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Out of the Past: A new species of *Tantilla* of the *calamarina* group (Squamata: Colubridae) from southeastern coastal Guerrero, Mexico, with comments on relationships among members of the group

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Abstract.—A new species of *Tantilla* in the *calamarina* group from southeastern coastal Guerrero, Mexico is described. This new species is part of a clade that contains *T. calamarina*, *T. cascadae*, *T. ceboruca*, *T. coronadoi*, *T. deppei*, *T. sertula*, and *T. vermiformis*. All of these species are endemic to Mexico, except for *T. vermiformis*, which is found along the Pacific coastal plain from El Salvador to northwestern Costa Rica. Members of this group of *Tantilla* show varying adaptations to fossoriality, which might reflect their phylogenetic relationships.

Keywords. *calamarina* group, centipede snake, fossoriality, phylogenetics, Reptilia, taxonomy

Resumen.— Describimos una nueva especie de *Tantilla* del grupo *calamarina* de la costa sureste de Guerrero, México. Esta nueva especie forma parte de un clado que contiene a *T. calamarina*, *T. cascadae*, *T. ceboruca*, *T. coronadoi*, *T. deppei*, *T. sertula* y *T. vermiformis*. Todas estas especies son endémicas de México, excepto *T. vermiformis*, que se encuentra a lo largo de la planicie costera del Pacífico desde El Salvador hasta el noroeste de Costa Rica. Los miembros de este grupo de *Tantilla* muestran diversas adaptaciones a la fosorialidad, lo que podría reflejar sus relaciones filogenéticas.

Palabras claves. Culebra ciempiés, fosorialidad, grupo *calamarina*, relaciones filogenéticas, Reptilia, taxonomía

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Introduction

A recent paper by Palacios-Aguilar et al. (2021) noted a specimen of *Tantilla* from Guerrero that was collected over a century ago (BMNH 1906.6.1.241). This specimen, a female clearly referable to the *Tantilla calamarina* group (Wilson and Meyer 1981), was discussed by Wilson and Mata-Silva (2014) and determined to be either an atypical individual of *Tantilla coronadoi* or a

representative of an unnamed taxon. Palacios-Aguilar et al. (2021) suspected the latter alternative because the three hitherto known specimens of *T. coronadoi* are consistent in key aspects of their scutellation, but they also declined to name a new species based on specimen BMNH 1906.6.1.241, which was collected in 1904 by Hans Gadow and reported as *Homalocranium miniatum* in his 1905 paper. According to Dixon et al. (2000), the name *H. miniatum* is a synonym of *T. rubra*.

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When the Palacios-Aguilar et al. (2021) paper appeared, one author of this paper (LDW) contacted the senior author and proposed reexamining the BMNH specimen to determine whether its status could be established more definitively, based on a modern understanding of the content and relationships within the *Tantilla calamarina* group. Consequently, the authors of this paper decided to collaborate in an attempt to determine on the status of this curious specimen, which has been lying in anonymity since it was collected 118 years ago.

The first four words of the title of this paper (*Out of the Past*) are used in reference to the period of time this specimen, which now becomes the holotype of a new species of *Tantilla*, has resided in the BMNH collection. These words also refer to the period of time that has elapsed since the person after whom this snake is being named began her journey in 1956 to find freedom from the tyranny in her homeland in her adopted land of Australia. For aficionados of cinema, *Out of the Past* will be recognized as the title of a well-regarded film noir, the 1947 work of French director Jacques Tourneur starring Robert Mitchum, Jane Greer, and Kirk Douglas.

Materials and Methods

During the last five decades, author LDW has been examining specimens of the genus *Tantilla*, resulting in the publication of several taxonomic treatments and species descriptions within this genus (e.g., Wilson and Meyer 1981; Wilson 1999; Wilson and Campbell 2000; Wilson and Mata-Silva 2014, 2015). While compiling information for the first taxonomic study of the *T. calamarina* species group (Wilson and Meyer 1981), measurements and scale counts were obtained for the specimen that now is the focus of this paper (BMNH 1906.6.1.241). Soon after that work started, the Senior Curator of Reptiles at the Natural History Museum, London, was contacted to obtain morphological data on the specimen, as well as high quality photographs. The photographs aided in making comparisons with the representatives of the *T. calamarina* species group.

In addition to the aforementioned works on the genus *Tantilla*, the comparisons in this paper benefitted from examinations of more recent literature specifically involving the *calamarina* species group (Canseco-Márquez et al. 2007; Cisneros-Bernal et al. 2020; Cruz-Sáenz et al. 2015; Dávalos-Martínez et al. 2021; Palacios-Aguilar et al. 2021; Ramírez-Bautista et al. 2014; Rocha et al. 2016), as well from the examination of comparative material housed at the Colección Nacional de Anfibios y Reptiles (CNAR) and the Museo de Zoología “Alfonso L. Herrera,” Facultad de Ciencias (MZFC), both at the Universidad Nacional Autónoma de México. Scale counts and digital photographs of specimens deposited in the herpetological collection of the University of Texas at Arlington (UTA-R) were also obtained. The measurements are indicated in millimeters, and the ventral scales were counted following the method proposed by Dowling (1951), with the segmental counts referring to the sum of the ventrals + subcaudals, excluding the cloacal scute.

Results

After detailed comparisons of the BMNH specimen with the pertinent published sources and specimens held in scientific collections, we determined that BMNH 1906.6.1.241 does indeed represent a new species of the genus *Tantilla*.

Tantilla carolina, new species

Figs. 1–2.

Suggested common name. Carolina’s Little Snake.

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Holotype. BMNH 1906.6.1.241, an apparent subadult or juvenile female from Tezonapan (= Tecopan), north of Ayutla, Guerrero, Mexico, collected by Hans Gadow in 1904.

Diagnosis. *Tantilla carolina* is a member of the *T. calamarina* group (Table 1). This species differs from *Tantilla calamarina* by the presence of more ventrals in females (156 versus [hereinafter = vs.] 118–140), more total segmental scales (194 vs. 146–179), a normally-sized preocular scale in contact with the postnasal scale (vs. a preocular with a tendency toward a decrease in size to complete the loss of the scale), two postocular scales (vs. one), seven supralabials (vs. usually six), a uniform dorsal head color followed by two pale postparietal spots (vs. a head pattern consisting of a spatulate dark anterior extension of the middorsal dark stripe flanked by

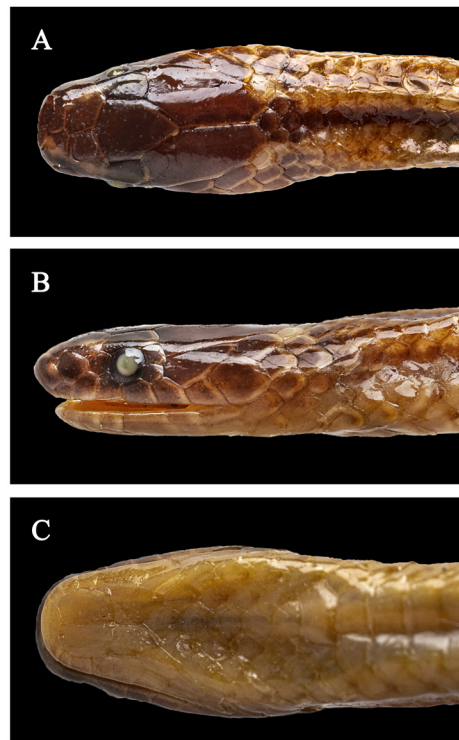


Fig. 1. Dorsal (A), lateral (B), and ventral (C) views of the head of the holotype of *Tantilla carolina* sp. nov. (BMNH 1906.6.1.241).



Fig. 2. Dorsal view of the holotype of *Tantilla carolina* sp. nov. (BMNH 1906.6.1.241).

prominent pale narrow longitudinal markings confluent with the pale postparietal spots), and a body pattern involving a dark lateral stripe that does not extend to the end of the body (vs. a dark brown lateral stripe on rows 3 and 4 extending the length of the body). The new species differs from *Tantilla cascadae* by the presence of more ventrals in females (156 vs. 139–144), more total segmental scales (194 vs. 176–192), seven supralabial scales (vs. six), and the dorsum of the head without a pattern but containing a pair of small pale postparietal spots (vs. a spatulate dark anterior extension of the middorsal dark stripe flanked by pale narrow longitudinal markings confluent with pale postparietal spots, or narrowly separated from the pale postparietal spots). The new species differs from *Tantilla ceboruca* by lacking a pattern and a pair of small pale postparietal scales on the dorsum of the head (vs. a spatulate extension of the middorsal dark stripe flanked by pale longitudinal markings confluent with postparietal spots and extending anteriorly along the sides of the parietal scales and across the supraoculars and prefrontals to join on the internasals), and a lateral portion of the head without a pattern (vs. one having each supralabial with a white border). The new species differs from *Tantilla coronadoi* by the presence of fewer ventral scales (156 vs. 165–178), fewer subcaudal scales (38 vs. 40–41), fewer total segmental scales (194 vs. 205–219), the anterior and posterior temporals in contact with one another (vs. those two scales separated from one another by contact of the 7th supralabial and the parietal scale), and the dorsal and lateral portions of the head lacking a pattern (vs. a dorsal head pattern consisting of a spatulate dark anterior extension of the middorsal dark stripe flanked by pale anterior extensions of the dorsolateral ground color, and a lateral head pattern consisting of supralabials with dark upper and pale lower portions). The new species differs from *Tantilla deppei* by the presence of fewer subcaudal scales (38 vs. 43–50), fewer total segmental scales (194 vs. 196–214), and the dorsal and lateral portions of the head lack a pattern and a pair of small pale postparietal

spots (vs. a spatulate dark anterior extension of the middorsal dark stripe flanked by pale anterior extensions of a middorsally-divided pale nuchal band). The new species differs from *Tantilla sertula* by the presence of fewer ventrals in females (156 vs. 161), more subcaudals in females (38 vs. 30), more total segmental scales (194 vs. 191), and the dorsal and lateral portions of the head lack a pattern (vs. a dorsal head pattern consisting of a spatulate dark anterior extension of the middorsal dark stripe flanked by prominent pale, narrow, longitudinal markings confluent with pale postparietal spots). The new species differs from *Tantilla vermiformis* by the presence of more ventral scales in females (156 vs. 120–129), more subcaudal scales (38 vs. 19–24), more total segmental scales (194 vs. 140–150), as well as by the presence of a small pair of pale postparietal spots confined to single scales (vs. a single pale spot crossing both parietal scales).

Description of the holotype (Figs. 1–2). An apparent subadult or juvenile female with 15 smooth dorsal scales throughout the trunk, 156 ventrals, a divided cloacal scute (= anal plate), 38 subcaudals, a total length of 112 mm, a tail length of 14 mm, and a tail/total length ratio of 0.125.

Nasal completely divided, posterior section in broad contact with a single preocular on both sides of head; two postoculars, approximately subequal in size; one anterior and one posterior temporal, in contact with one another, anterior temporal separating supralabials five, six, and seven from parietal, posterior temporal shorter than anterior temporal, approximately the shape of a dorsal body scale, although somewhat larger; supralabials 7–7, the 1st in contact with rostral, prenasal, postnasal, and 2nd supralabial, the 2nd with postnasal, preocular, and 3rd supralabial, the 3rd with preocular, orbit, and 4th supralabial, the 4th with orbit, lower postocular, and 5th supralabial, the 5th with lower postocular, anterior temporal, and 6th supralabial, the 6th with 5th supralabial, anterior temporal, and 7th supralabial, the 7th with the 6th

Table 1. Comparison of selected morphological features among the eight members of the *Tantilla calamarina* group. Data summarized from Wilson and Campbell (2000); Savage (2002); Canseco-Márquez et al. (2007); Wilson and Mata-Silva (2014); Cruz-Sáenz et al. (2015); Rocha et al. (2016); and Palacios-Aguilar et al. (2021).

Features	<i>T. carolina</i>	<i>T. calamarina</i>	<i>T. cascadae</i>	<i>T. ceboruca</i>	<i>T. coronadoi</i>	<i>T. deppei</i>	<i>T. sertula</i>	<i>T. vermiformis</i>
Total length (mm)	112	72–202	158–196	175–200	161–183	95–273	89–152	157
Tail length (mm)	14	13–36	30	33–35	25–31	16–62	12–21	—
Relative tail length	0.125	0.110–0.211	0.138–0.190	0.164–0.194	0.155–0.169	0.166–0.254	0.121–0.157	0.096–0.150
Ventrals in males	—	106–133 (119.7)	—	138–146	158	142–154 (145.9)	153?	115–123 (119.6)
Ventrals in females	156	118–140 (129.0)	139–144 (141.5)	153–178	165–178 (171.5)	148–168 (160.1)	160–161	120–129 (124.2)
Subcaudals in males	—	30–43 (36.8)	—	42–47	35+ (?)	54–62 (57.2)	37?	23–28 (25.3)
Subcaudals in females	38	22–43 (28.8)	37–48 (42.5)	36–41	40–41 (40.5)	43–58 (46.2)	30–33	19–24 (21.0)
Ventrals + subcaudals in males	—	145–166 (156.9)	—	180–193	—	196–213 (203.1)	190?	141–147 (144.5)
Ventrals + subcaudals in females	194	146–179 (158.0)	176–192 (184.0)	189–219	205–219 (212.0)	196–214 (206.3)	191–193	140–150 (144.7)
Preocular	Present, in contact with postnasal	Tendency toward decrease in size to complete loss	Present, in contact with postnasal	Present, in contact with postnasal or not	Present, in contact with postnasal	Present, in contact with postnasal	Present, in contact with postnasal	Present, in contact with postnasal, sometimes fused with prefrontal
Number of postoculars	2	1	2	2	2	2	2	2
Number of supralabials (number entering orbit)	7 (3+4)	Usually 6 (3+4)	6 (3+4)	7 (3+4)	7 (3–4)	Usually 7	6–7	7

Table 1 Continued. Comparison of selected morphological features among the eight members of the *Tantilla calamarina* group. Data summarized from Wilson and Campbell (2000); Savage (2002); Canseco-Márquez et al. (2007); Wilson and Mata-Silva (2014); Cruz-Sáenz et al. (2015); Rocha et al. (2016); and Palacios-Aguilar et al. (2021).

Features	<i>T. carolina</i>	<i>T. calamarina</i>	<i>T. cascadeae</i>	<i>T. ceboruca</i>	<i>T. coronadoi</i>	<i>T. deppei</i>	<i>T. sertula</i>	<i>T. vermiformis</i>
Anterior and posterior temporals separated	No	No	No	No	Yes	No	No	No
Fusion of anterior temporals and sixth supralabial	No	No	No	No	No	No	No	Occasionally
Dorsal head pattern	Dorsum of head without pattern; pale postparietal spots limited to single scale located posterior to juncture between posterior temporal scale and parietal scale	Spatulate dark anterior extension of middorsal dark stripe flanked by prominent pale narrow longitudinal markings confluent with pale postparietal spots	Spatulate dark anterior extension of middorsal dark stripe flanked by pale narrow longitudinal markings confluent with pale postparietal spots or narrowly separated from postparietal spots	Spatulate extension of middorsal dark stripe flanked by pale longitudinal markings confluent with pale postparietal spots, and extending anteriorly along sides of parietals, and across supraoculars and prefrontals to join on internasals	Spatulate dark anterior extension of middorsal dark stripe flanked by pale anterior extensions of dorsolateral ground color	Spatulate dark anterior extension of middorsal dark stripe flanked by prominent pale narrow longitudinal markings confluent with pale postparietal spots	Spatulate dark anterior extension of middorsal dark stripe flanked by prominent pale narrow longitudinal markings confluent with pale postparietal spots	Dark brown dorsally and laterally with tan, pale lavender, or pale brown blotches on posterior portion of parietals
Lateral head pattern	Uniform in color	—	—	Each supralabial scale with a white border	—	—	Uniformly dark brown in color	—
Body pattern	Dark lateral stripe does not extend to end of body	Tan to brown with variously-sized dark middorsal stripe and a dark brown lateral stripe on rows 3 and 4	Pale brown with dark middorsal stripe occupying middle of middorsal scale row; dark lateral stripe on rows 3 and 4 only in neck region	Dark brown with dark middorsal stripe covering middle of middorsal scale row on most of body; dark lateral stripe on adjacent halves of rows 3 and 4	Tan to brown with dark middorsal stripe occupying middle of middorsal scale row and dark lateral stripe on row 3 or rows 2 and 3; diffuse dark stripe on rows 3 and 4	Tan to brown with diffusely dark variously-sized middorsal stripe and dark lateral stripe on row 3 or rows 2 and 3; diffuse dark stripe on row 5	Dorsum pale brown on rows 5 to 7, dark brown on rows 1 to 4; dark middorsal stripe on middle of middorsal row, narrowing to series of disjunct longitudinal dashes continuing to end of tail	Pale brown to brown dorsum with poorly-defined, disjunct dark middorsal stripe confined to middorsal row
Ventral pattern	Immaculate cream	Immaculate cream	Cream to pale greenish yellow, with slight amount of dark pigment at lateral apices	Immaculate cream to pale greenish yellow	Immaculate cream to white	Immaculate cream	Immaculate cream	Immaculate white, cream, pale yellow, or pale pink

supralabial, anterior and posterior temporals, and two post-cephalic scales, with the 7th the largest; infralabials 6–6, with the 1st pair separated by contact of mental and anterior chinshields, the first four in contact with anterior chin shields, with the 4th largest; and anterior chinshields larger than posterior pair.

In preservative, the dorsal and lateral portions of the head are uniform dark brown, without a pattern (Fig. 1). A pair of pale postparietal spots, pale yellow in color, are present on the single scales located at the juncture of the parietal and posterior temporal scales, one each on either side of the head (Fig. 1). The dorsal ground color in preservative is brown with a dark brown middorsal stripe confined to the middorsal scale row, which extends to the end of the tail, breaking up into isolated dark spots, one per scale on the posterior region of the body and tail (Fig. 2). The remainder of the dorsum lacks a pattern. The venter is a uniform (perhaps cream) color in preservative.

Distribution. Known only from the type locality (Fig. 3). Tecoanapa is the seat of the municipality of Tecoanapa in the Pacific lowlands of southeastern Guerrero (coordinates 16°53'N, 99°24'W). Tecoanapa is a city located on Mexico Highway 95, east-northeast of Acapulco and south-southeast of Chilpancingo. The town lies at an elevation of 431 m (<http://PueblosAmerica.com>; accessed 30 March 2022).

The vegetation in the region consists of a mixture of tropical deciduous forest (*selva baja caducifolia*), oak forest (*bosque de encino*), and agricultural lands, according to the available maps (CONABIO 1999).

Conservation assessment. The Environmental Vulnerability Score (EVS) for *Tantilla carolina* can be calculated as $6 + 8 + 2 = 16$, which places its score in the middle of the high vulnerability category, as explained by Wilson et al. (2013).

Etymology. We are privileged to name this small snake in honor of the Hungarian Freedom Fighter Karolina Laszlo (Fig. 4), in recognition of her dedication to the maintenance of human rights for all peoples in the face of totalitarianism, beginning with the Hungarian Revolution in 1956. As a young woman, Karolina was forced to join the exodus of her country people, in the company of her new husband, a soldier, Ede Károly Fucskó, who bravely defied the Hungarian dictatorship, communism, and the invading Soviet army. Ede Károly Udvarhelyi was adopted at an early age, when his mother remarried and thus kept the surname Fucskó. As the couple roamed through several European countries, in search of a refuge from the terror of oppressive political regimes, they escaped to England before seeking asylum in Australia. Due to unforeseen circumstances, however, the family of

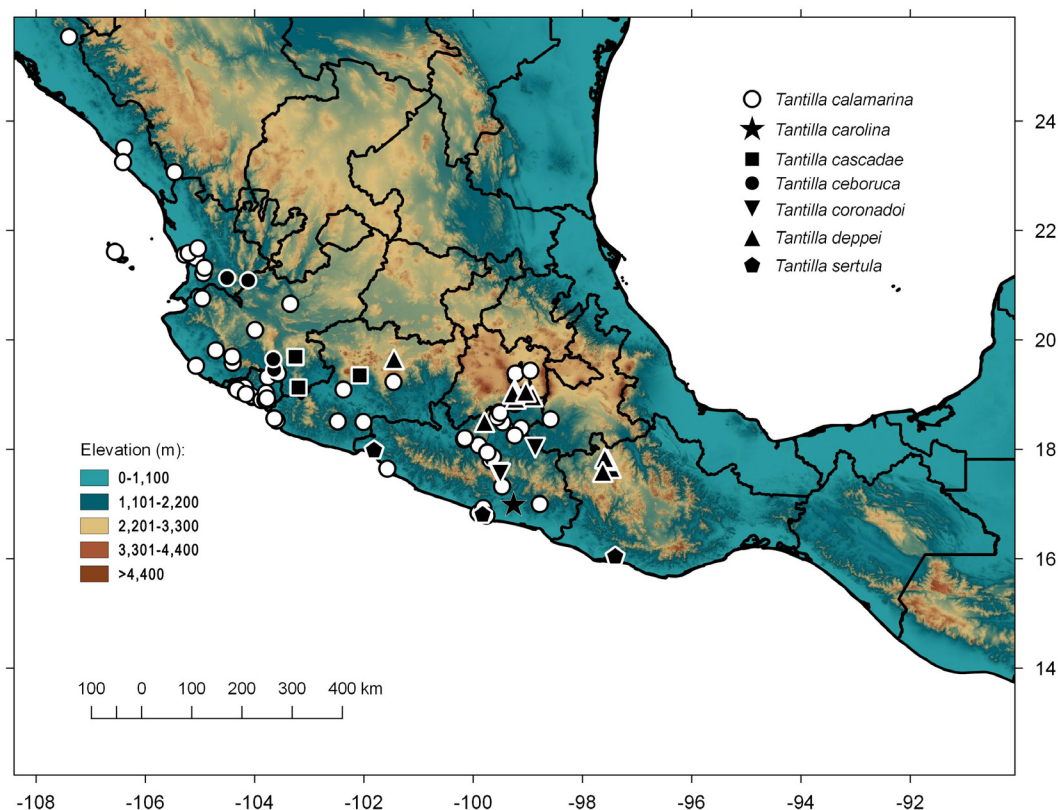


Fig. 3. Geographic distribution of the *Tantilla calamarina* group species in western Mexico. The black star represents the type locality of *Tantilla carolina* sp. nov. described herein.

Key to the members of the *Tantilla calamarina* group

1. Anterior and posterior temporals separated by contact of 7th supralabial and parietal. *T. coronadoi*
Anterior and posterior temporals in contact, not separated by contact of 7th supralabial and parietal 2
2. Postocular single *T. calamarina*
Postoculars two. 3
3. Ventrals fewer than 130; subcaudals fewer than 30 *T. vermiformis*
Ventrals 130 or more; subcaudals 30 or more 4
4. Ventrals 144 or fewer *T. cascadae*
Ventrals 153 or more 5
5. Dark lateral stripe present 6
Dark lateral stripe absent 7
6. Dark lateral stripe on adjacent halves of rows 3 and 4 *T. ceboruca*
Dark lateral stripe on row 3 or on rows 2 and 3 *T. deppei*
7. Dorsal head pattern consists of a spatulate dark anterior extension of the middorsal dark stripe occupying dorsum of head, flanked by pale, narrow, longitudinal stripes broadly separated from pale postparietal spots occupying portions of three dorsal scales immediately posterior to the posterolateral portion of each parietal scale. *T. sertula*
Dorsum of head without pattern, uniform brown in color; pale postparietal spots each confined to single postparietal scales *T. carolina* **sp. nov.**

five later travelled back to Hungary, residing there for several years before escaping again to Vienna, Austria, then travelling to Italy, and from there they journeyed to South Africa. There, they dared to oppose the policy of apartheid but eventually, under duress, had to flee as interracial tensions escalated into further hostilities and reprisals. Finally, the family found relative solace in the democratic land of Australia, where life remained challenging in such a strangely beautiful land. During this long trek to find a life of freedom, Karolina and Ede were accompanied by their three children, John Edward, Stephen Charles, and a co-author of this paper, Lydia Allison Fucsko. Therefore, in Karolina's honor, we named this snake *Tantilla carolina* **sp. nov.**, with a reference to the meaning of the name Carolina in Spanish as "the prettiest woman of the town," an apt descriptor for this truly lovely, indomitable, and spirited lady whose humanitarian efforts continue to inspire future generations.

Discussion

Wilson and Meyer (1981: 2–3) established a case for the recognition of the *Tantilla calamarina* group, which they maintained consisted of four species, including *T. calamarina*, *T. coronadoi*, *T. deppei*, and a species they described as new, *T. cascadae*. The justification for their recognition of the *calamarina* group primarily was based on a "similarity in head pattern." Wilson and Meyer (1981: 2) detailed that all four species they recognized as part of this group "have the central portion of the parietals covered with a spatulate anterior extension of the middorsal dark stripe, which continues anteriorly to cover the remainder of the head. On either side of this central head mark is a postparietal pale spot that usually grades posteriorly into the ground color of the dorsolateral field [...] and, in its best-developed state, connects

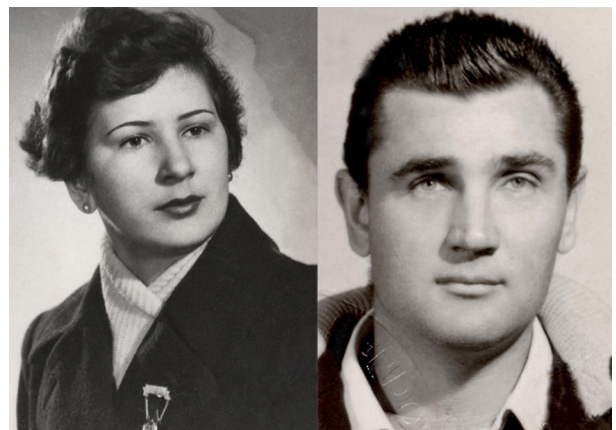


Fig. 4. (Left) The Hungarian Freedom Fighters, Karolina and Ede Károly Fucskó, in Hyde Park, London, England, 1958. (Right) Enduring photographs of Karolina and Ede Károly Fucskó.

anteriorly with a narrow extension that proceeds along the side of the parietal, over the supraocular and onto the side of the prefrontals and internasals.” The members of this group also exhibit a dark middorsal stripe occupying some portion of the middorsal scale row and, in some cases, a portion of the adjacent dorsal scale rows.

In subsequent years, another species of *Tantilla*, *T. vermiformis*, was allocated to the *calamarina* group (Wilson 1999). This allocation, however, was questioned by Holm (2008: 98), who stated that “[his] results [lead him] to not include *T. vermiformis* in the *T. calamarina* group as suggested by Wilson et al. (1999) and Wilson and Campbell (2000). Similarities between these taxa may be due to convergent adaptations for fossoriality and the dark vertebral line is a shared primitive trait.” Other hypotheses worth testing when sufficient molecular material becomes available would include whether *T. vermiformis* is more closely related to the members of the *T. melanocephala* group (Wilson and Mena 1980) or to some other member or members of the genus not yet identified.

In 2000, Wilson and Campbell described *Tantilla sertula* based on a single specimen from Pacific coastal Guerrero, Mexico, and allocated this species to the *calamarina* group. A second specimen of this species was documented from the coastal plain of Guerrero by Canseco-Márquez et al. (2007). Thereafter, Rocha et al. (2016) reported a third specimen of this species from the lower foothills of the Sierra Madre del Sur of southern Oaxaca. Finally, Canseco-Márquez et al. (2007) described *Tantilla ceboruca* from southern Nayarit, Mexico. These authors also placed this species in the *calamarina* group.

Thus, with the description of *T. ceboruca* in 2007, the *calamarina* group was considered to consist of seven species, including, in order of year of description: *T. vermiformis* (Hallowell 1861), *T. calamarina* (Cope 1866), *T. deppei* (Bocourt 1883), *T. coronadoi* (Hartweg 1944), *T. cascadae* (Wilson and Meyer 1981), *T. sertula* (Wilson and Campbell 2000), and *T. ceboruca* (Canseco-Márquez et al. 2007). With the description of *T. carolina*, the genus *Tantilla* currently is known to contain 68 species (The Reptile Database, <http://www.reptile-database.org/>; accessed 15 May 2022).

Most species in the *calamarina* group are distributed in the western portion of Mexico, from northern Sinaloa to south-central Oaxaca, except for *Tantilla vermiformis*, which is found along the Pacific coastal plain of Central America from El Salvador to northwestern Costa Rica (Wilson and Mata-Silva 2015; Antúnez-Fonseca et al. 2020a). The northernmost-occurring and most widely-distributed species in the group is *T. calamarina*, which is known from northern Sinaloa to south-central Guerrero, including the Tres Marias Islands (Isla María Madre) lying off Nayarit; the elevational range for this species is from near sea level to 1,677 m asl. In comparison, the remaining species in the group are narrowly distributed, as follows: *T. cascadae* (1,430–1,858 m asl from south-central Jalisco to central Michoacán); *T. ceboruca* (1,233–2,094 m asl from southeastern Nayarit to north-central Jalisco); *T. coronadoi* (650–1,524 m asl in northeastern and central Guerrero); *T. deppei* (1,524–

2,438 m asl in northern Morelos, northern Guerrero, and northwestern Oaxaca); *T. sertula* (near sea level–487 m asl from northwestern Guerrero to south-central Oaxaca); and *T. vermiformis* (40–520 m asl from El Salvador to northwestern Costa Rica).

One of the most obvious features of the species presently allocated to the *calamarina* group is that they show varying adaptations to a fossorial existence. Ramírez-Bautista et al. (2014) developed a so-called “index of fossoriality” to quantify the degree of fossorial adaptation among the seven members of this group, as then comprised, based on features of cephalic scutellation and segmental counts. These features were documented in Table 1 of that paper, converted to character states that were placed in Table 2 of that paper, which then were collated to produce an index of fossoriality. The reader should refer to that paper for a more thorough explanation of the index of fossoriality. These authors concluded their analysis of fossoriality in the *calamarina* group by stating (pp. 803–804) that “low indices [of fossoriality] are found in the more generalized *calamarina* group species, such as *T. sertula* and *T. deppei*..., intermediate values are found in the more adapted species, such as *T. ceboruca*, *T. coronadoi*, *T. cascadae*, and *T. vermiformis*..., and high indices in the most adapted species, i.e., *T. calamarina* and *G. redimitus*.”

Using the methodology employed by Ramírez-Bautista et al. (2014), we determined the index of fossoriality for *Tantilla carolina* as follows:

- Preocular present—1
- Preocular in contact with postnasal—1
- Preocular fused with prefrontal and supraocular—1
- Number of postoculars—1
- 5th supralabial separated from parietal—1
- 6th supralabial fused with anterior temporal—1
- 7th supralabial and parietal in contact—1
- Number of supralabials—1
- Supralabials entering orbit—1
- Number of ventrals—1
- Number of subcaudals—2

The sum of these 11 character-values for *T. carolina* is 12, the same value as calculated for *T. sertula* by Ramírez-Bautista et al. (2014). This index of fossoriality is the lowest among the members of the *calamarina* group, in which the indices range from 12 to 24 (including that for *Geagras redimitus*, which was included in the *calamarina* group by Holm [2008]). This determination indicates that *T. carolina* and *T. sertula* are the two members of the group that are the least adapted for a fossorial existence. The indices of fossoriality for the other species involved, in increasing value, are as follows: *T. deppei* (13); *T. ceboruca* and *T. coronadoi* (both 14); *T. cascadae* (15); *T. vermiformis* (16); *T. calamarina* (21); and *G. redimitus* (24).

As noted by Ramírez-Bautista et al. (2014), the index of fossoriality is not intended to elucidate the phylogenetic relationships within the *calamarina* group, but it is tempting to hypothesize that this index perhaps is reflective of the phylogenetic relationships that could

be substantiated by a molecular analysis, should such an analysis ever become possible. The timeline for such an analysis is difficult to predict, especially because most of the species involved are known from only a handful of preserved specimens (or only one).

If and when a molecular analysis of the phylogenetic relationships of this group of snakes becomes possible, five questions of principal interest to answer would be the following: (1) Is *Geagras redimitus* closely related enough to the members of the *Tantilla calamarina* group to be subsumed into this group, as per the conclusion of Holm (2008)? (2) Is *Tantilla vermiformis* closely related enough to the unquestioned members of the *calamarina* group to be included within it, or do its closest relationships lie elsewhere in the genus *Tantilla*? (3) Is *Tantilla carolina* closely related enough to the unquestioned members of the *calamarina* group to be included within it? (4) What are the phylogenetic relationships of the nine species involved to one another? and (5) What are the relationships of these species to the other members of the genus *Tantilla*?

In their treatment of the *Tantilla* clade, Wilson and Mata-Silva (2015) noted that the genus *Tantilla* contained 61 species at that point. With the description of *Tantilla carolina*, the genus now contains 68 species, and it remains the second largest genus of snakes in the Western Hemisphere after *Atractus* (currently containing 146 species, according to The Reptile Database, <http://www.reptile-database.org/>; accessed 9 April 2022). Only one other snake genus contains more species than *Tantilla*, the Old-World genus *Oligodon* (presently consisting of 88 species, according to The Reptile Database, <http://www.reptile-database.org/>; accessed 9 April 2022). The seven species of *Tantilla* described since the Wilson and Mata-Silva (2015) paper was published are (listed alphabetically): *T. berguidoi* Batista et al. 2016; *T. excelsa* McCranie and Smith 2017; *T. gottei* McCranie and Smith 2017; *T. lydia* Antúñez-Fonseca et al. 2020b; *T. stenigrammi* McCranie and Smith 2017; and *T. tjiasmantoi* Koch and Venegas 2016. Six of these seven species are allocated to the *Tantilla taeniata* group. The remaining species (*T. tjiasmantoi*) was not placed in a species group by the original authors, but its unusual pattern of dark banding on a pale ground color might suggest that this species is allied with another South American species that sometimes is banded, *T. semicincta* (Wilson 1976).

In the last two decades, about 40 new species of snakes have been described from Mexico, including four that are known to occur on the Pacific Coastal Plains (PCP), where the holotype of *T. carolina* was obtained (i.e., *Tantilla sertula* Wilson and Campbell 2000; *Thamnophis rossmani* Conant 2000; *Coniophanes michoacanensis* Flores-Villela and Smith 2010; and *Rhadinella dysmica* Campillo et al. 2016). Surprisingly, this region has received less attention when compared with the adjacent elevations of the Sierra Madre del Sur, and few collections have been made in this area (e.g., Holman 1964; Liner and Dundee 1969; Saldaña de La Riva and Pérez Ramos 1987; Schätti and Stutz 2016). Recent scattered reports have recorded several species of snakes with hitherto restricted ranges that were found hundreds of kilometers from their previously known localities (Siria-Hernández et al. 2006; Rocha et al. 2016; Blancas-Hernández et al. 2019; Arrazola-Bohórquez and Palacios-Aguilar 2022), which apparently reinforces the

proposal of Flores-Villela and Goyenechea (2001) that this province serves both as a corridor for lowland species and as a barrier for montane species of amphibians and reptiles. Nonetheless, there are areas of the PCP where interesting sets of microendemic species of reptiles are found (Palacios-Aguilar et al. 2018), and overall, a high proportion of endemic amphibians and reptiles occur in this province (Johnson et al. 2017), which might suggest that it is not as homogeneous as previously considered and that biotic subprovinces may be present within it. Detailed, objective biogeographic studies are necessary to test this hypothesis, now that novel information on species previously known from few localities or specimens is emerging.

Incomplete information and sampling biases affect what we know about biodiversity. The biodiversity *shortfalls* such as the Wallacean, the limited knowledge on the distribution of species, and the Linnean, the proportion of undescribed diversity, are two of the most important limiting factors that beset our understanding and knowledge of the natural world (Hortal et al. 2015). The effect that roads have on the vertebrate fauna of southern Mexico has been reported (Bojórquez-Tapia et al. 1994, 1995), and it is expected to diminish progressively as collectors and researchers reach previously inaccessible regions. In recent decades, it has been reported that species extirpations and extinctions have been augmented in an unprecedented way due to the negative impact of human activities (Dirzo et al. 2014). This highlights the importance of having accurate and reliable sources of biological information, such as scientific collections, that help us to diminish the effects of these shortfalls and allow us to provide an accurate image of how many, where, and which species exist in a particular region. Also, one should note that not all taxa have the same rate of species descriptions, and particularly in snakes, the *shelf-life* that specimens have from their collection to their description ranges from 0 to 146 years (mean 7.5 years, Guedes et al. 2020), inasmuch as the conduct of taxonomic treatments is one of the factors that boosts species discovery. The new species described herein has “awaited” being described for 118 years, which makes it a snake species with one of the longest shelf lives, and thanks to the conduct of a taxonomic treatment and the adequate housing of the individual in one of the world’s largest scientific collections, it was possible to identify it as a novel taxon. We can only imagine how many more species in Mexico (and the world) probably are now on a shelf awaiting discovery.

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Víctor H. Jiménez Arcos is an Associate Professor and the head of the Herpetology Lab, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México. Through studies on ecology and evolutionary biology, his laboratory focuses on understanding the evolution of the phenotypic diversity of amphibians and reptiles, as well as the changes and losses of geographical range associated with anthropogenic factors. He also works intensively with human communities and the Mexican government agency in charge of Natural Protected Areas (CONANP) to achieve the conservation of amphibian and reptile species in the short, medium, and long term.



Larry David Wilson is a herpetologist with lengthy experience in Mesoamerica. He was born in Taylorville, Illinois, USA, and received his university education at the University of Illinois at Champaign-Urbana (B.S. degree) and at Louisiana State University in Baton Rouge (M.S. and Ph.D. degrees). He has authored or co-authored more than 465 peer-reviewed papers and books on herpetology. Larry is the senior editor of *Conservation of Mesoamerican Amphibians and Reptiles* and a co-author of seven of its chapters. His other books include *The Snakes of Honduras*, *Middle American Herpetology*, *The Amphibians of Honduras*, *Amphibians & Reptiles of the Bay Islands and Cayos Cochinos, Honduras*, *The Amphibians and Reptiles of the Honduran Mosquitia*, and *Guide to the Amphibians & Reptiles of Cusuco National Park, Honduras*. To date, he has authored or co-authored the descriptions of 75 currently recognized herpetofaunal species, and seven species have been named in his honor, including the anuran *Craugastor lauraster*, the lizard *Norops wilsoni*, and the snakes *Oxybelis wilsoni*, *Myriopholis wilsoni*, and *Cerrophidion wilsoni*, as well as the oligochaete annelid *Pheretima wilsoni* and the coccidian parasite *Caryospora wilsoni*. In 2005, he was designated a Distinguished Scholar in the Field of Herpetology at the Kendall Campus of Miami-Dade College. Currently, Larry is a Co-chair of the Taxonomic Board for the website *Mesoamerican Herpetology*.

A new *Tantilla* species in the *calamarina* group from Guerrero, Mexico



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Appendix

Appendix I. In addition to published sources, the following comparative material was examined. All localities are in Mexico.

Tantilla calamarina. GUERRERO: Acapulco de Juárez, Viveros “El Huayacán,” La Poza (CNAR 29208–220, MZFC 13810–815), Puerto Marqués (CNAR 18729–735); Apaxtla de Castrejón, Tecolhuiztle (MZFC 2206); Arcelia, Campo Morado, Cañada El Limón (MZFC 19793, 19798–801), Campo Morado, Cañada El Naranjo (MZFC 19795, 19797), Agua Zarca (MZFC 19794, 19796); Eduardo Neri, San Miguel, Rancho del “Patillas” (MZFC 35822, 35826); Pilcaya, Parque Nacional Grutas de Cacahuamilpa (CNAR 28923–924).

Tantilla ceboruca. JALISCO: Road between Copala and Ciudad Guzman, N of Nevado de Colima (UTA-R 58516).

Tantilla coronadoi. GUERRERO: Copalillo, 2.5 km NE Papalutla (MZFC 25507).

Tantilla deppii. OAXACA: 3.2 km SW of Yosocuno (MZFC 33820, 33822); San Pedro Nopala, Maguey Verde (MZFC 33747).