



An adult male Isthmian Alligator Lizard, *Coloptychon rhombifer*, from Cerro San Juan de Rincón, Cantón de Osa, Provincia de Puntarenas, Costa Rica, elev. 500 m. For a century, this enigmatic anguid lizard was known from only three specimens. Although more individuals have been found, the lizard is largely a mystery. Its habits in the wild, diet, reproductive behavior, and osteology remain unknown. When approached closely, *Coloptychon* is prone to bite defensively. 📷 © César L. Barrio-Amorós



The gerrhonotine genus *Coloptychon* (Sauria: Anguidae)

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ABSTRACT: We discuss the provenance, history, and literature pertaining to the poorly known lizard *Coloptychon rhombifer* (Anguidae: gerrhonotinae). We include English translations of both the original description of this species by Peters (1876) and the first extensive re-description by Bocourt (1878) from the German and French, respectively. We report on six recently discovered individuals, increasing the total number known to 13. We also discuss habitat and distribution, ontogenetic variation in color and pattern, and provide pertinent observations of captive behavior.

Key Words: *Coloptychon rhombifer*, Chiriquí, Costa Rica, gerrhonotinae, *Gerrhonotus*, Panama

RESUMEN: Discutimos el origen, historia y literatura perteneciente sobre la poco conocida lagartija *Coloptychon rhombifer* (Anguidae: gerrhonotinae). Incluimos traducciones en inglés de la descripción original de dicha especie por Peters (1876) y de la primera re-descripción exhaustiva por Bocourt (1878) en idioma Alemán y Francés, respetivamente. Ofrecemos datos sobre seis individuos recientemente descubiertos, aumentando el número total de ejemplares conocidos hasta 13. También discutimos hábitat y distribución, variación ontogenética de color y patrón, y proveemos observaciones pertinentes sobre comportamiento en cautiverio.

Palabras Claves: *Coloptychon rhombifer*, Chiriquí, Costa Rica, gerrhonotinae, *Gerrhonotus*, Panama

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INTRODUCTION

In an analysis of generic relationships among the Recent Anguidae, Tihen (1949) coined the term “gerrhonotine lizards” for members of this family with four well-developed limbs and the presence of a lateral fold. They

also share an hourglass-shaped frontal bone, and a relatively elongate temporal bone. Gerrhonotines (*sensu lato*) commonly are called “alligator lizards,” and they comprise six genera and over 50 species ranging from the Pacific Northwest region of North America south to western Panama. Some of these species are Critically Endangered (www.iucnredlist.org), and some rank among the most beautifully colored of lizards (Campbell and Frost, 1993; Savage, 2002; Lamar, 2004; Campbell et al., *In Press*). The southernmost gerrhonotine comprises the monotypic genus *Coloptychon*. The Isthmian Alligator Lizard, *Coloptychon rhombifer*, until recently was one of the least known and most enigmatic reptiles in the world (cover illustration). For 94 years it was known from a single specimen of uncertain (apparently Panamanian) origin. From 1970 until 2013 only three additional specimens were reported.

The herpetological specimen catalog in the Museum für Naturkunde of the Humboldt-Universität zu Berlin (ZMB) contains data for a lizard holotype (Fig. 1), as follows: “8655, *Gerrhonotus rhombifer* Ptrs.*, Chiriqui, g. Möschler.” The catalog entry was made by Wilhelm C. H. Peters, at that time serving as the Director of the Zoologisches Museum (as it was then called). Peters, a consummate zoologist, also was the greatest German herpetologist of the 19th century and his collections, along with those of H. C. M. Lichtenstein, comprise the most important part of the museum’s reptile and amphibian holdings. Through the courtesy of Frank Tillack (pers. comm.), we have learned more about the background of the holotype of *Gerrhonotus rhombifer*.

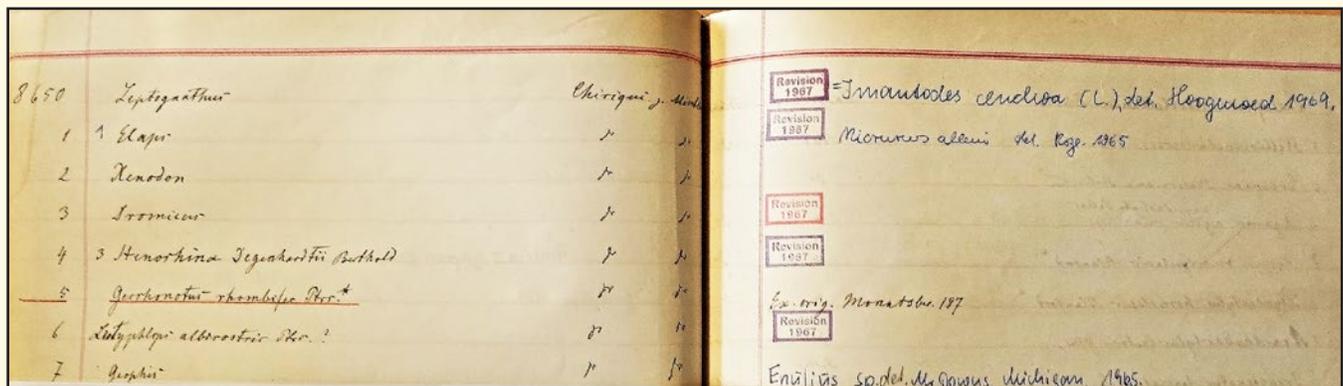


Fig. 1. The herpetological specimen catalog in the Museum für Naturkunde of the Humboldt-Universität zu Berlin showing Peters’ entry for a “*Gerrhonotus*” from “Chiriqui.” Courtesy of Frank Tillack.

The catalog information indicates the specimen was purchased from a person with the surname Möschler. The museum’s Department of Historical Research contains a large folder with over 400 pages of correspondence sent by Heinrich Ferdinand Möschler and his son Heinrich Benno Möschler from the years 1854 to 1890. Both of these men provided zoological specimens to the museum. Heinrich Benno Möschler (1831–1888) resided in Kronförstchen near Bautzen, Saxonia, Germany. He was a merchant, entomologist, and dealer of zoological objects (F. Tillack, pers. comm.).

On 14 November 1875, H. B. Möschler sent Peters a letter (Fig. 2A) and shipment of amphibians and reptiles. Through the courtesy of Gunther Köhler of the Senckenberg Museum the translation of the letter from Kurrent (old German script) is as follows:

Dear Professor,

Attached I send you some snakes and lizards from Central America – Chiriqui. Maybe some of these are of use for you. Please put names on those specimens that you send back. And allow the question how high a price I shall put on *Dryophylax Olfersii*, *Oxyropus multifasciatus*, *Botrops* [sic] *lanceolatus* and *Xenodon rhabdocephalus*, since I believe you already have these species, I have not sent these along. However, they are available if needed.

Best wishes

A list of the specimens included, which was compiled by Peters and written on the reverse of Möschler’s letter (Fig. 2B), mentions “3. *Gerrhonotus*.” Peters had numbered the items contained, so item 3 would appear to be the first reference to what he would subsequently describe as *Gerrhonotus rhombifer*. Inasmuch as there were no other letters mentioning herpetological material from “Chiriqui,” it seems likely that the type of *G. rhombifer* was the lizard in this shipment. Möschler’s collecting activities apparently were confined to Germany, and he received his extralimital material from other persons.

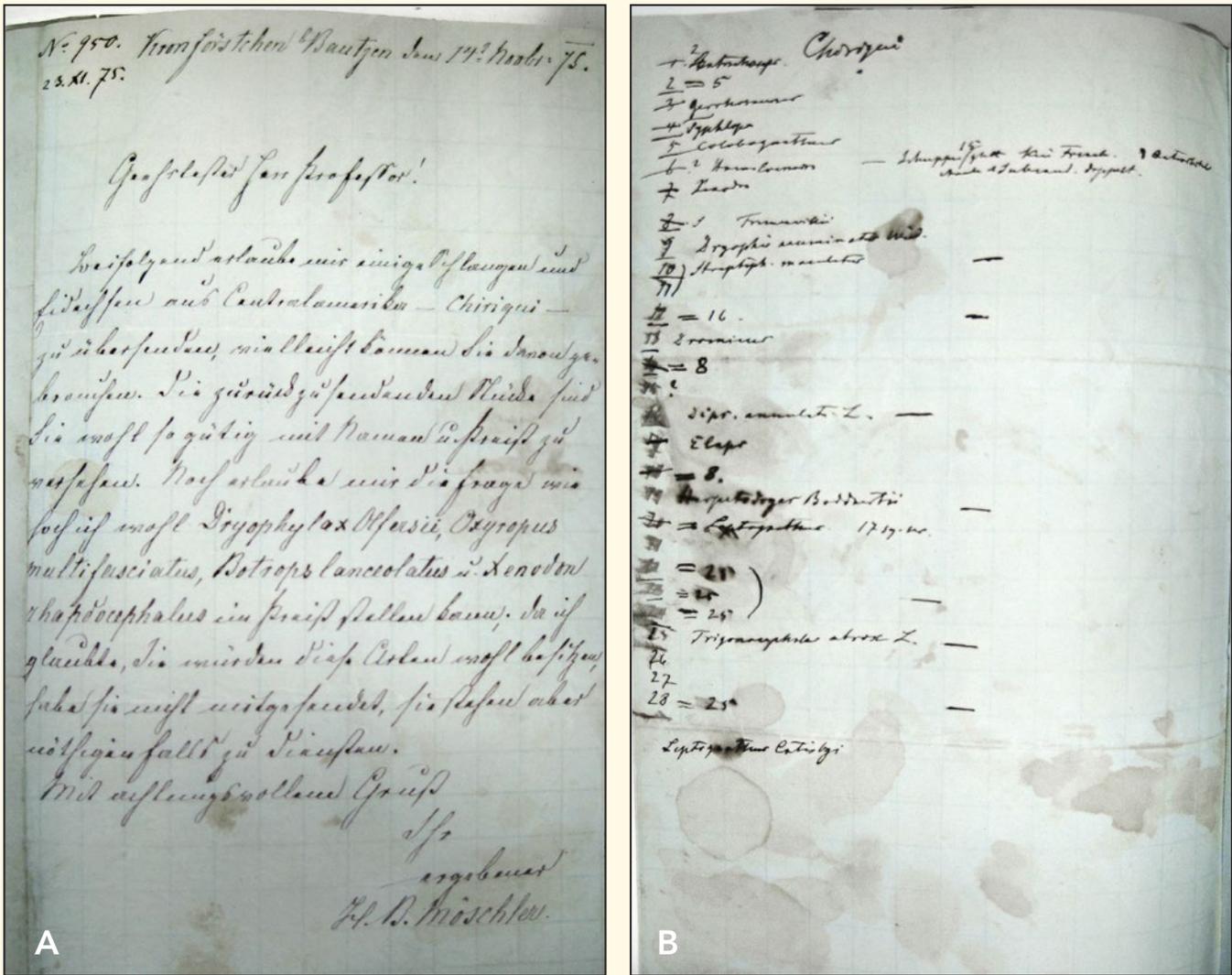


Fig. 2. (A) Letter from H. B. Möschler to Wilhelm Peters which accompanied some specimens from Chiriquí, including the holotype of *Gerrhonotus rhombifer*. (B) Wilhelm Peters’ notes and provisional identifications written on the back of Möschler’s letter. Courtesy of Frank Tillack.

Möschler made no mention of a collector in his letter accompanying the “Chiriqui” material, but his other correspondence with the museum indicates he often obtained specimens from missionaries. Because no other locality data exist, it is assumed that “Chiriqui” refers to modern-day Chiriquí Province, in Panama (but see discussion of Bocourt’s comment below). Subsequently, the species has not been reported from Panama. Importantly, the other specimens in the shipment are varieties found in Chiriquí, such as *Enulius*, *Imantodes*, *Stenorrhina*, and *Xenodon*. One of the specimens is *Elaps (Micrurus) alleni*, a snake with a Pacific versant distribution in Panama that is restricted to mesic forest in southwest Chiriquí (Campbell and Lamar, 2004). Based on additional Costa Rican material, this also would be the most likely place in Chiriquí for Peters’ holotype to have been collected.

Peters (1876) described *Gerrhonotus rhombifer* on the basis of a single specimen BM (= ZMB) 8655 from “Chiriqui.” His description, translated from German, is as follows:

2. *Gerrhonotus rhombifer* n. sp.

A species that is readily characterized its long flattened head, the flattened body, the long tail, and the thin, smooth scales.

Upper body scales in 16 to 18, ventral scales in ten longitudinal rows, separated from each other only by a very narrow lateral furrow.

Three nasorostrals, the medium one rhombiform; behind this, two supranasals, in contact with each other, then a single, anteriorly convex internasal, then two prefrontals, the elongate, hexagonal, at its sides convex frontal, separated from the frontoparietals by the hexagonal interparietal, and behind the parietals a row of rather scale-like occipitals. The long nasal is perforated by the nostril on its posterior end and contacts with its lower angles the first and fourth supralabial, so that it contacts four supralabials. Behind the nasal first two vertically arranged nasofrenals, then two vertically arranged frenals of first and a large frenal of second row. Four supraorbitals, five supraciliaries except for a second row of smaller, three infraorbitals. Fourteen supralabials, of which the 9th through 11th are below the eye; 11 to 12 low infralabials. Four preanal scales.

The upper side of the head broad, irregularly rhomboidal transverse bands, separated from each other by narrow black interspaces and developing into complete rings of yellow color on tail. A black transverse band, descending from the frenal, fuses with that of the other side below the chin, a second one connects the same way from below both eyes by meeting the one of the other side in the middle of the lower chin, a third one descends from the angle of the jaw and hits the one from the other side at the posterior end of the lower chin, two to three additional, more irregular ones of the anterior neck and chest, converging in the shape of a V, start at the sides of the neck. In front of the eyes begins a black band that meets the one of the other side in a large ark behind the occiput. On the lower parts of the body sides transverse yellow blotches. Venter predominantly black. Limbs predominantly black with yellow, serrated transverse lines and blotches.

Total length 0.150 [mm]; head 0.012 [mm]; tail 0.100 [mm]; forelimbs 0.011[mm]; hind limbs 0.014 [mm].

A specimen from Chiriqui (No. 8655 M.B. [= ZMB 8655]).

Among the known species, this species is closest to *Gerrhonotus fasciatus* and *G. Deppei* Wiegmann, of which Gray formed a special genus *Abronia* by splitting the genus *Gerrhonotus* of Wiegmann into four genera, based only on external characters, an action that may not be justified in view of the transitions the species show in their external appearance.

19TH CENTURY HISTORY OF *GERRHONOTUS RHOMBIFER*

Cope (1877) briefly discussed gerrhonotid generic characteristics and mentioned *G. rhombifer*. Bocourt (1878) provided excellent drawings of the holotype (Fig. 3, A–B), which he examined closely. His report, in French, is translated as follows:

4. *GERRHONOTUS (ABRONIA) RHOMBIFER*¹, Peters

(Pl.XXI B, fig.4, 4a [see Fig. 3A, B])

Characteristics: Head flat and elongated. Nasal scale separated from rostral scale. Anterior edge of the ear drum edged with small conical scales and spicules (see Pl.XXI B fig 4a [see Fig. 3B]). Eight supranasal scales on the region between rostral and prefrontals. No supranasals. Eyes relatively large. Smooth dorsal crests, barely smaller than the abdominal plates. Shallow lateral fold. Rather long tail.

Trunk decorated with brown transverse bands which are separated from each other by yellowish white rhombic spaces.

Description: Head long, depressed and covered with smooth plates; its length, from the tip of the snout to the middle of the ear opening does not quite equal a quarter of the space between the chin and the anus. The snout is elongated, covered with eight supra-nasal scales between the rostral and prefrontal scales; the three first are in contact with the rostral scale; next two, placed at the level of the nasal plate, form the second row; the sixth and seventh, a little bit less small, form the third row; at last the eighth, much larger and hexagonal, is in contact with the previous two, with each side in contact with the upper loreal and posteriorly with the prefrontal plates; these ones, similar in their dimensions to the previ-

ous scales, offer five edges; the frontal, very elongated, is of the same shape of the scales that we just described; the interparietal, almost as long as the frontal, is in contact forward with the latter and the two frontoparietals, to the right and to the left with the parietals, and posteriorly with two occipitals much larger than those that cover the neck; the suborbital areas are each protected by nine plates; the five largest delimit the inner-outline, the four other, much smaller, cover the opposite side, which is bordered with a series of superciliary scales (see Pl.XXI B *fig 4a* [see Fig. 3A]). The opening of the circular nostril pierced in the center of the nasal scale, which is related with a scale of the supranasal region of the first row, superiorly with the scales of two series, below with the second and third supralabial, and back with two postnasals; the upper one, exceedingly small, then we see two superimposed loreals; lower, larger and directed backwards, is based on a part of the fifth and the sixth supralabials; its scales are followed by two postloreal also superimposed; the upper offers five unequal sides, and its inferior angle is not in contact with supralabials; the other, placed more in the back, offers the form of a trapeze and are supported by the sixth and seventh supralabial; the preocular, very small, is followed by subrectangular scales of similar sizes forming a nearly complete, half circular suborbital row (see Pl.XXI B *fig 4a* [see Fig. 3B]). We count fourteen small supralabials and eleven to twelve infralabials; behind the mental, there is a small divided scale, followed to the right and to the left by four big sub-mandible plates which are separated from the infralabials by a longitudinal row of scales. Triangular ear opening, bordered in front by three small translucent tubercles. Shallow lateral fold, begins in front of the arm and finishes at the opening of the cloaca. Smooth or slightly swollen dorsal patches and constituting sixteen to eighteen longitudinal series, while abdominal strips [rows], a little smaller, do make ten in the same direction, to the mid part of the trunk; the last row of the anal area is composed of only four scales.

Total length of holotype 0''', 145 [mm]

Length of the head from snout until the middle of the ear 0 013 [mm]

Width of the head at the level of the temporal region 0 007 [mm]

Length of the body from chin to vent 0 049 [mm]

Length of the tail 0 096 [mm]

Length of the arm until the extremity of the middle finger 0 011 [mm]

Length of the leg until the extremity of the longest finger 0 013 [mm]

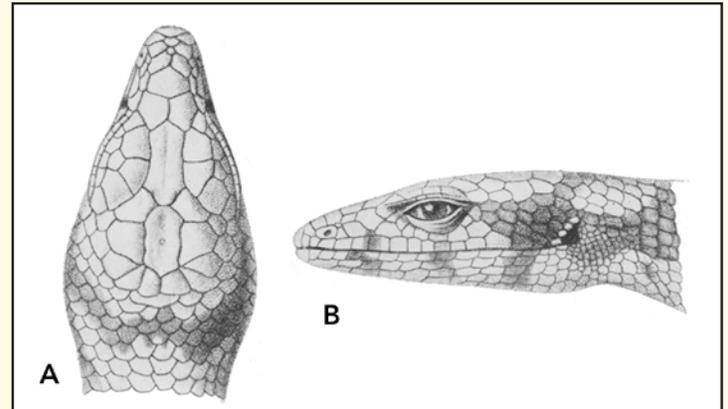


Fig. 3. (A) Dorsal cephalic scutes and (B) lateral cephalic scutes in *Coloptychon rhombifer*. Figure adapted from Bocourt (1878).

Coloration: The top of the head is yellowish white, surrounded with black from the front part of the eye until the occiput; this color extends widely on the temporal region, then down the throat forming a cross-shaped chevron band; in front of it, we see others, one originating below the eye, the other at the sixth supralabial scale (see Pl.XXI B *fig 4a* [see Fig. 3B]). The upper portions of the neck and snout are adorned with eight irregular patches of rhombic shape, tinted, like the top of the head, yellowish white, separated from each other by a narrow space of a dark brown, which ends in the lower regions of the neck and chest with narrow lines directed from front to back. The belly is blackish, laterally marked with small yellowish spots. On the tail we count seventeen rings of this latest color, divided by brown spaces: some of these rings placed at the base have a rhombic form like those above the trunk.

This beautiful small species, with its long and depressed head, and remarkable by its yellow rhombic spots that adorn the superior areas of the body, is also recognizable by its front and interparietal plates well developed length-wise as well located plates on the top and sides of the muzzle, on the contrary, are small and therefore more numerous than in other known species. It is also to be noted that we see in front of the ear opening small tubercular scales (see Pl.XXI B *fig 4a* [see Fig. 3B]) that are close to the two following species: *Gerrhonotus vasconcelosii* and *Gerrhonotus auritus* (see Pl.XXI A, *fig.7a et 8a*).

The holotype of *Gerrhonotus rhombifer* that Professor W. Peters kindly presented us originates from Chiriquí (Veragua province). This species is not present in the herpetological collection of the Museum.

We cannot account for the discrepancy between Peters' and Bocourt's measurements of total length of the holotype; specimen shrinkage in preservative is a possibility. Bocourt's mention of "Veragua Province" is puzzling. The Province of Veraguas, which name is derived either from that of an indigenous chieftain ("Verahua") or from the possibility of seeing both the Atlantic and the Pacific from a point in the uplands ("ver aguas" or, see the waters) (Bollaert, 1863), was the name applied to several territorial entities beginning with the Spanish colonial occupation of Central America and at one point including what presently comprises the Provincia de Chiriquí in Panama. The province was established while Panama was still part of Colombia and some 50 years prior to Bocourt's publication, but his inclusion of "Veragua" is unsupported by any further documentation and would seem to represent a *lapsus*. Chiriquí (a Guaymí Indian name meaning "Valley of the Moon") is Panama's westernmost province, and it borders the portion of Costa Rica from which all subsequent specimens of Peters' anguid have been discovered. The Provincia de Veraguas lies to the east of Chiriquí. Boulenger (1885) and Günther (1885) included descriptive information on the specimen, and Günther, evidently repeating what Bocourt previously had published, also mentioned "Veragua" as part of the locality. Cope (1887) did the same thing.

20TH CENTURY HISTORY OF *COLOPTYCHON* (*GERRHONOTUS*) *RHOMBIFER*

Pointing out differences between *Gerrhonotus rhombifer* and members of *Abronia* and the *Gerrhonotus-Elgaria-Barisia* complex, and indicating that, "there is no possibility of assigning *rhombifer* to any of the other genera of Gerrhonotinae," Tihen (1949) erected the genus *Coloptychon* to accommodate this species (but see Pyron et al., 2013 for a different view). Moreover, he considered *Coloptychon* the most primitive of all the living gerrhonotinae. His diagnostic characters for the genus and the species were the same, as follows: (1) a weakly developed lateral fold; (2) sides of the neck nearly angular; (3) 10 or more scales across the nape; (4) anterior internasals present; (5) two azygous postrostrals; (6) the circumorbital series not differentiated into a preocular, subocular, and postocular; and (7) 10 ventral scale rows.

Tihen (1949) postulated a Cenozoic origin for gerrhonotine ancestral stock, with the northern Mexican Plateau as the likely dispersal center (but see Good, 1988, and Macey et al., 1999 for more detailed hypotheses). He envisioned an early and rapid modification and spread of the group and wrote, "The only place where a form closely

resembling the original primitive stock has managed to survive is at the extreme southern periphery of the range—Panama; *Coloptychon* represents a slightly modified remnant of this group...Also, the inundation of southern Nicaragua during the Upper Eocene must have effectively isolated the *Coloptychon* prototype from the more centrally located members of the group.” Stebbins (1958) recognized the distinctiveness of *Coloptychon*, but, like Tihen, did not examine the holotype. Wermuth (1969) synonymized *Coloptychon* with *Gerrhonotus* without comment. Waddick and Smith (1974) rejected this move and supported Tihen’s conclusions, and also cited the presence of two postrostrals as unique to *Coloptychon*. The discovery of a second specimen, in 1970 (Colección de Herpetología, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica [UCR] 3143), and a third in 1976 (UCR 6971) from Costa Rica, barely made a ripple in the scientific community. Roy McDiarmid, in an unpublished 1975 presentation (Williamsburg, Virginia, United States, conference) discussed UCR 3143 (R. McDiarmid, pers. comm.); and *Coloptychon* was cited without further comment as occurring in the southwest portion of the country by Savage (1973, 1976, 1980). Savage and Villa R. (1986) also cited it, without comment, for southwestern Costa Rica.

McDiarmid and Good (1987) compared the three known specimens and stated that their analysis of character states of scalation supported recognition of the genus *Coloptychon* and suggested that *C. rhombifer* is the sister taxon to a clade containing all other gerrhonotine lizards. In an examination of phylogenetic relationships among gerrhonotine lizards, Good (1988: p. 66) listed a series of derived features for this group of lizards to diagnose *Coloptychon*, stating that, “the presence of two postrostrals and five pairs of large chin shields are [sic] restricted to *Coloptychon*” and all other characters “are shared through homoplasy with other gerrhonotines.” Nonetheless, Good (1988) also indicated that *Coloptychon* lacks a number of derived features found in all other gerrhonotine genera, and that certain derived aspects of coloration, primarily the dorsal and ventral banding patterns, are diagnostic of *Coloptychon*. Furthermore, Good noted that some of the characteristics cited for this species by previous authors, such as enlarged neck scales and a lack of prefrontal-superciliary contact, actually are not present. The translations of Peters and Bocourt contained herein plus a careful reading of Boulenger, and Gunther, and perusal of Bocourt’s drawings nowhere indicate that these authors ever mentioned these characters as being present in *Coloptychon*. Tihen, however, (1949) does state, and Bocourt’s lateral view (Fig. 3B) drawing implies, that the anterior superciliary does not contact the prefrontal. Bocourt’s dorsal view drawing (Fig. 3A) shows no contact. Following Bocourt’s drawing, Tihen (1949) called the neck scale condition “nearly agranular,” and stated that the granular scales were restricted to an area just behind the ear.

At the time of Good’s study, *Coloptychon* was known from three specimens—the holotype from Panama and two specimens (UCR 3143 and 6971) from southwestern Costa Rica (see map in Good, 1988: fig 26, and a photograph of a preserved adult [UCR 3143] on p. 33). Savage (2002) and Köhler (2000, 2003, 2008) presented a summary of the known information for *Coloptychon*, with Savage providing more extensive diagnostic, descriptive, and distributional data, including an elevational range for the species of 50–500 m. Owing to a lack of further information, *Coloptychon* in Panama has been presumed to occupy the Pacific Lowland physiographic region (see Campbell, 1999; Jaramillo et al., 2010). The lack of specimens has resulted in the exclusion of *Coloptychon* from modern osteological studies that include gerrhonotine anguid lizards (Criley, 1968; Rieppel, 1980; Gauthier, 1982; Good, 1987; Savage, 2002).

On 1 August 2000, Alejandro Solórzano obtained a recently injured adult male *C. rhombifer* that apparently had been dropped by a predator, possibly a raptorial bird. The specimen (UCR 15000) was found near Golfito, in a now-defunct neighborhood previously known as “Hong Kong” (A. Solórzano, pers. comm.), Provincia de Puntarenas, Costa Rica; its total length is 505 mm, the record size at that time for the species. Initially the specimen was frozen, but later was photographed and an image appears on the cover of *Herpetological Review*, for which Lamar (2004) provided information. In addition to the aforementioned cover photograph, images of non-preserved *Coloptychon* have appeared in Savage (2002; a different image of the same UCR specimen); Muñoz and Johnston (2013; photographed by Andrés Vega at Rancho Quemado, inland from Bahía Drake, Península de Osa, Puntarenas Province, Costa Rica); and Arias and Bolaños (2014), who reported the presence of *C. rhombifer* at Reserva Forestal Los Santos, San Isidro de Dota, Provincia de San José, Costa Rica, based on a photograph with locality data. Dwyer and De Plecker (2013) provided photographs (UTADC 7635–7636) of an individual collected at San Andrés de Matapalo, Cantón Aguirre, Provincia de Puntarenas, Costa Rica; from the photographs, the individual appears to be an adult female (Fig. 4).

In addition to the seven specimens of *C. rhombifer* in museum collections or otherwise reported in the literature, herein we provide information on six additional individuals (Table 1). We include data from two juveniles with striking color patterns, as well as from four subadult-to-adult lizards. All individuals, save the holotype, were found in Costa Rica, at elevations ranging from near sea level to 986 meters (Fig. 5). All have been found along the Pacific versant in habitats ranging from Tropical Wet Forest up to Premontane Wet Forest and Premontane Rain Forest (Bolaños, et al., 1999). The climate is characterized by moderate to high temperatures with an annual minimum of two meters of rainfall occurring mostly from March through December (Solano and Villalobos, 2001).

Table 1. Known occurrences of *Coloptychon rhombifer* based on specimens, individuals, or sightings with photographs. Numbers correspond to those on map (Fig. 5).

Number	Locality	Voucher	Elevation (m)	Date	Reference
1	Costa Rica: San José: Pérez Zeledón, Pejibaye	UCR 3143	700	1970	McDiarmid and Good (1987)
2	Costa Rica: Puntarenas: Golfito, Cerro Purruja	UCR 6971	485	13 June 1970	McDiarmid and Good (1987)
3	Costa Rica: Puntarenas: Golfito	UCR 15000	5	1 August 2000	Lamar (2004)
4	Costa Rica: Puntarenas: Buenos Aires, San Francisco Salitre	Photo by Jason Vargas	986	20 May 2014	This work
5	Costa Rica: Puntarenas: Aguirre, Londres de Quepos	Photo by Stephanie Joseph Segura	540	22 March 2013	This work
6	Costa Rica: San José: San Isidro de Dota	Photo voucher	800	Not stated	Arias and Bolaños, (2014)
7	Costa Rica: Puntarenas: Savegre, San Andrés Matapalo	Photo by Juan Andrés López	515	7 October 2012	Dwyer and De Plecker (2013)
8	Panama: Chiriquí	ZMB 8655	?	1876	Peters (1876)
9	Costa Rica: Puntarenas: Rainmaker, 22 km NNW Parrita	Photo by Luis Fernando Peña	124	15 March 2013	This work
10	Costa Rica: Puntarenas: Cantón de Osa, Cerro San Juan de Rincón,	Alive at Parque Reptilandia	500	19 August 2011	This work
11	Costa Rica: Puntarenas: Dominicalito, near the Escaleras cell phone tower	Photo by José Luis Segura Navarro	ca. 300 m	August 2014	This work
12	Costa Rica: Puntarenas: Península de Osa, Rancho Quemado, inland from Bahía Drake	Photo by Andrés Vega	200	?	In Muñoz Chacón and Johnson (2013)
13	Costa Rica: Puntarenas: Cantón Aguirre, San Andrés de Matapalo, finca Bocaracá	Photo by Juan Andrés López	348 m	October 2014	This work



Fig. 4. Adult *Coloptychon*, probably female, from Cantón Aguirre, San Andrés de Matapalo, finca Bocaracá, Provincia de Puntarenas, elev. 348 m. When encountered on the ground, this lizard undulates in snake-like fashion with the limbs adpressed. © Juan Andrés López



Fig. 5. The distribution of *Coloptychon rhombifer* based on all known sightings and specimens. Numbers correspond to those in Table 1. Inasmuch as the specific locality for the holotype is unknown, we simply made an indication in suitable habitat in Chiriquí, Panama.

COLOR IN LIFE, PATTERN, AND ONTOGENETIC VARIATION

The designation of a ground color versus a band/ring color in *Coloptychon* largely is a matter of semantics, with Peters describing the lizard one way, and Bocourt doing the reverse.

Two neonates (unrelated; Fig. 6A–C) in life bore the following color and pattern:

Dorsum of head yellowish to grayish tan; snout tan dorsally; sides of face white with three blackish brown bars, one distal to nasals, one below eye, and one below temporal region. The first two bars extend across the infralabials and onto the venter; the third crosses the rictus and also extends onto the venter. The same dark pigment begins on side of head just anterior to the eye and widens as it extends posteriorly, encompassing the orbital region and covering the temporal region before merging with the nuchal band (of the same color), which then passes just posterior to the parietals. A second band of the same color lies directly above the insertion of the forelimbs, which are similarly colored but with a few scattered white dashes and specks.

Six dark brown bands of variable length cross the body and another straddles the pelvic region with the same color extending onto the hind limbs, save for a few thin white transverse lines. The body bands become 16–17 irregular rings on the tail. The dorsal ground color on body is pearly white with a faint suffusion of pinkish tan on body being most apparent anteriorly. On the tail, this pale ground color is nearly immaculate, and the tail tip is the same color. The body bands coalesce laterally, reducing the pale ground color. The iris is black. The tongue is medium blue. The ventral color and pattern of neonates are unknown.

Color in life and pattern of adults:

The dorsal surface of the head varies from grayish to pinkish tan in young adults, and tan to medium brown with a suffusion of yellow on snout and over eyes in adults. Yellow pigment scattered on the snout and head becomes more pronounced with age. The labial region is white to pinkish white with tan to medium brown bars, sometimes with weak yellow pigment in older individuals. The area below and behind the eye is white with tan/brown markings and, in older animals, yellow pigment may surround the orbital region. The small scales surrounding the anterior edge of the ear opening are slightly darker than the adjacent area. The sides of the neck are pinkish tan/brown. The iris is pale bronze, darker peripherally. The pupil is round and black and the orbital tunic is dark gray.



Fig. 6. Neonate *Coloptychon*, as follows: (A) Londres de Quepos, Aguirre, Puntarenas Province, elev. 540 m. (B, C) Two views of the same individual from Rainmaker private reserve, 22 km NW Quepos, Provincia de Puntarenas, elev. 124 m.

© Stephanie Joseph Segura (A) and Luis Fernando Peña (B, C)

The interior of the mouth is pink, with a grayish pink mandibular floor. The tongue is slightly bifurcate and uniformly pale blue. Six to eight rhomboid bands are present on the body (between the anterior border of the hind limbs and the occiput), and these measure 1–4 dorsal scales in length. The interspaces they delimit also tend to be rhomboidal. On the body, these bands expand laterally and tend to fade, and when viewed dorsally the paler interspaces may appear as diamond-shaped blotches. The body bands are reddish tan with moderately defined borders that contain sparse areas of darker pigment. The tail contains 14–17 irregular reddish tan to grayish tan rings, which tend to be rhomboid in shape owing to dorsal expansion. The rings are slightly dark-edged and measure 1–5 dorsal scales in length, as do the paler interspaces.

The upper surfaces of the limbs may be pinkish tan (young adults) to tan, becoming grayish tan on the sides. The front toes are yellowish tan, the claws are horn-colored, and the interstitial skin above the insertion of the front legs is yellow. The hind toes essentially are the same as the ground color, but with a slight yellow hue. The palms and soles are a dirty yellowish tan. The sides of the body are patterned with fading coalescing bands, tan to brown, all coloring the smaller granular scales that form the dorsal border of the weak lateral line. The sides of the tail are colored the same as the dorsum. The underside of the tail ranges from ringed with gray-stippled whitish interspaces to uniform tan to brown in older individuals.

The ventral scales are white anteriorly, but suffused with pinkish tan such that from mid-venter posteriorly the color is a paler version of the dorsum. Five to seven distinct white triangular-to-square markings with slight dark edges are located paraventrally along the abdomen, beginning at the lateral line and extending downward. Ventrally, the throat and chin region are white with the dark labial bars extending down and posteriorly until fusing in a V-shape and forming a mid-ventral line that extends until the subsequent V-shaped fusion.

The tendency is for successive loss of distinct pattern elements with age, such that *Coloptychon* begin life as boldly banded and ringed lizards, nearly bicolored, and become progressively more muted until they display a nearly patternless dorsum that is tan, reddish tan, or medium brown, with a somewhat paler mottled tan venter (Figs. 7, 8). This progression has been demonstrated in a captive as follows:

In August of 2011, a live individual of *C. rhombifer* was brought to Parque Reptilandia. The lizard (Fig. 9), a juvenile male measuring 95 mm in snout–vent length (SVL), 170 mm in tail length (T), and 265 mm in total-length (TL), was collected at Cerro San Juan de Rincón, Península de Osa, Provincia de Puntarenas, Costa Rica, elev. ca. 500 m. Its coloration at the time was quite distinct as compared with neonates, yet bolder in every way from that of adults.

After 14 months, when the individual measured 150 mm SVL, the rhomboid pattern on the dorsum and tail had faded to the point of being nearly



Fig. 7. A subadult *Coloptychon rhombifer* from Dominicalito, Provincia de Puntarenas, Costa Rica, elev. ca. 300 m. This individual, estimated to measure 30–40 cm, still retains a strong pattern element. © José Luis Segura Navarro



Fig. 8. An adult *Coloptychon rhombifer* found dead on the road at finca Bocarácá, San Andrés de Matapalo, Cantón Aguirre, Provincia de Puntarenas, Costa Rica. The strong juvenile pattern has faded almost completely.

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Fig. 9. Juvenile male *Coloptychon rhombifer* from Cerro San Juan de Rincón, Cantón de Osa, Provincia de Puntarenas, elev. 500 m. Pattern elements, while more marked than those of adults, are losing their neonatal intensity.

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Fig. 10. Same individual as Fig. 9, 14 months post-capture. The pattern has become more uniform as adulthood is reached.

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indistinguishable, but slightly more evident on the tail (Fig. 10). Also, the white on the sides of the head, and the vertical crossing bars faded, and only the striking white triangles beneath the lateral fold remained distinct. At the time of this writing, the same specimen measures ca. 165 mm SVL with a TL of at least 522 mm (Fig. 11), making it the largest *Coloptychon* thus far measured. The pattern elements have continued to fade, while diffuse yellow pigment in the cephalic region has become more pronounced (see cover image). The white paraventral markings remain distinct (Fig. 12).

During its four years in captivity this individual not only matured, but also has displayed some behavioral traits worth noting. The lizard is housed in a spacious, planted outdoor enclosure, in an area within the potential distribution of *Coloptychon*, and is fed a diet of crickets (*Zoophoba*) and other local insects. Geckos (*Gonatodes*) and small anoline lizards have been refused as food items. Large arboreal katydids, including *Steirodon stalii* and *Aegimia elongata* (Orthoptera: Tettigoniidae, Phaneropterinae), however, are especially relished and constitute the only food item the lizard will accept from the hand. These katydids are unusual in that they are obligate vegetarians that inhabit several layers of forest canopy (Gwynne, 2001), and are sympatric with other foliage mimicking katydid species including several conocephalines capable of inflicting significant defensive bites (WWL, pers. observ.). The *Coloptychon* consistently handles katydids by grasping the head and dispatching the insect. The lizard often will hang by its tail into a food dish for feeding, waiting for food to be introduced. This individual only rarely visits the ground or low branches within its enclosure. The tail is highly prehensile (Fig. 13), and the lizard sleeps coiled on branches and exposed like many diurnal colubrid snakes. No interest is shown in hollow logs on the enclosure's floor. When threatened, it uses a controlled fall as a defense

wherein the lizard will launch the body from its perch onto a lower branch, using its tail to stop or change direction. We have observed similar behavior in some species of *Abronia*. The lizard is alert, knows its environment, readily makes eye contact, and is prone to defend itself vigorously by biting if approached too closely (see Introductory Page image). Like many anguids, it seldom basks and prefers dim light. Based on the tail morphology of this species and the captive behavior of this individual, *Coloptychon* apparently is arboreal and likely a canopy dweller, as postulated by Lamar (2004). Interestingly, the eyes are oriented such that the lizard can easily gaze in a downward direction (Figs. 12, 14), which presumably would be advantageous in arboreal situations.



Fig. 11. Same individual as Fig. 9, 42 months post-capture. Allowing for slight body contortions inside the acrylic tube, the individual measures minimally 165 mm SVL and 522 mm TL. This individual presently is the longest *Coloptychon* measured. © Roel De Plecker



Fig. 12. Same individual as Fig. 9, showing distinctive paraventral triangular white patches, which remain distinctive while other pattern elements fade with age. © Roel De Plecker



Fig. 13. Same individual as Fig. 9, using the highly prehensile tail as an anchor.

📷 (UTADC 7638) © César L. Barrio-Amorós



Fig. 14. A subadult individual from San Francisco Salitre, Buenos Aires, Provincia de Puntarenas, elev. 986 m. Note the orientation of the eyes, permitting downward vision.

📷 © Jason Vargas

This individual and the two neonates were captured on the ground while crossing paths. In fact, all but two of the specimens herein discussed were found on the ground; the others were in low bushes. Museum records of other arboreal reptile species often are biased toward encounters on the ground, but logically this is where humans will see them. Individuals of *Coloptychon* likely descend from the canopy to lay eggs, to seek new territory (subadult males), or to disperse (neonates). When on the ground and engaging in escape behavior, this anguid moves in a decidedly snake-like fashion by undulating the body and tail.

The Isthmian Alligator Lizard, *Coloptychon rhombifer*, 139 years after its description, despite a range that includes easily accessible forest that has been intensely studied by scientists, remains known from only 13 specimens/individuals. A single tissue sample is being analyzed and nothing is known about its osteology. Much remains to be learned about this arboreal, enigmatic reptile.

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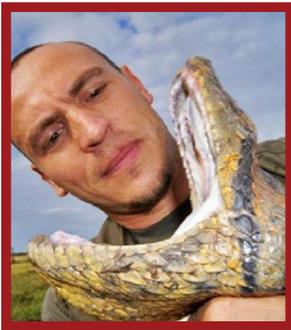
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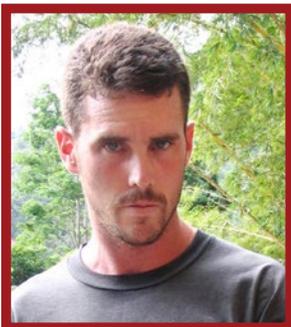




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