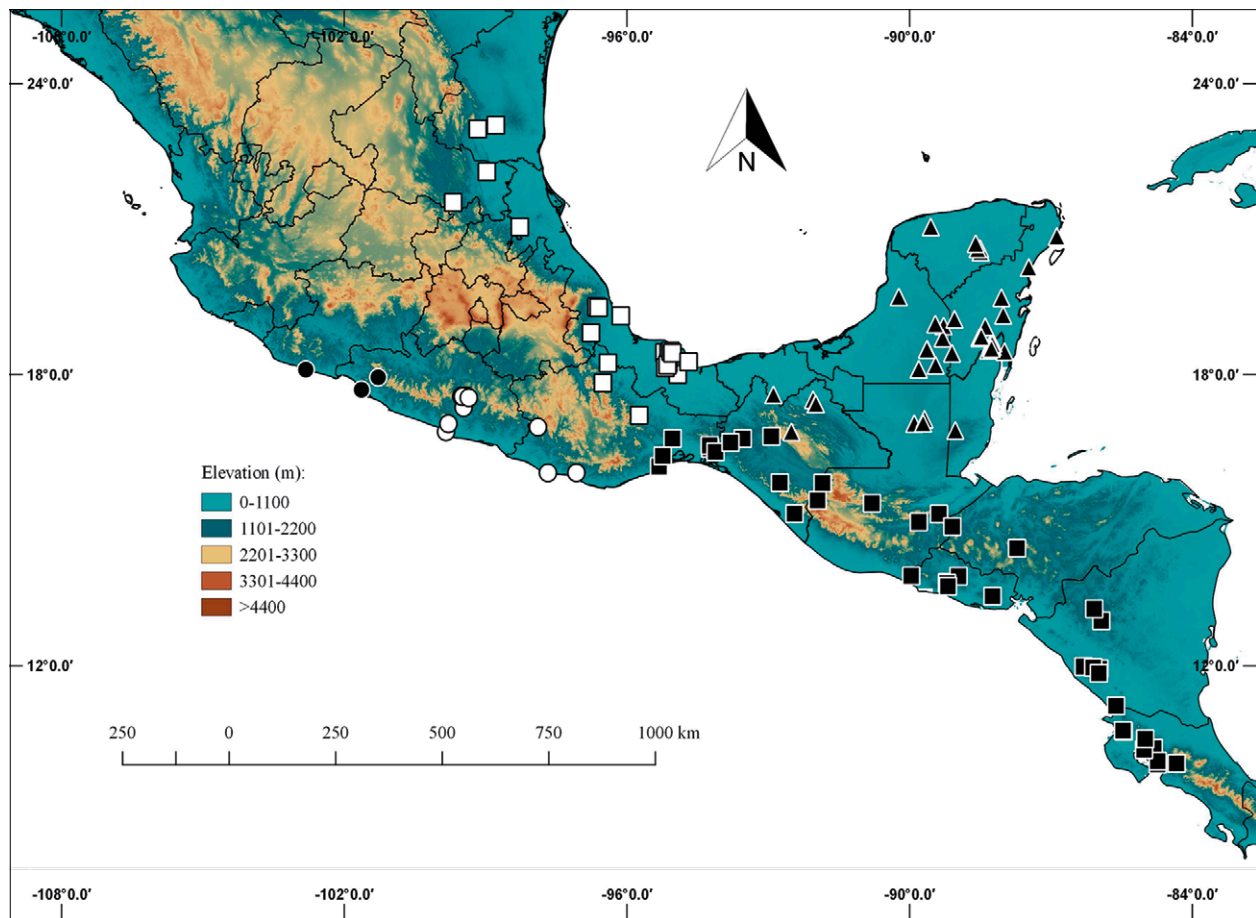


Fig. 6. Geographic distribution of the *Coniophanes piceivittis* group. *Coniophanes michoacanensis* (closed circles), *C. piceivittis* (closed squares), *C. schmidt* (closed triangles), *C. taeniat* (open squares), and *C. taylori* (open circles).

terial exhibiting these traits becomes available to help us elucidate this issue.

As for the taxonomic identity of *C. sarae* we regard the morphological characters used by PONCE-CAMPOS & SMITH (2001) as ambiguous as they fall within the observed variation of *C. lateritius*. The ventral scales, subcaudals, dorsal, and post-collar coloration overlap to a large degree, and it was demonstrated that the alleged geographic isolation of the species is a collection artifact when recent records of *C. lateritius* from Guerrero and Michoacán became available (SUAZO-ORTUÑO *et al.*, 2014; PALACIOS-AGUILAR *et al.*, 2018). These new records came from the northern and southern limits of the range of *C. sarae* and one of the specimens from Guerrero (MZFC 31980) exhibits pale coloration, like that of the type series of this taxon. These observations lead us to state that *C. sarae* cannot be differentiated from *C. lateritius* and should be considered its junior synonym.

Coniophanes melanocephalus is apparently restricted to the Balsas Depression in the states of Guerrero, Michoacán, Morelos, and Puebla (CASTRO-FRANCO & BUSTOS-ZAGAL, 2004; SOLANO-ZAVALA *et al.*, 2014), and it is likely that it reaches the Estado de México, Jalisco, and Oaxaca. The differences in color pattern noted by PONCE-CAMPOS & SMITH (2001) are consistent in our lim-

ited sample, and differences in hemipenis and maxillary morphology, in addition to a geographic isolation lead us to support the taxonomic conclusion of those authors.

The *piceivittis* group

The taxonomic status of the taxa within this group have been discussed elsewhere (HARRISON, 1992; FLORES-VILLELA & SMITH, 2009), however the status of the Atlantic populations of the nominal species has not been examined recently by researchers. Based on morphological evidence (presence of light spots on the nape, lack of a continuous dark stripe from the anterior margin of the eye to the tip of the snout, long papillae surrounding the calyces of the hemipenis capitulum and a robust maxillary bone with an anterior maxillary process enlarged towards the base) and distribution, here we propose that these populations be known under the name *Coniophanes taeniat* (Peters, 1869 [1870]). With the addition of this taxon, the *Coniophanes piceivittis* group is now composed of five species: *C. michoacanensis*, *C. piceivittis*, *C. schmidt*, *C. taeniat* and *C. taylori*.

The type locality of *C. taeniat* was restricted to Puebla by SMITH & TAYLOR (1945) most probably because of the mention of the state in the title of the original



Fig. 7. Head shape comparison between *Coniophanes taeniatus* (ZMB 6672, holotype) and *C. piceivittis* (MZFC 34556) in dorsal (upper), ventral (middle) and lateral (lower) views. Scale bar = 5 mm.

publication. However, CAMPBELL & SAVAGE (2000) have argued that some species described in that same paper might have been collected on the Atlantic lowlands of Veracruz and in adjacent Puebla. Wilhelm Peters never visited the Americas but described some species from there based on the donation of several samples collected by other colleagues, a common practice at the time (BAUER *et al.*, 1995). Most of the amphibian and reptile species reported by PETERS (1869 [1870]) in the paper describing *C. taeniatus* are commonly found in the lowlands of Veracruz, such as: *Anolis laevis*, *Boa imperator*, *Dipsas cenchoa* (*Imantodes cenchoa*), *Elaps corallinus* (*Micrurus diastema*), *Ficimia olivacea*, *Geophis semidoliatus*, *Hylodes berkenbuschii* (*Craugastor berkenbuschii*), *Pliocercus elapoides*, *Stenostoma dulce* (*Rena dulcis*), and *Streptophorus sebae* (*Ninia sebae*); and others from the eastern region of the Transmexican Volcanic

range: *Bufo compactilis* (*Anaxyrus compactilis*), *Conopsis nasus*, *Gerrhonotus lichenigerus* (*Barisia imbricata*), *Hyla eximia* (*Dryophytes eximius*), *Hyla microtis* (*Rheohyla miotympanum*), *Phrynosoma orbiculare*, *Phymatira bairdi* (*Salvadora bairdii*), *Pityophis deppei* (*Pituophis deppei*), *Sceloporus aeneus*, *S. microlepidotus*, *S. spinosus*; and a small portion of the Balsas Depression: *Dipsas biscutatus* var. *latifascia* (*Trimorphodon tau*), *Elaps marcgravi* var. *laticollaris* (*Micrurus laticollaris*), *Tachymenis melanocephala* (*Coniophanes melanocephalus*). This list leads us to suggest that the collections of Louis Berkenbusch donated to the Zoologisches Museum of Berlin originated in Veracruz. Berkenbusch and his team landed in the Port of Veracruz, and probably went on to Córdoba and Orizaba, then all the way to Puebla, from whence they went southwards to the Balsas River Basin where Izúcar de Matamoros is located. Given this

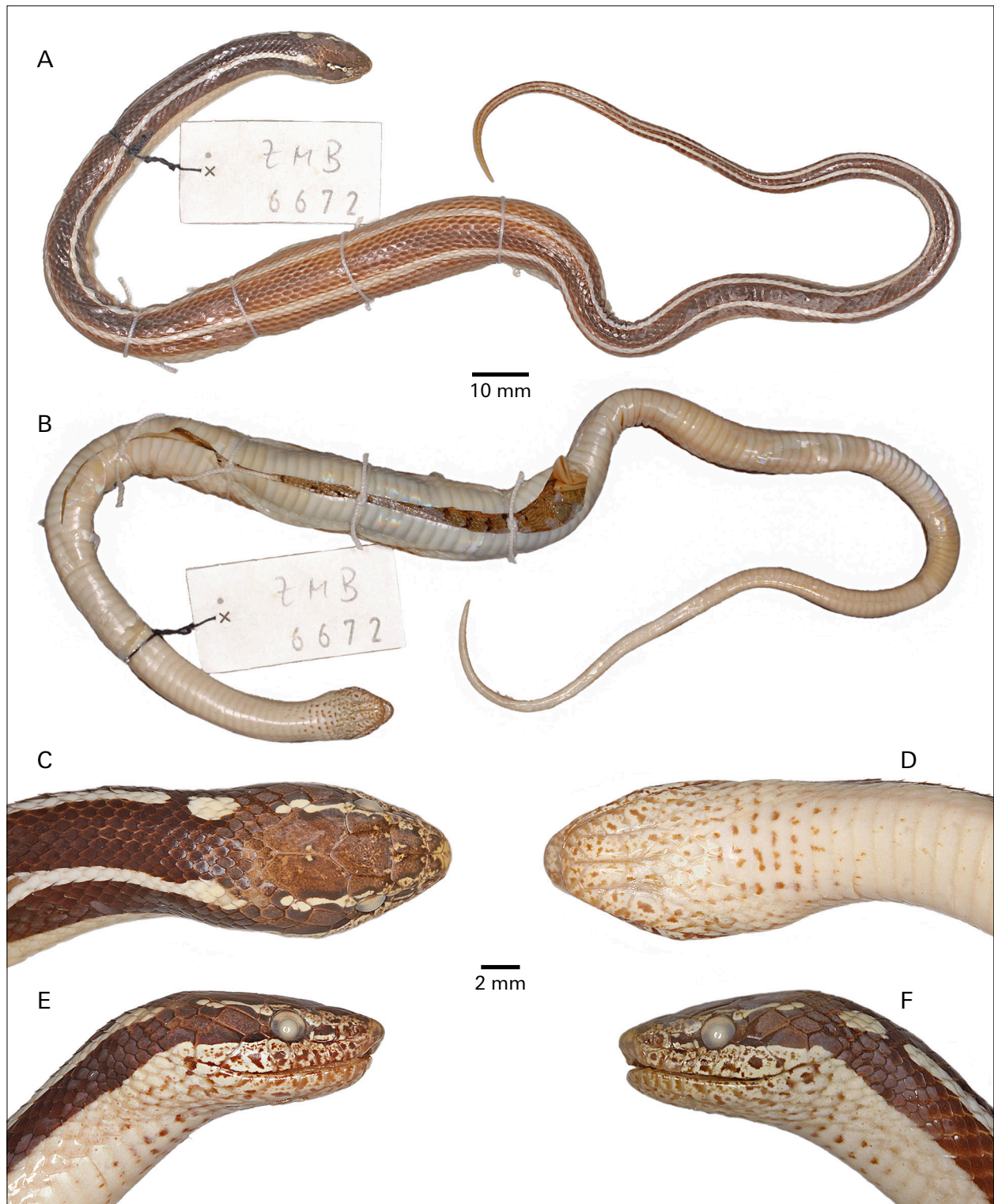


Fig. 8. Holotype of *Tachymenis taeniata* (ZMB 6672). Dorsal (A) and ventral (B) views of the body, dorsal and ventral (C and D, respectively), right and left lateral (E and F, respectively) views of the head.ventral (middle) and lateral (lower) views.

route, we propose that the type locality of *C. taeniatus* be restricted to the Port of Veracruz, Veracruz, Mexico instead of Puebla, taking into account that there are specimens from this locality (UMMZ 122031) and its surroundings, and knowing that this was the point of entry for European travelers and collectors for decades, during the 19th and 20th Centuries.

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Appendix 1. Material examined

***Coniophanes lateritius*. — MEXICO:** COLIMA: Ixtlahuacán, 1.45 km E of turnoff to La Salada, on road to Ixtlahuacán (MZFC 26944); 2.3 km E of to La Salada, on road to Ixtlahuacán (MZFC 26945); 3 mi NW Tamala (MZFC 26947); Reserva de la Biósfera Sierra de Manantlán, Cerro Grande, El Terrero (MZFC 25938); GUERRERO: Municipio de Chilpancingo de los Bravo, Ejido Zoyatepec, Cerro La Imagen (MZFC 31980); Municipio de Zihuatanejo de Azueta, near the San Antonio-Ciudad Altamirano highway (MZFC 32626); JALISCO: 2.8 miles (by Mex Hwy 80) W Puerto Los Mazos (BYU 41302); 7.5 miles north of Magdalena (BYU 13793, neotype); Ejido Miguel Hidalgo, municipio de La Huerta (INIRENA 1639); Entre Autlán de Navarro y El Zapotillo (MZFC 19749); Reserva de la Biosfera La Huerta, arroyo Careyes (MZFC 20571); Municipio de Casimiro Castillo, 4.3 km (air) SW Casimiro Castillo (MZFC 26948); MICHOACÁN: On road to Coahuayana-Palos Marías (INIRENA 1069); SINALOA: 2.6 km W Concordia, on Hwy 40 (MZFC 26948).

***Coniophanes melanocephalus*. — MEXICO:** GUERRERO: 0.3 mi (by road to Chichihualco) W Mex. 95 (LSUMZ 36253); 3.2 mi N Zumpango del Rio (UF 24780); 12 miles S Puente de Ixtla (FMNH 100032); 400 m along the turnoff to Tecolapa from the Olinalá-Papalutla road (MZFC 28840); MICHOACÁN: Villa Eréndira, municipio de Nuevo Urecho (INIRENA 1618); Benito Juárez, en huerta de guayabas (INIRENA 1760); Taretán, Hoyo del Aire (UAA 323); MORELOS: Calera Chica, Jiutepec (UTA R 56408); PUEBLA: Jolalpan, Rancho El Salado (CNAR 25730).

***Coniophanes michoacanensis*. — MEXICO:** GUERRERO: Municipio de Zihuatanejo de Azueta, Mata de Sandía (MZFC 34561); MICHOACÁN: Municipio de Aguila, El Farito, 8 km NW Caleta de Campos (MZFC 10393, holotype).

***Coniophanes piceivittis*. COSTA RICA:** GUANACASTE: Liberia, Santa Rosa National Park (UTA-R 44958); **GUATEMALA:** no locality data (UTA-R 28297); ZACAPA: Among cabins at Usumatlán on CA9 where the road crosses a river 20.5 km N of El Rancho (UTA-R 32965); Cabañas El Arenal (UTA-R 52276); Gualán, Aldea Arenal, Km 164, Carretera al Atlántico (UTA-R 44764); HUEHUETENANGO: Cuilco, Caserío Mojuba (UTA-R 39184); 9.2 km N Cuatro Caminos at Río Azul (UTA-R 42312); QUICHÉ: Chicam, N Chixoy (UTA-R 42464); **HONDURAS:** COMAYAGUA: Playitas, Aldea Lo de Reina (UTA-R 41256); COPÁN: Copán (UMMZ 65620); Santa Rita Copán (UTA-R 53236); **MEXICO:** CHIAPAS: 6.9 mi E Chiapa de Corzo (AMNH R 158325); Pijijiapan, Subteniente Pedro Sánchez (MZFC 34560); OAXACA: 2-3 mi S Tapana-tepec (UTA-R 4338); Carretera San Pedro Pochutla-Puerto Ángel (UTA-R 51863); Cerro Arenal, near Tenango (AMNH-R 68030); Cerro Las Flores (MZFC 34562); Ciudad Ixtepec, Arroyo del Cerro Naranjo, Cerca de “Los Mangos” (CNAR 13017); Quiengola (half-way), Tehuantepec (AMNH-R 64583, 66804); San Blas, Tehuantepec (CNAR 7639); Santo Domingo Zanatepec, Camino a las Lagunas Sol y Luna (MZFC 25265); Santo Domingo Zanatepec, Montañas N Zanatepec (MZFC 25269); Santa Lucia, near Tehuantepec (AMNH-R 68028); San Pedro, near Tehuantepec (AMNH-R 68029); Tehuantepec (AMNH-R 65886); Mex 200, Carretera Pochutla-Santo Domingo Tehuantepec (MZFC 17292).

***Coniophanes “sarae”*. — MEXICO:** MICHOACÁN: 12 mi S Arteaga (UMMZ 118954, paratype); Chinicuila, Tehuantepec (MZFC 13030, holotype).

***Coniophanes schmidtii*. — GUATEMALA:** PETÉN: 6.4 km N El Caoba on El Remate-Tikal Road (UTA-R 39163); ca. San José (UTA-R 37249-50); ca. San José, N shore Lago Petén-Itzá

(UTA-R 37251); Gringo Perdido, NE side of Lago Petén-Itzá, near El Remate (UTA-R 50293-94); **MEXICO:** CAMPECHE: 64 Km N X-Pujil, Km 2.5, Camino a Rancho San Isidro (ECOSUR 954, 958); Brecha a Flores Magón, El Papagayo (ECOSUR 1327); Carretera a la Zona Arqueológica de Calakmul (ECOSUR 1204); Zona Arqueológica de Calakmul (ECOSUR 1197, 1267, 1446; MZFC 22080); CHIAPAS: Ocosingo, Campamento Yaxchilán (MZFC 13133); QUINTANA ROO: Carretera a Laguna Guerrero (ECOSUR 3466); Carretera Carrillo Puerto-Valladolid (ECOSUR 303-05, 360); Carretera costera entre Calderitas y ruinas Oxtankah (ECOSUR 2930, 3425); Chetumal, Centro de Investigación de Quintana Roo (ECOSUR 8, 69, 346, 921; MZFC 10898); Col. FOVISSSTE Quinta Etapa (ECOSUR 3982); Ejido X-Hazil Sur (ECOSUR 2807); Entre Bacalar y Reforma (ECOSUR 4020); Entre Calderitas y Laguna Guerrero (ECOSUR 3119, 3245, 3496, 3662); Entre Calderitas y Ruinas de Oxtankah (ECOSUR 3741, 4025); Entre Luis Echeverría y desviación Laguna Guerrero (ECOSUR 2931, 3242, 3244); Felipe Carrillo Puerto, Reserva de la Biosfera Sian Kaan, Zona 5, Transecto 3 (ECOSUR 1966); Laguna Negra (Lag. Sn. Felipe) por Reforma (ECOSUR 2723); Nuevo Tabasco camino a la aguada El Metate (ECOSUR 2455); Othón P. Blanco, Ejido Caobas, en el pueblo (ECOSUR 2699); TABASCO: Piscifactoría José Narciso Roviroso, Teapa (MZFC 14885); YUCATÁN: Chankom (ECOSUR 3463); Cholul (UTA-R 28298); Entre Chankom y la carretera costera del Golfo (cruzamiento), 2.65km antes de llegar a Chankom (ECOSUR 3785); Ticimul (ECOSUR 3623); Valladolid, Pisté (UTA-R 53430).

***Coniophanes taeniatus.*—MEXICO:** OAXACA: San Felipe Usila, Santiago Tlapeusco (CNAR 24749); San Juan Cotzocón, Rancho ADAMK (MZFC 27526); QUERÉTARO: Arroyo Seco village

near Rio Santa María Canyon (UMMZ 143726); SAN LUIS POTOSÍ: 13 mi N Ciudad Valles (AMNH-R 162006); TAMAULIPAS: 5 mi NE of Gómez Farias along Río Sabinas at Pano Ayuctle (UMMZ 104048); Rancho El Cielo (MZFC 34557); VERACRUZ: 1/2 mi E Plan del Río (UMMZ 101160, holotype of *Coniophanes frangivirgatus*); 1 mi S Juan Díaz Covarrubias (UTA-R 2827); 4 mi NW Acayucan, Rancho Las Hojitas (UMMZ 114532-33); 18.6 mi S bridge at W end of Lago Catemaco (UTA-R 6863); 23 mi SE Xalapa (TNHC 27446); 26.2 mi (by Mex 140) SE Jalapa (AMNH-R 106563); Catemaco, Acuyal (CNAR 19289); Catemaco, Instalaciones Parque de la Flora y Fauna Tropical, UV, Cerro Pipiapan (CNAR 19288); Near Los Mangos, S edge of town (UMMZ 122833); Near San Andrés Tuxtla on by pass around town (UMMZ 122832); Veracruz (UMMZ 122031); No other locality data (ZMB 6672, holotype).

***Coniophanes taylori.* — MEXICO:** GUERRERO: 2 km W Puerto Marqués (CNAR 9452); 8 km E Chilpancingo (FMNH 126631, paratype); Agua de Obispo (FMNH 100868, holotype); Aproximadamente 100 m del Centro de Salud de Tecotcintla, sobre carretera Tixtla-Zacatzonapa (MZFC 30003); Cerro de la Cantera Holcim (MZFC 34558-559); Colonia Cerro Las Torres, Chilpancingo de los Bravo (MZFC 34556); Colonia Cooperativa, Chilpancingo de los Bravo (MZFC 30002); Km 357 on highway, near Acapulco (FMNH 126630, paratype); Las Torres, Colonia Omiltemi, Chilpancingo de los Bravo (MZFC 30002); Zoyatepec (SMF 100276-77); OAXACA: Villa de Tututepec de Melchor Ocampo, Parque Nacional Lagunas de Chacahua (CNAR 23852).

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