

A PHENACOSAUR FROM CHIMANTÁ TEPUI,
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ABSTRACT. A new species of the genus *Phenacosaurus* is described from Chimantá Tepui, close to *P. neblininus*. It differs from *P. neblininus* (and other known phenacosaurus) in having the interparietal smaller than the ear and in having the circumnasal in broad contact with the rostral and only barely touching or not all in contact with the first supralabial. It also differs from *neblininus* in a generally darker coloration and having the belly with bold dark reticulation.

INTRODUCTION

Until Lazell (1969) described the new species *Phenacosaurus orcesi* from two localities in Ecuador, the anoline lizards separated as the genus *Phenacosaurus* had been known only from Colombia and from just over the border in Venezuela. A summary of new information has been reported in Williams *et al.* (1996).

Now still another small but distinctive new species, represented by a unique specimen, deposited in the collections of the Sociedad de Ciencias Naturales "La Salle," Caracas, most similar to the other tepui species, *P. neblininus*, from Cerro de La Neblina, provides the easternmost representative of the genus from Chimantá Tepui in Venezuela.

The new species is named after the late Carlos Todd, long active in conservation work (Gorzula, 1987), who participated in the exploration of Chimantá Tepui that resulted in the discovery of the new species *Phenacosaurus carlostoddi*.

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DESCRIPTION

Phenacosaurus carlostoddi, new species

Holotype. SCN 10351, adult female, coll. S. Gorzula and A. Farrera, February 1, 1984.

Type Locality. The southern high plateau of Abacapa-tepui (05°12'N, 62°19'W) (CHIMANTÁ V.), Estado Bolivar, Venezuela, 2,200 m.

Diagnosis. A small phenacosaur closest to *P. neblininus*, but differing from it and all other phenacosaur in having the ear opening larger than the interparietal, rather than smaller or much smaller, in having the circumnasal in broad contact with the rostral not at all in contact with the first supralabial, instead of having a scale intervene between the circumnasal and the sulcus between the first supralabial and rostral, and an apparently generally darker coloration, and in having the belly with bold dark reticulation.

It (and *neblininus*) differs from the *orcesi* group, to which *neblininus* was first referred, in the condition of the fourth toe. Lamellae (scales wider than long, distally imbricate) in the fourth toe are restricted to phalanges ii and iii.

Description. *Head*: Casque indicated by distinct lateral and occipital ridges.

Dorsal head scales (Fig. 1): Antorbital area—Scales smooth or weakly rugose, small at the tip of the snout and posterior to the circumnasals and between the canthals and a median row of larger scales. Post rostrals 8, including the circumnasals and the anteriormost loreals of both sides. *The latter on both sides just exclude the circumnasals from the sulcus between the rostral and the first supralabial*. Dorsally 4 scales between the circumnasals.

Canthals 6 on the left side, 7 on the right, rounded or very bluntly keeled. On both sides the anteriormost canthal separated from the circumnasal by 2 scales, one behind the other. Six scales between the second canthals across the frontal depression.

Frontal depression shallow, the scales within it all larger than those at the tip of the snout.

Orbital area—Scales of the supraorbital semicircles large, smooth or lightly rugose, 2 pairs in contact. Scales of the supraocular area smooth or very weakly shagreened. On each side the 3 largest of

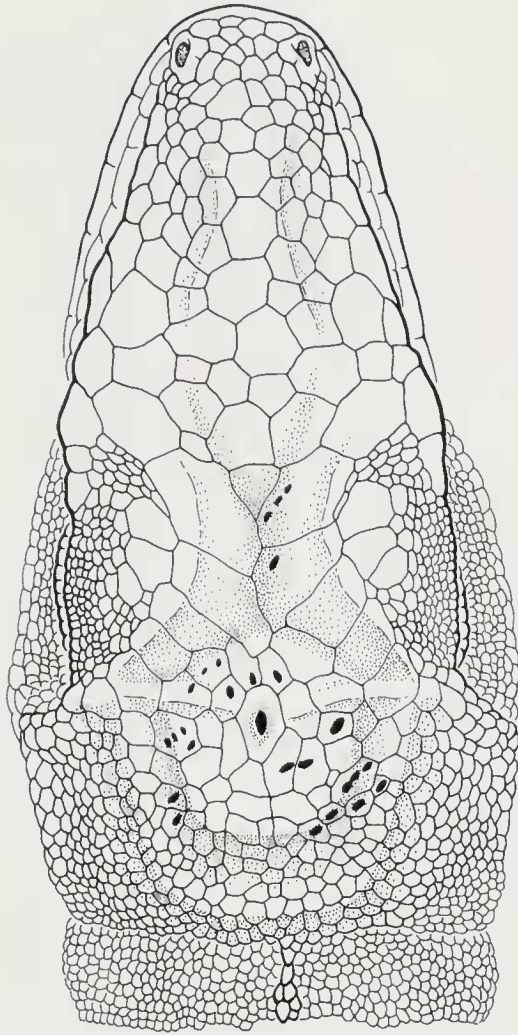


Figure 1. *Phenacosaurus carlostoddi*, holotype, SCN 10351: Dorsal view of head. The black areas on the parietal scales and on some scales of the semicircles represent the characteristic pustulations referred to in the text.

the supraocular scales forming a medial arc, the 2 largest of these in contact with the supraorbitals, the third separated by granules. Lateral scales of the supraocular region somewhat enlarged medially, but always sharply smaller than the medial supraoculars and becoming granular at the superciliary border. One (right side) or 2 (left side) anteriormost superciliaries short, bluntly keeled, quadrate or wedge-shaped, and followed only by granules not distinguishable from the adjacent granules of the supraocular region.

Parietal area—Scales on the boundary ridges of this area not significantly larger than adjacent nape or supratemporal scales.

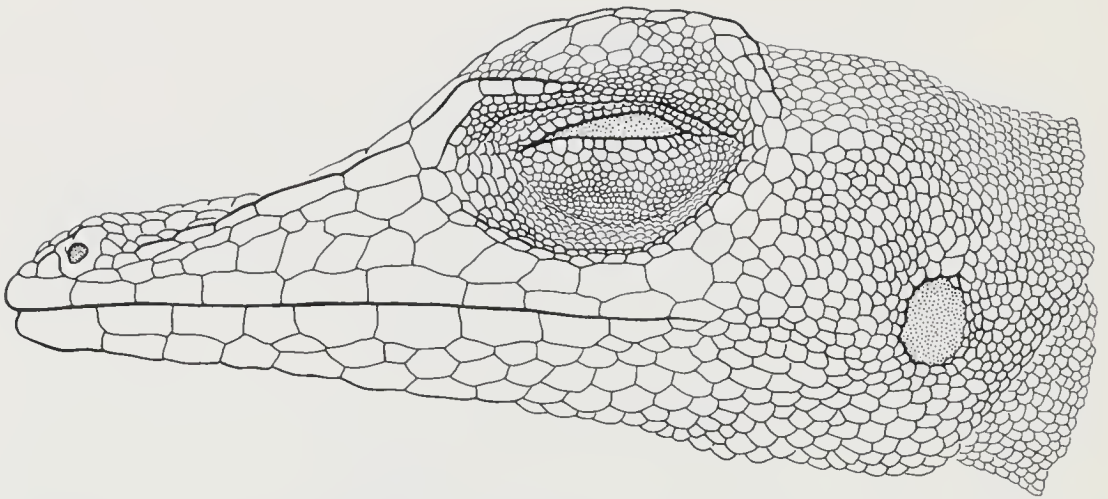


Figure 2. *Phenacosaurus carlostoddi*, holotype, SCN 10351: Lateral view of head.

No pustulations or rugosities on the scales of the lateral and occipital ridges. About 3 rows of scales lateral and posterior to the interparietal and 1–2 rows anterior to it distinctly enlarged. These enlarged parietal scales and the interparietal itself distinctly smaller than the larger scales of the frontal depression. An indistinct parietal eye. The interparietal scale diamond-shaped, small, smaller than the rather large ear, and separated by 1–2 scales from the semicircles. All scales surrounding the interparietal swollen, rugose with irregular raised areas and abundant pustulation, characteristic of other phenacosaur species also, overlying rugosities on the underlying bone. Some scale borders difficult to see. About 7 or 8 scales, decidedly irregular in shape and size between the interparietal and the subgranular nape scales.

Lateral head scales (Fig. 2): Loreal rows 3 on each side. Total number of loreals 17 on right side, 14 on left.

Preoculars 2 on each side, the uppermost in contact with the second canthal. Suboculars 4 on right side, 5 on left. Postoculars not well defined grading into the lower temporals. Seven to 8 supralabials to below the center of the eye.

Lower temporal scales slightly convex, smooth, juxtaposed, larger near the postoculars into which they grade. A weakly differentiated intertemporal zone of 1 row grading from the largest next to the postoculars to scales not distinguishable from nape scales.

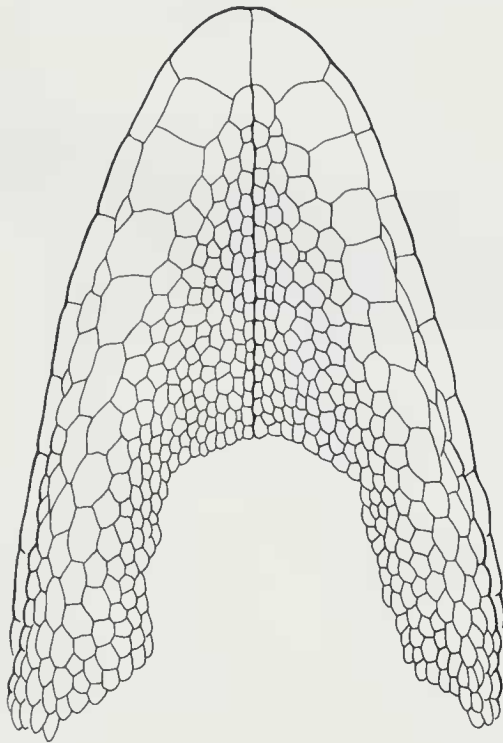


Figure 3. *Phenacosaurus carlostoddi*, holotype, SCN 10351: Ventral view of throat.

Upper temporals immediately above the intertemporal row small, flat, and smooth, subequal, abutting above on a zone demarcated by a slight ridge, surrounding the parietal area.

Ear opening on both sides, vertically ovoid, the narrower end above, its vertical dimension 6–8 times the height of the highest crest scales, relatively larger than the ears of any other species of the genus, larger than the interparietal.

Ventral head scales (Fig. 3): Mental almost completely divided, very bluntly indented, in contact with 4 postmentals between the infralabials, 1 first sublabial on each side, each about 4–5 times the size of the 2 medial gulars, which are themselves somewhat larger than the gulars posterior to them. Two additional sublabials on the right side, 3 on the left, in contact with the infralabials.

Central gulars small, smooth, swollen, juxtaposed, subrectangular, becoming somewhat larger and distinctly polygonal toward the sublabials.

Trunk (Figs. 5 and 6): An indistinct and at intervals interrupted crest of triangular scales, sometimes in 2 rows, sometimes in 1 row, always low, but of varying heights, and never much larger

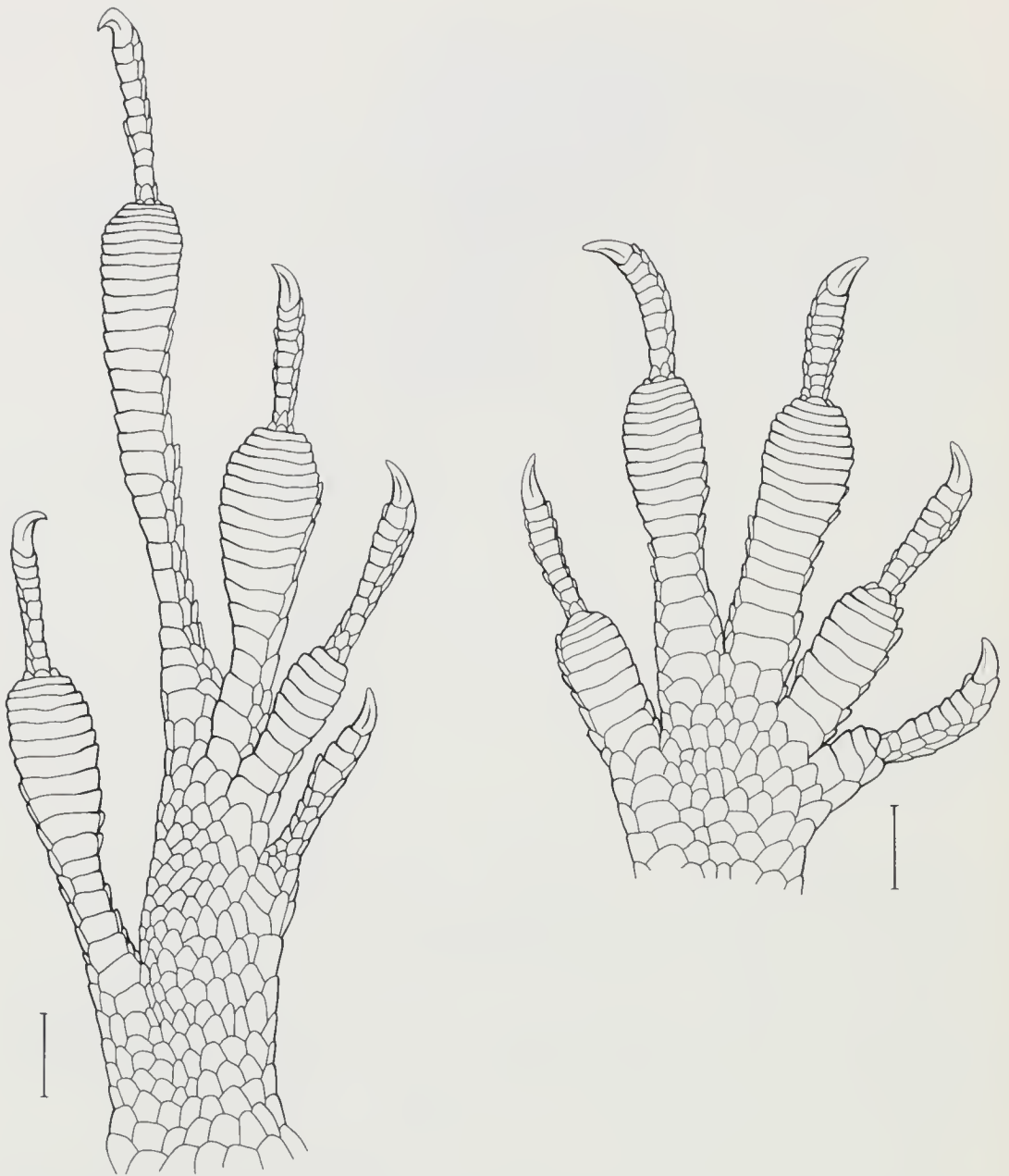


Figure 4. A subdigital view of the toes and hands of the holotype of *P. carlostoddi*, SCN 10351, to show that the fourth toe has the lamellar condition restricted to phalanges ii and iii. This feature has been confirmed in two paratypes of *P. neblininus*, USNM 322911 and 322912.

than the paravertebrals. Paravertebral and flank scales subequal, flat or slightly swollen, round, weakly rugose, tending to be in transverse rows, in contact paravertebrally, separated on lower flanks by naked skin or, in part, by granules, grading into ventrals. Ventrals smooth, oval, in transverse rows, subimbricate or separated by naked skin, larger than any dorsals.

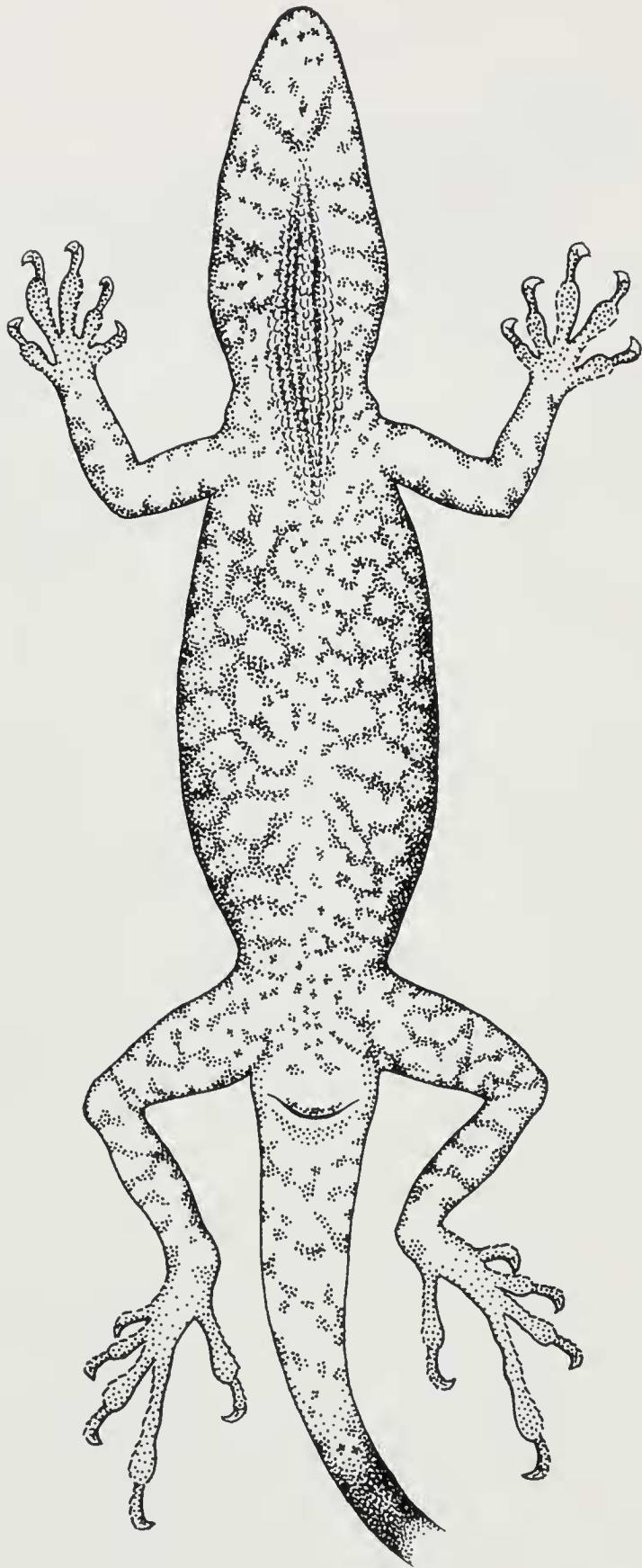


Figure 5. *Phenacosaurus carlostoddi*, holotype, SCN 10351: Lateral view of entire animal.

Limbs (Fig. 4): Upper arm scales smooth, larger and imbricate anteriorly and ventrally, smaller and juxtaposed or separated dorsally, posteriorly, and ventrally. Lower arm scales keeled, imbricate anteriorly and ventrally, smooth, juxtaposed or subimbricate dorsally, posteriorly and ventrally. Thigh scales anteriorly keeled, imbricate, posteriorly smooth subgranular. Supradigitals rugose rather than keeled. *The toe pad of the fourth toe restricted to the intermediate phalanges (ii and iii).* (Two or 3 scales are again wider than long at the insertion of the proximal phalanx of the fourth toe into the palm, but they are not believed to be lamellae. They are described as lamella-like.) All other toes are subdigitally totally lamellar. *Eighteen lamellae under phalanges ii and iii of fourth toe. All fingers subdigitally lamellar.*

Tail (Fig. 5): Distinctly compressed. A single median crest (except on the tail base where the relevant scales are low and small), becoming larger, sharply keeled and conspicuously dentate about 10 mm behind the hindlimbs. Lateral scales not keeled near base of tail, small, quadrate, rugose, becoming larger and distinctly keeled posteriorly. No enlarged postanals (female). Scales behind vent smooth, becoming keeled only 20–22 mm behind vent.

Dewlap (Figs. 5 and 6): Posteriorly just reaching beyond the level of the insertion of the forelimbs. Edge scales much smaller



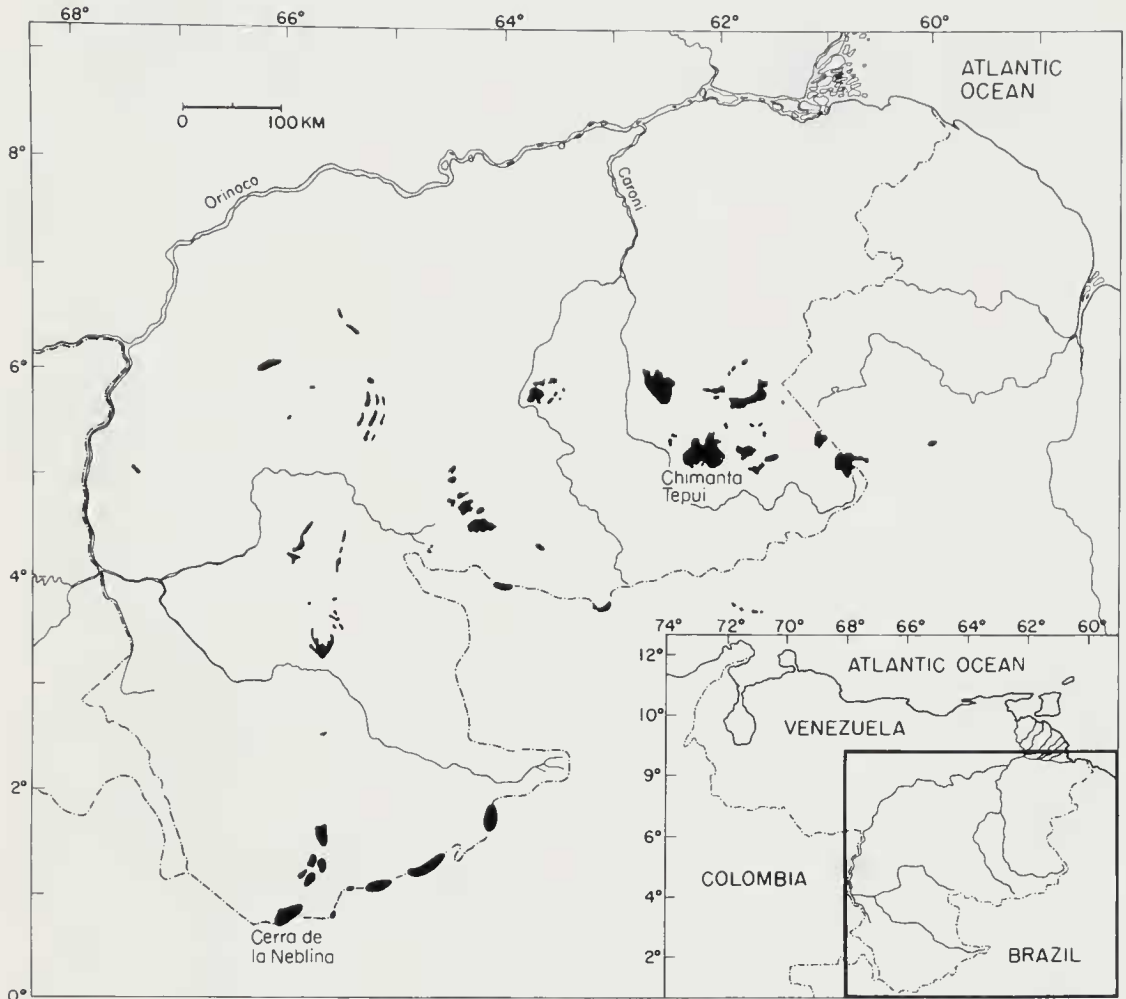


Figure 7. "Pantepui" *sensu* Mayr and Phelps (1967), showing the locations of Cerro de la Neblina and Chimantá Tepui.

than ventrals, oval. Lateral scales abruptly larger, but still smaller than ventrals, in rows, triangular or trapezoidal.

Size: Snout-vent length (SVL) 55 mm, tail 73 mm.

Color in Life (from Gorzula's Field Notes). "Distinct black markings on an off-white background on the head. Dorsum with light brown markings. Bluish gray color on the gular fan when extended."

Color as Preserved. Head and body black dorsally, with very vaguely indicated coarse lighter mottling. Suboculars and su-

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Figure 6. *Phenacosaurus carlostoddi*, holotype, SCN 10351: Ventral view of entire animal.

pralabials light with spotting below middle of eye and below second canthals. Loreals mostly light on right side, mostly dark on left side. Light spotting in front, above, and behind arms and in axilla. Limbs above black, vaguely spotted or mottled. Throat with small black spots and streaks. Belly and anterior tail boldly reticulate with black, the reticulations broken at midline. Limbs below light centrally with black spotting on anterior and posterior margins. Posterior two-thirds of tail black.

Habitat. Found at about 11:00 A.M. in a small crack in the sandstone, near the top of a deep crevasse on a very exposed rock escarpment. There were only some stunted *Bonnetia roraimae* scrub and patches of vegetation within a radius of about 100 m.

Comment. *Phenacosaurus carlostoddi* would appear to be genuinely rare. From 1983 to 1987, 22 localities were explored on the Chimantá Massif. Gorzula visited and collected the herpetofauna of 16 of these localities, and others made similar collections at five of the remaining six localities. Collecting parties usually stayed 3–5 days at each locality. Gorzula has also collected amphibians and reptiles on the adjacent Angasima and Adanta tepuys, on Aprada Tepui, on Ptari Tepui, at a dozen or so localities on the Auyan Tepui Massif, at localities on the “Los Testigos” chain of tepuys, at three localities on Ilu Tepui, on Yuruani Tepui, and at two localities on Cuquenán Tepui. Gorzula has also collected at dozens of localities at intermediate elevations in the Gran Sabana. He reported the following:

There was usually no problem in collecting “tepuí species” once their habitat was known. *Phenacosaurus carlostoddi* and *Atractus steyermarki* were exceptions to this general rule. The only other high elevation anole was *Anolis chrysolepis ewei*, a short-legged rock-dweller, that turned up on widely separated tepuys at elevations above 1,700 m.

Associated Species. Also collected from “Chimantá V” were *Ololygon* sp. (an undescribed species common around swamps on most tepuys in the Gran Sabana region) [now *Scinax* sp. *vide* Duellman and Wiens, 1992], *Arthrosaura* sp. (an undescribed species collected at various localities but only on the Chimantá Massif) and *Stefania ginesi* (very common in swamps and in adjacent *Brocchineae hectioides*, apparently

endemic to the Chimantá Massif but with closely related species or subspecies on most other tepuys in the Gran Sabana region [Duellman and Hoogmoed, 1984].

DISCUSSION

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It is especially necessary to begin to sort out the similarities and differences within *Phenacosaurus* with seven new taxa described since the last revision (Lazell, 1969), which recognized just three species.

Three groups are currently recognizable in the genus: the *heterodermus* group, the *orcesi* group, and the *neblininus* group:

- I. The *heterodermus* group (two subgroups) is defined by scale heterogeneity: the round flat enlarged scales intermingled with smaller scales and granules. All the subdigital scales of the hands and feet are always totally lamellar (wider than long and with a distal free edge), as in the species *heterodermus*.
 - (1) The *heterodermus* subgroup *sensu stricto* (strongly heterogeneous flank scalation, well-developed casquing, moderate to giant size) includes *heterodermus* Duméril and Duméril, 1851 (maximum SVL 76 mm), the Colombian giant *inderenae* Rueda and Hernández-Camacho, 1988 (maximum SVL 118 mm), and the Ecuadorian giant *vanzolinii* Williams, Orces, Matheus, and Bleiweiss, 1996 (maximum SVL 104 mm).
 - (2) The *nicefori* subgroup (weakly heterogeneous flank scalation, casquing dependent on size, small or near giant) includes *nicefori* Dunn, 1944, a species now known to be smaller than *heterodermus* (maximum SVL 63 mm) and *tetarii* Barros, Williams, and Vilorio, 1996, (maximum SVL 85 mm), a near-giant species tentatively referred to *nicefori* by Alemán (1953) and Lazell (1969) and now shown by an additional two specimens to be a valid species.
- II. The *orcesi* group differs from the *heterodermus* group by the absence of heterogeneity in flank scales (the enlarged flat round scales). All subdigitals of the hands and feet are totally lamellar, as in the *heterodermus* group.

The *orcesi* group (homogeneous flank scalation, relatively poorly developed casquing, small size) includes Ecuadorian *orcesi* Lazell, 1969 (maximum SVL 59 mm), and Venezuelan (and probably Colombian: the Sierra de Perijá occurs on both sides of the border) *euskalerriari* Barros, Williams, and Vitoria, 1996 (maximum SVL 53 mm) and a single juvenile from Peru (Williams and Mittermeier, 1991) (SVL 32 mm), which was left unnamed because of its juvenile status.

- III. The *neblininus* group again differs from the *heterodermus* group in the absence of heterogeneity in its flank scalation but is defined by the fourth toe of the hindfoot having the most distal and the most proximal phalanx nonlamellar (the distal scales narrow = nonlamellar and two or three of the most proximal lamella-like). All the subdigitals of the hands and four of the five digits of the feet are lamellar.

The *neblininus* group (homogeneous flank scales, poorly developed casque, small in size) are confined thus far to two tepuys in south-central and eastern Venezuela: the *neblininus* Myers, Williams, and McDiarmid, 1993, from Cerro de la Neblina (maximum SVL 63 mm) and *carlostoddi* Williams, Praderio, and Gorzula, 1996 (this paper) (maximum SVL 55 mm).

All the species of *Phenacosaurus* are poorly known, some because of the difficulty of collection, as may well be true of the *neblininus* group (Myers *et al.*, 1993:12–14; S. Gorzula, see earlier under Habitat). For the *heterodermus* group, the difficulty may be quite different. Special difficulty in species discrimination results from the extraordinary variability of *P. heterodermus*, as currently recognized.

It is almost certain, however, that the present concept of *P. heterodermus* is an unresolved complex of sibling species. Old material, discolored to a muddy brown by formaldehyde that was too strong and, as well, from inexact localities, is nearly useless for discrimination of species. New material collected from precise localities and preserved in a fashion that does not obscure color and pattern will be necessary to solve this problem. Above all, it will also be necessary to find new characters.

The fourth toe of the *neblininus* group is anomalous among the phenacosaurus. All the other phenacosaurus have all subdigitals

lamellar. The *neblininus* group overlaps the variation ascribed to *Anolis* totally. In the fourth toe of the *neblininus* group phenacosaur only the most restricted anoline toe pad—the subdigitals under phalanges ii and iii—is lamellar (wider than long, imbricate distally), as in some *Anolis*. In many other *Anolis*, some fraction of the subdigitals of the proximal phalanx is lamellar. Peterson (1983:270) cited *Anolis aequatorialis* as having half to two-thirds of the anterior portion of the proximal phalanx lamellar. *Phenacosaurus* was cited as possibly “unique” in having lamellae on all the subdigitals of the proximal phalanx of the fourth toe.

The discovery that the fourth toe of the *neblininus* group was anomalous for *Phenacosaurus* was very late, much too late for the fact to be recorded in Myers *et al.* (1993), indeed, well after the manuscript for this description of *carlostopodi* was “completed.” In fact, in only two of the paratypes of *neblininus* has this “anomaly” been verified. Peterson (1983) was writing 10 years before the description of *neblininus*, before any but three species were considered valid. Peterson saw only *heterodermus*, but of the nine species now current only the two show the fourth toe of the hindfoot as anything but totally lamellar.

The paraphyly of *Anolis* relative to *Phenacosaurus* was suggested by Etheridge and de Queiroz (1988:312). Presumably the assumption of paraphyly would make *carlostopodi* and *neblininus* the most primitive known phenacosaur, but this is not unequivocal. The *neblininus* group still shows the presumed synapomorphy of all the subdigitals of the hand and four of five of the feet (Fig. 4) being lamellar. Possibly the “anomaly” could be a homoplasious loss of the lamellar condition for the proximal phalanx of the fourth toe in only the *neblininus* group of phenacosaur. Perhaps a totally lamellar condition of all the fingers and toes was the original condition of all the anolines.

Perhaps the reverse of the Etheridge and de Queiroz supposition is true. *Phenacosaurus* is not derived from within *Anolis*. Instead of the Venezuelan tepui species being most primitive, and the Colombian species being most derived, with *P. orcesi* and related forms being intermediate, the evolutionary scene might be very different. Instead, the totally lamellar condition of the subdigitals of the hands and the feet may be primitive for anoline lizards, the heterogeneous flank scalation primitive for the genus *Phe-*

nacosaurus, and a well-developed casque primitively restricted to large phenacosaurus.

Intriguing as this discussion might be, it would obviously be inappropriate to append this extensive and still incomplete work to a species description.

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