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A NEW GIANT PHENACOSAUR FROM ECUADOR

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ABSTRACT. A new giant *Phenacosaurus* from the eastern Andes (La Bonita-Santa Bárbara Region) of Sucumbíos Province of Ecuador is described. It, like *P. inderenae* Rueda and Hernandez, 1991, differs from all other species in reaching a maximum size of more than 100 mm and differs from *inderenae* in the smaller size of the largest class of heterogeneous scales (flat flank scales interspersed with smaller scales and granules). In the density of the largest class of scales, it resembles *heterodermus* and differs from *nicefori* Dunn, 1944, and *tetarii* Barros, Williams, and Vilor, 1996. From all the remaining species, it differs in having heterogeneous scales.

INTRODUCTION

The first giant phenacosaur, *Phenacosaurus inderenae* (>100 mm in snout-vent length [SVL]), was described by Rueda and Hernández-Camacho (1988) from Gutiérrez, in the southeast of the Department of Cundinamarca, Colombia, on the eastern slopes of the Cordillera Oriental of the Andes, syntopic or sympatric with *P. heterodermus*.

Since that description, there has been an explosion of information concerning these lizards. New species belonging to several subgroups have been described: *tetarii* Barros, Williams, and Vilor, 1996, and *euskalerriari* Barros, Williams, and Vilor, 1996, both from the Venezuelan side of the Cerro de la Perijá; *neblininus*

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Myers, Williams, and McDiarmid, 1993, from the Cerro de la Neblina, at the border of Brazil and Venezuela; and an unnamed juvenile (Williams and Mittermeier, 1991) from Venceremos, Department of San Martín, Peru. Two more require description, a second giant from Ecuador, formally described herein, and another small species from Chimantá Tepui, Venezuela (Williams, Praderio and Gorzula, 1996).

Sorting out at least the similarities and differences of the several new described and undescribed species within the genus seems necessary at this time. The justification of the genus will be postponed until a separate paper.

It has only been possible to separate *P. inderenae* and the species described later by comparing the whole type series of *inderenae* with the whole type series described later. Both type series are small, four in the case of *inderenae*, eight (but one was found dead and is now a skeleton) in the new species later, but each comes from a well-defined local area. We find that the large, flat, round scales are consistently smaller in the Ecuadorean species as compared with *P. inderenae* and, on that basis, describe the former as a new species. To facilitate future research, we have described the holotype separately and in detail. We discuss variation within the remainder of the type series of the new species in the same format as the description of the type, except that we describe a probable hatchling separately. We then deal with the variation in the type series of *inderenae* in the same style and format.

The material of the new species is deposited in four museums: the type and the first found of the paratypes (now a skeleton) in the Museo Ecuatoriano de Ciencias Naturales (MECN), four of the paratypes in the Escuela Politécnica Nacional (EPN), two of the paratypes in the Museum of Comparative Zoology, and one paratype in the National Museum of Natural History (USNM).

The new species, which is very close to *P. inderenae* in many characters in addition to size, is here named for the distinguished Brazilian scientist, Paulo Emilio Vanzolini.

Phenacosaurus vanzolinii, new species

Holotype. MECN 0309, adult male.

Type Locality. ECUADOR: S La Alegría, at an elevation of 2,360 m, ca. 14 km by road from La Bonita (77°37'42"W,

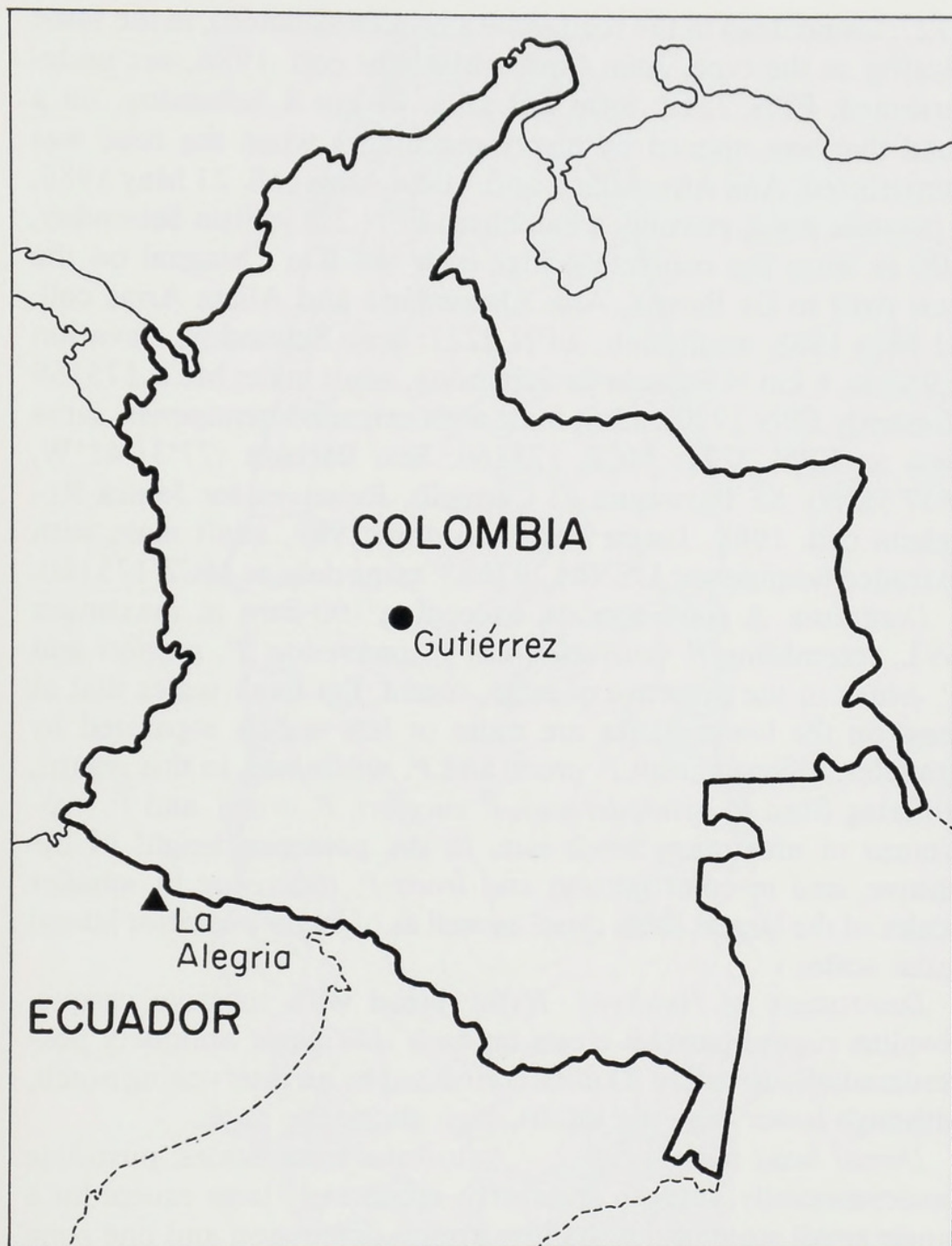


Figure 1. The regions of the type localities of *Phenacosaurus inderenae* (circle) and *Phenacosaurus vanzolinii* (diamond).

0°27'30"N), Provincia de Sucumbíos (formerly the northwest part of Provincia de Napo), Robert Bleiweiss and Juan Carlos Matheus coll. 15 March 1985.

Paratypes. All ECUADOR: Provincia de Sucumbíos: MECN

0327: found dead in the road (now a broken skeleton), at the same locality as the type, Juan Carlos Matheus coll. 1986, sex undetermined; EPN 2218: Sitio Las Ollas, 4 km S Sebundoy, on a road that was opened by heavy machinery when the road was constructed, Ana Almendáriz and Alicia Arias coll. 21 May 1988, a juvenile male, possibly a hatchling; EPN 2219: Sitio Sebundoy, 100 m from the concrete bridge over the Río Chingual on the new road to La Bonita, Ana Almendáriz and Alicia Arias coll. 21 May 1988, adult male; EPN 2221: Sitio Sebundoy, elevation 1,950 m, 6 km N Escuela de Sebundoy, adult male; MCZ 175159 (formerly EPN 2220): adult male with extruded hemipenes, same data as EPN 2221; MCZ 175160: Sta. Bárbara (77°31'41"W, 0°37'58"N), SE Parroquia El Carmelo. Relatives for Janira Regelado coll. 1988. Janira Regelado don. 1989, adult male with extruded hemipenes; USNM 293683: same data as MCZ 175160.

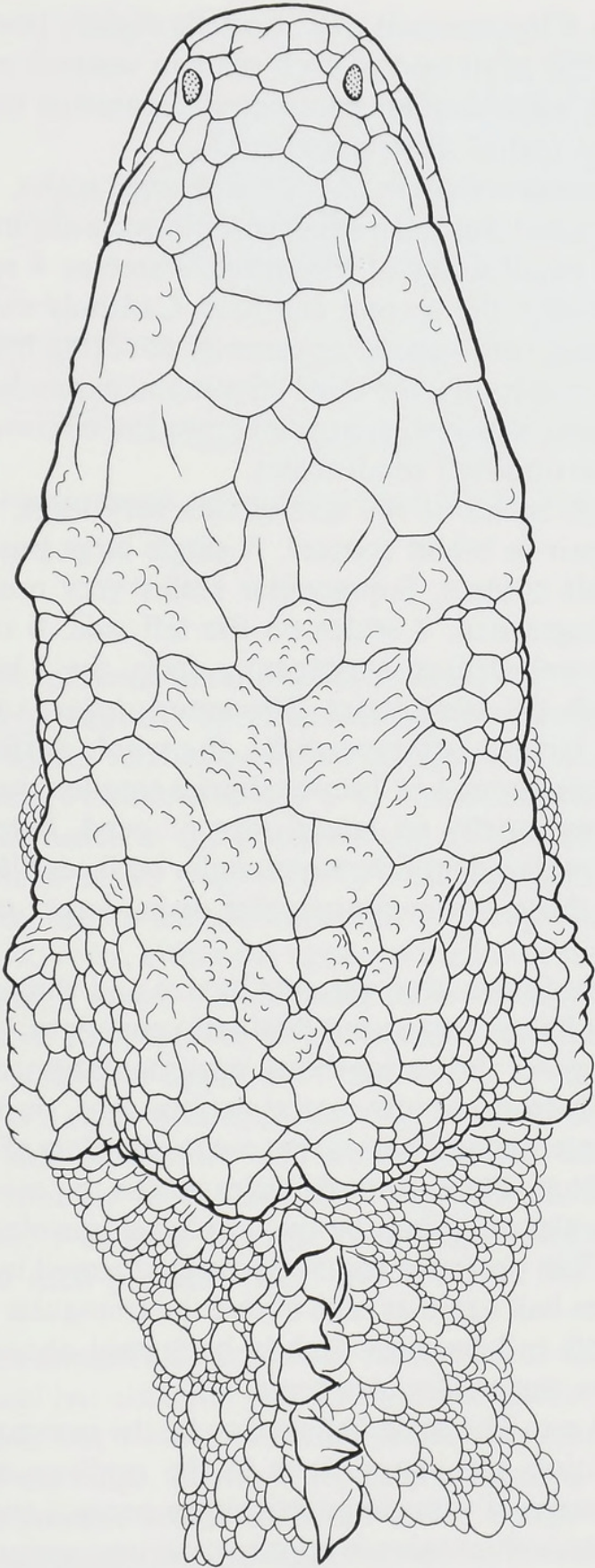
Diagnosis. A giant species, exceeding 100 mm in maximum SVL, resembling *P. heterodermus*, *P. inderenae*, *P. nicefori* and *P. tetarii* in the presence of large, round, flat flank scales that at least on the lower flanks are more or less widely separated by granules; differing from *P. orcesi* and *P. neblininus*, in this regard; differing from *P. heterodermus*, *P. nicefori*, *P. orcesi*, and *P. neblininus* in maximum adult size, in the posterior height of the casque, and in color pattern and from *P. inderenae* by smaller scales of the largest flank class, as well as of larger posterior lateral gular scales.

Description of Holotype. Head: Head with massive casque. Swollen rugose parietal crests on each side angle obliquely posteromedially to end in 2 knobs connected by an intervening notch, although lower than the knobs, high above the nape.

Dorsal head scales (Fig. 2)—Antorbital area: Scales, pustulate posterolaterally, smooth anteriorly, moderately large except for a single small scale in the shallow frontal depression and one zone of small scales posterior to the circumnasals, another such zone on each side between the anterior canthals and the medial series

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Figure 2. *Phenacosaurus vanzolinii*, holotype, MECN 0309, Dorsal view of head.



of large scales. Circumnasals oval, nostrils slightly posterior within the scales, the acute end of each scale in contact with the first supralabial. A subtriangular postrostral separating each circumnasal from the rostral. Five postrostrals.

Frontal depression shallow. A rosette of larger scales, very weakly rugose or pustulate, around a small smooth scale about equivalent in size to the small scales of the snout. Three or 4 scales across the snout between the second canthals. Canthals swollen, their edges raised and very rugose, apparently covering bony encrustations, four on each side, the third largest and expanded medially, the anteriormost smallest, separated from the circumnasal of its side by 2 superimposed small scales.

Orbital area: Scales of the semicircles very large, rugose and pustulate, 1 pair in broad contact. A single large pustulate scale anterior to this contact. Supraocular scales very much smaller, very finely shagreened, 4 scales on the left side, 6 on the right side in rather well-defined supraocular disks, the 2 largest scales in contact with the semicircles. The anteriormost superciliaries of both sides largest, subtrapezoidal, the whole surface exposed dorsally, the remaining 6 or 7 superciliaries smaller, quadrangular, in a single row mostly on lateral face of head, barely exposed dorsally. The remainder of the supraocular surfaces filled by scales smaller than those of the supraocular disks, larger than the superciliaries.

Parietal area: Scales very variable in size and shape, moderate to small, most lightly rugose but distinctly pustulate. Lateral crest scales very rugose, indicating bony ornamentation underneath, arising abruptly from the low central parietal area, sloping upward toward the posterolateral bosses that are the borders of a moderate but narrow notch. Three smooth scales across the median notch. The several scales covering the two eroded posterolateral bosses also smooth. The posterior transverse ridge formed by the bosses and notch rises half again as high above the triangular nape scales as they are tall and projects slightly backward above the small interval before the crest scales begin.

No parietal eye. The scale believed to be the interparietal identified on position and shape. It is in the midline anteriorly, a rather small, narrow triangle anteriorly in contact with the semicircles. Lateral to this scale are apparent parietal scales, the largest

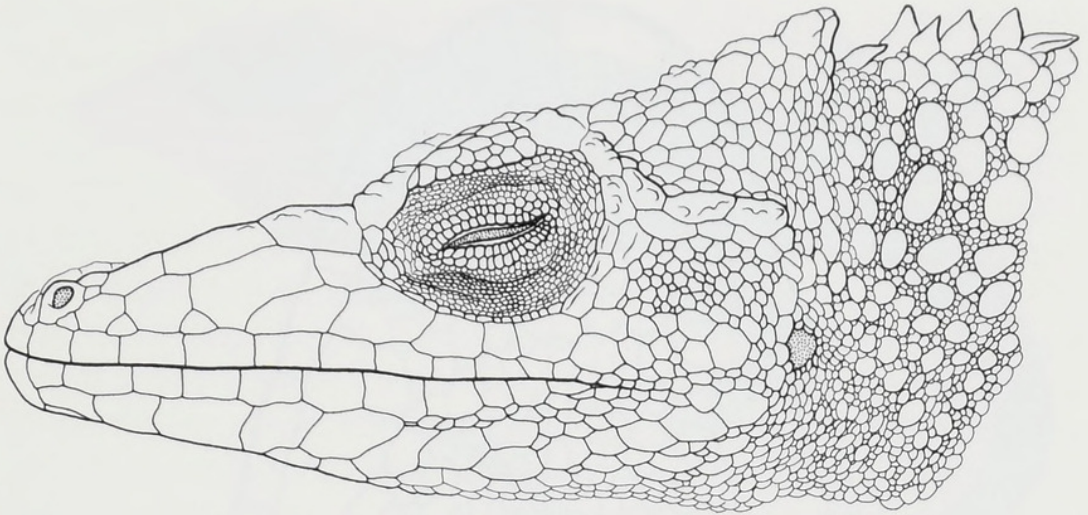


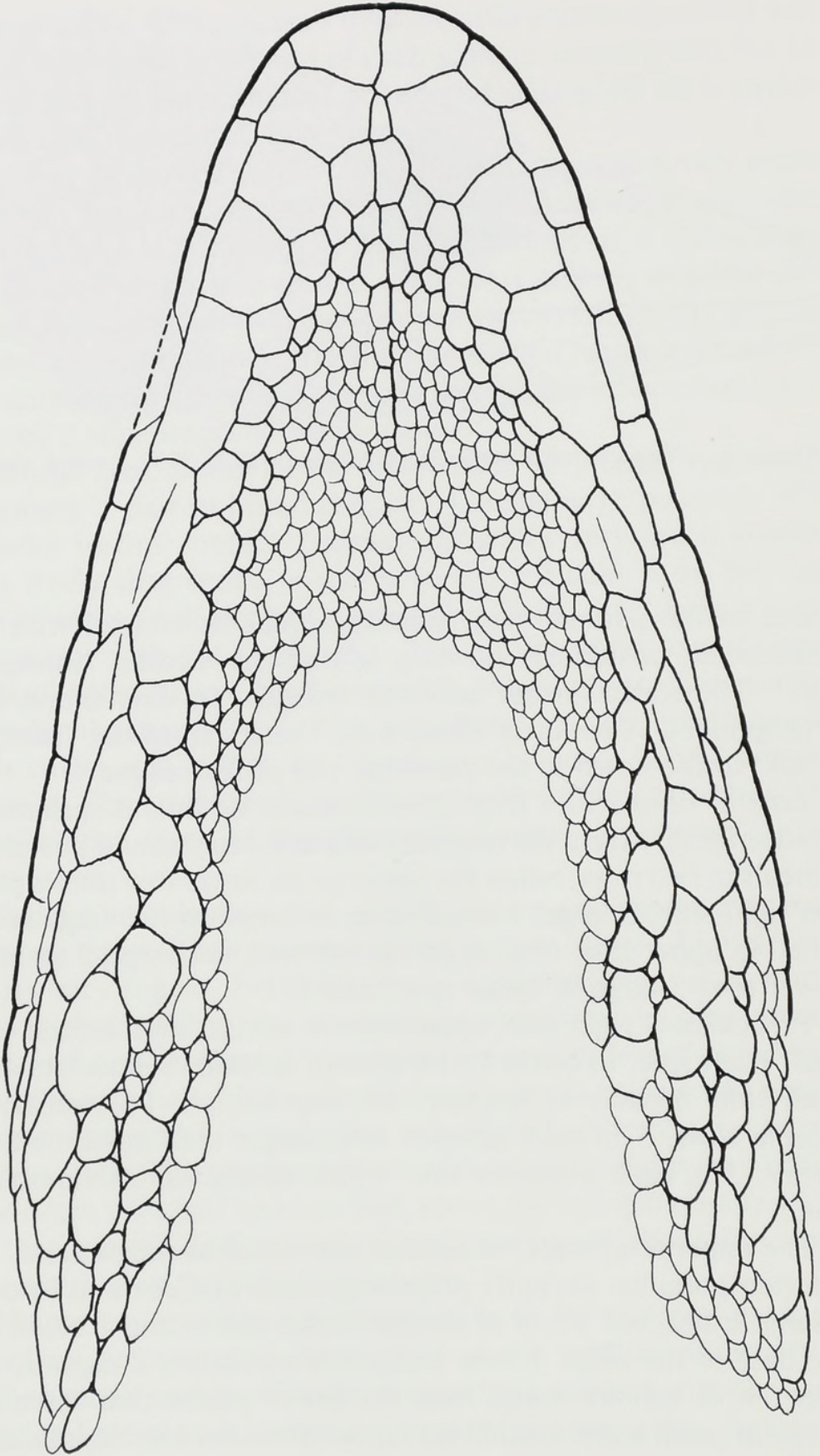
Figure 3. *Phenacosaurus vanzolinii* holotype, MECN 0309, Lateral view of head.

scales in the parietal area, subtrapezoidal, in contact with the semicircles, posteriorly meeting behind the median “interparietal.” The scales further posterior irregular in size, shape, and arrangement. A count of about 6 to 7 scales from the “interparietal” to the notch at the posterior end of the casque.

Lateral head scales (Fig. 3)—All scales on lateral surfaces of head smooth, except the canthals, which are rugose and pustulate. Loreals in two rows, either the upper or the lower row interrupted. On right side, 5 large, 1 small scale in lower row, 1 large and 1 small in upper row, total 8; on the left side, one large, 3 small in lower row, 3 large in upper row, total 7.

Preoculars 2 right side, uppermost in contact with second canthal, 1 left side, in contact with second canthal. Suboculars 4 on each side, broadly in contact with supralabials. Postoculars in double rows, 5 in each anterior row, larger than adjacent temporals, 3 in each posterior row, which meets the intertemporal bar.

The upper temporals variable in size, small to subgranular. An intertemporal bar abruptly projecting, shelf-like, covered by only 3 large scales, but 1 row of smaller scales above and 1 below on the base of the ridge. Lower temporals exhibiting 2 regions, the upper with smaller scales than the lower except that there are irregular small scales around the corner of the mouth. Supralabials



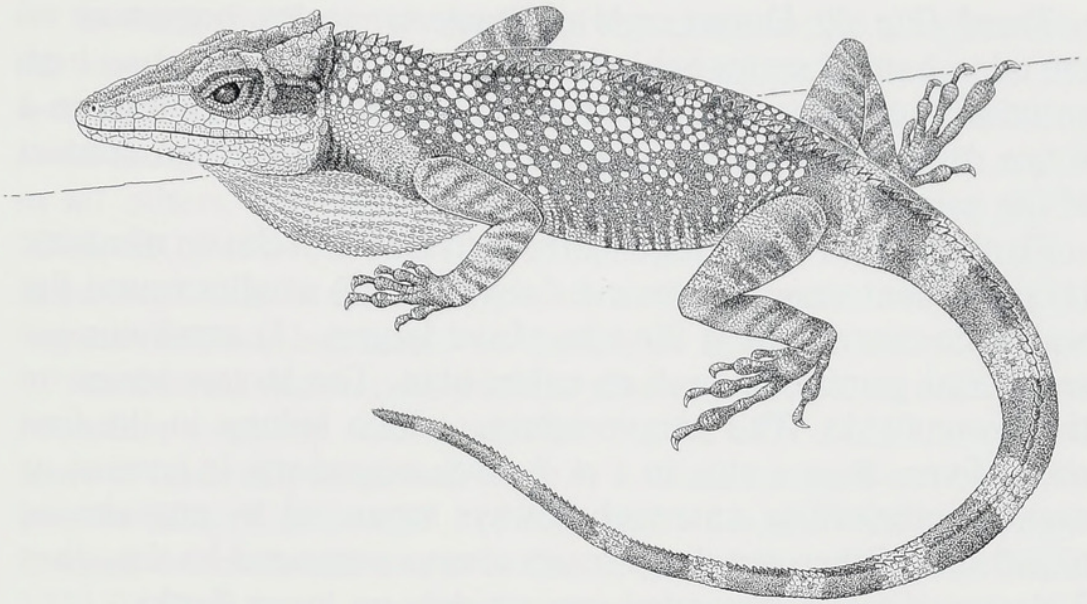


Figure 5. *Phenacosaurus vanzolinii*, holotype, MECN 0309, Lateral view of entire animal.

elongate rectangles, 8–9 on both sides to below the center of the eye.

Ventral head scales (Fig. 4)—Mental partly divided, deep, sub-pentagonal, not indented, in contact with 3 scales between the infralabials. Nine infralabials on right side, 10 on left. Very large first sublabials, each more than $5 \times$ the size of the single median gular. Three somewhat smaller sublabials on each side, in series with the first, in contact with the infralabials. Total sublabials on each side five. Central gulars smooth, swollen, variable in size, largest adjacent to the sublabials. Posterolaterally, posterior to the sublabials, the lateral gulars mostly much enlarged, but very variable in size, in several distinct rows.

Dewlap (Fig. 5): Edge scales convex, smooth, smaller than ventrals. Lateral scales about the same size as the edge scales, in single rows separated by naked wrinkled skin.

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Figure 4. *Phenacosaurus vanzolinii*, holotype, MECN 0309, Ventral view of head.

Trunk (Fig. 5): Dorsal crest of triangular scales, beginning on the nape 2 small scales behind the abruptly vertical casque, high anteriorly, only low above the sacrum. Nearly continuous in a single row, interrupted at irregular intervals by median contact of the paravertebrals.

Flank scales very heterogeneous, with at least 3 classes of scales: (1) prominent very large round flat scales, (2) smaller round flat scales, no more than $\frac{1}{4}$ the size of the largest, (3) small convex scales and granules as well as naked skin. The largest scales on the lower flanks. The paravertebrals, which belong to the first class of very large scales, in 1 or 2 rows, posteriorly in contact or slightly imbricating, anteriorly always separated by granules or naked skin. Other very large scales always separated by the other 2 classes of scales, separated most widely on lower flanks.

Axilla and groin granular. Ventrals smaller than the largest flank scales, averaging a little larger than the second class of flank scales, rather irregular in size and shape, imbricate or subimbricate.

Limbs (Fig. 5): Anterior face of forelimbs mostly with separated flat smooth scales. Anterior face of hindlimb mostly with scales in contact. Posterior face of upper arm and thigh with granules separated or in contact, of lower arm and leg with small scales mostly in contact. Supradigitals smooth. Subdigitals all lamellar. Lamellae under phalanges ii and iii of fourth toe 25–26.

Tail (Fig. 5): Strongly compressed, with a crest of larger sharply keeled, dentate scales. All scales keeled except a few rows above at the base of the tail and about 8 rows immediately behind vent. Postanals much enlarged (male).

Color in life: No descriptions of the color in life of the type series exist. Fortunately, we do have slides of the holotype. It is revealed to be dorsally greenish in background with the underparts totally white. The large round scales are often yellow or lighter green. There is some vague tendency to banding. The head scales have an orangish cast when not overlaid by green smudging. A broad white band unites the supralabials. There is yellow banding on the limbs and digits.

Variation: The Adult Paratypes. Head: The casque is high to very high posteriorly and its lateral crests are always significantly raised above the central parietal roof.

Dorsal head scales—Antorbital area: Pustulations may extend

far forward but never to the tip of the snout or the area between the circumnasals. Small scales may extend only alongside the fourth (anteriormost) canthal or reach the anterior end of the third as in the holotype. There are 3 postrostrals in EPN 2221 and 4 in all others. The rostral area is injured in 3 specimens (EPN 2219, MCZ 175160, and USNM 293683), in all the circumnasals appear to be, as in the holotype, narrowly in contact with the first supralabial, and separated on each side from the rostral by one of the frontal depression there is always a rosette of scales surrounding a central scale or scales, but in EPN 2221 the central scale is relatively large and there is a small scale off center to the left. In EPN 2219, MCZ 175160, and USNM 293683 there are 2 small or moderate scales at the center of the rosette. In MCZ 175159 there are 2 rosettes, the posterior with a small scale, the anterior with a large scale in center but a small scale just off center. The large scales of the rosette may be pustulate or with none or few pustules.

The canthals are always 4 and the anteriormost always separated from the circumnasals by at least 2 superimposed scales. The third is always largest and expanded medially. The first canthal may or may not be expanded medially. These scales are nearly smooth in MCZ 175159, except for a few pustulations, but more or less wrinkled in the other paratypes, which are more or less heavily pustulate as well.

Orbital area: The scales of the semicircles are always pustulate to heavily pustulate except the extreme posterolateral scales, which may entirely lack pustules. The supraoculars, on the other hand, and the superciliaries, are always smooth or very finely shagreened. A single pair of the scales of the semicircles may meet medially or these may be wholly separated by 1 row of rather large pustulate scales. The supraoculars are relatively few in number, the enlarged scales in 2 or 3 rows, with the largest scales medial and in contact with the semicircles, and one or more of the lateral enlarged scales in contact with the superciliaries. A few smaller scales, variable in size and number, fill the remainder of the supraocular area. The anteriormost 1 or 2 of the superciliaries in all of the type series fully exposed dorsally, larger, and subtriangular or subtrapezoidal. The remainder of the single row of superciliaries is quadrate, subequal or the posteriormost again

larger, and in 5 of 6 specimens barely exposed dorsally, mostly on the lateral surface of the head. In MCZ 175160, the entire row is fully exposed dorsally, and the anteriormost element best described as quadrate like the other superciliaries.

Parietal area: These scales in the paratypes are extraordinarily variable, not only in size and shape but also in rugosity and pustulation. EPN 2219 shows an extreme in pustulation with very little rugosity; MCZ 175160, on the contrary, is extreme in rugosity, which nearly conceals all pustulation.

The lateral crests, as in the holotype, slope upward toward posterior bosses that, however, are either the lateral borders of a more or less deep notch or of a transverse occipital ridge. A notch like that of the holotype occurs only in EPN 2219. In USNM 293683 and EPN 2221, a series of 4 bosses unite to form a transverse ridge. In MCZ 175160 and MCZ 175159, there are 4 transversely oriented bosses but a narrow and deep notch.

No parietal eye in any adult specimen. In EPN 2221 and MCZ 175160, a smaller and shorter scale occurs in the position of the "interparietal" of the holotype, but the scales called "parietals" in the holotype are broken up in both specimens. In the 3 remaining adult paratypes, the scales are so irregular or asymmetric that no interparietal is plausibly demonstrable. In consequence, counts from interparietal to the posterior crest of the casque can only be made in EPN 2221 (4 or 5) and MCZ 175160 (6 or 7).

Lateral head scales—All lateral scales are smooth in the paratypes except USNM 293683, which has the canthals pustulate as in the holotype. Only MCZ 175160 has a single loreal row on both sides. The total number of loreals in this specimen is 4 or 5, the series grading in size anteriorly. On both sides the very large and long preocular has a dorsal vertical groove at the middle of its length, indicating that 1 loreal has fused with the preocular on each side. If so, the true total count of loreals would be 5 and 6, respectively. The other paratypes have 2 rows, 1 row, upper or lower, always interrupted. The total number of loreals in these paratypes varies from 7 to 9. Preoculars are 2 in 3 of the paratypes as in the holotype. In EPN 2219 and 2221, however, there is only 1 preocular on each side. In all cases, the preocular is in contact with the second canthal. The suboculars vary from 3 to 4 in 4 paratypes and are 5 only on one side of EPN 2219. Postoculars

are in 2 rows behind the eye (on the bony ridge that is the junction of jugal and postorbital). The number of postoculars in each row varies from 3 to 5; only in MCZ 175159 does the number of postoculars rise to 6 in each of the 2 rows on the right side and to 6 on the posterior row, 7 in the anterior row on the left. The supralabials are elongate rectangles in all specimens, and the number to the center of the eye varies from 7 to 10.

The temporal area is in all specimens divided into supra- and infratemporals by a very prominent projecting, shelf-like intertemporal ridge (marking externally the squamosal–postorbital bar that is the lower border of the upper temporal fenestra). The edge of the intertemporal ridge is covered by 2 large horizontally extended scales in all paratypes. The number of scale rows entering the ridge base from the supratemporals or infratemporals varies from 0 to 1 on the upper or lower side independently.

The supra- and infratemporals are quite smooth. Where in the supratemporal region a scale overlaps the edge of the casque, the scale is always smooth on the supratemporal side, always wrinkled, rugose or pustulate on the parietal side. Most of the supratemporals are subequal and polygonal, but occasional smaller polygonal or narrow scales intervene posteriorly. The infratemporals divide abruptly into 2 regions differing in the size of their scales. The abrupt size difference is coincident with the margin between dark and light pigment in this lower temporal region. This condition is consistent in all the paratypes as well as in the holotype, but in the paratypes as in the holotype, just below the intertemporal ridge larger scales again occur, and at the lower margin around the corner of the mouth quite small scales are found.

Ventral head scales—The mental is always semidivided. It varies somewhat in width but is always as deep as it is wide, and not or only slightly indented by the sublabials or medial gulars. The first sublabials vary much in size and may be significantly different in size on the 2 sides of the same animal. However, they are always at least $4\text{--}5 \times$ as large as the medial gulars that lie between them, although these also vary very much in size. The first sublabials are in series with a row of sublabials, each of which may be as large or larger than the first. A total of $4\text{--}7$, always counting the first, may be in contact with the infralabials. The central gulars,

those that cover the throat posterior to the medial gulars that lie between the sublabials, are always smooth, mostly juxtaposed, swollen, elongate, and larger anteriorly, becoming smaller and more rounded, subimbricate in the center of the throat. Granules are visible between some of the central gulars. Those gulars that lie next to the sublabials are consistently larger than those occurring centrally.

Lateral to and behind the sublabials and lateral to the insertion of the dewlap are lateral gulars. The anterior ones are tiny, barely separating the sublabials from the infralabials. These become larger posteriorly and, indeed, become as large as the posterior sublabials from which they are distinguished by their orientation.

Dewlap (all paratypes are males): Moderate, not extending posteriorly much beyond the insertion of the arms. Edge scales, smooth, imbricate, smaller than ventrals. Lateral scales, about the same size as edge scales, in very regular single rows, the scales well separated by wrinkled skin or by wrinkled skin with very occasional minute scales.

Trunk: A dorsal crest of a single row of triangular interrupted at irregular intervals by 2 paravertebral scales joining across the midline, highest on the nape, lowest on sacrum.

There are 3 classes of flank scales: (1) round, flat scales, varying in size but larger than crest scales; (2) round, flat scales much smaller than class 1 ($\frac{1}{4}$ their size or less); (3) convex granules, large or small, some almost as large as some class 2. One or more rows of paravertebrals of class 1 size are always in contact or separated by only 1 row of class 3 granules or scales. Class 1 scales lower on the flank, on the other hand, are always separated by 2–5 rows that include class 2 scales and/or smaller class 3 scales or granules.

The ventrals are always smooth, flat or slightly convex, imbricate and about the size of class 2 scales or slightly larger.

Limbs: Anterior upper arm scales smooth, variable in size, sometimes imbricate. Posterior upper arm scales granular, juxtaposed.

Anterior lower arm scales smaller, narrower, smooth, subimbricate. Posterior lower arm scales granular, juxtaposed.

Manus with weakly multicarinate scales, imbricate dorsally on carpus, palm scales narrower, subimbricate. Supradigitals multicarinate. All subdigitals lamellar.

Thigh scales anteriorly large, smooth, subimbricate proximally, imbricate at knee, posteriorly with narrow scales, subimbricate or juxtaposed. Tibial scales smooth, small, narrow and imbricate anteriorly, subgranular and subimbricate posteriorly. In EPN 2219, larger scales are found among the granules.

Pes with scales dorsally and on the sole indistinctly carinate and subimbricate. Supradigitals weakly multicarinate. All subdigitals lamellar. Lamellae under phalanges ii and iii of fourth toe 24–28.

Tail: Always strongly compressed and with a distinct crest of keeled scales, which, however, varies in height but, in most paratypes, has a dentate appearance. The lateral caudal scales are always keeled, except dorsally at the base and ventrally for 5–10 rows behind the vent.

Variation: The Juvenile Paratype. The juvenile EPN 2218 requires a separate description. Many of the differences are surely ontogenetic, but it is not obvious that all of them are. Differences between this specimen and the remainder of the type series are italicized.

Head: *There is no casque* but its margins are partially indicated by low ridges (lateral parietal crests) bounding the parietal area.

Dorsal head scales — Antorbital area. *There are no pustulations.* Scales at the tip of the snout and 2–3 rows posterior to the circumnasals and a few scales between the canthals and a larger median row of scales are small. A total of 7 postrostrals, 5 almost granular postrostrals in addition to the larger circumnasals. Each circumnasal is broadly in contact with the first supralabial of its side. There are 3 small scales between the circumnasals dorsally.

The frontal depression is very shallow with large scales forming a rosette around small scales in the center.

The canthals are 6 *on the left side*, 5 on the left, gently arched, not keeled, the first (posteriormost) widened medially on both sides, third largest, also expanded medially, *the anteriormost on the left side in contact with the circumnasal, that on the right separated from the circumnasal by 1 small scale.*

Orbital area: The supraorbital semicircles are separated medially by a single row of scales only slightly smaller than those of the semicircles. One especially large supraocular in contact with the semicircles on each side. Two to 3 enlarged supraoculars in

a second row, not in contact with the superciliaries. Other scales of the supraocular region smaller. Two or 3 short polygonal anterior superciliaries followed by quadrate subgranular scales.

Parietal area: A parietal eye indicated by a light spot in the hexagonal interparietal, the largest scale in the parietal area and separated from the semicircles by a large scale on the left side and by 2 small scales in a row on the right side.

There are moderate-sized scales that abut laterally on the interparietal but they do not meet behind it and intervening scales of small or moderate size separate these from the semicircles as well as others that separate them from scales that cover the lateral parietal crests and are larger than any scales of the parietal area except the interparietal.

The lateral parietal crests converge but do not meet. There is, instead, a wide gently convex medial area, presumably marking the position of the future posterolateral bosses and the median notch. Over this gentle convexity, 4 rows of small scales, here called "notch scales," precisely comparable in size to the nape scales, enter the parietal area to abut against the 4–5 rows of abruptly larger (moderate-sized) scales behind the interparietal.

Lateral head scales—Two loreal rows, 8–10 total loreals, 4 large and 4 small on the right side, 4 large and 6 small on the left side.

Preoculars 2, counting on each side the upper scale that overlaps the loreal rows and excludes the lower preocular from contact with the second canthal. Five suboculars each side, broadly in contact with the supralabials. Eight to 10 supralabials to below the center of the eye.

Temporals smooth, flat. Lower temporals variable in size, but a vaguely indicated division by scale size with the scales averaging smaller in the upper pigmented region and larger in the lower unpigmented region. A well-defined intertemporal row beginning with a single large elongate scale and continuing as a double row of slightly enlarged scales. Upper scales subequal with an abrupt transition at the lateral parietal ridges where the enlarged scales of the parietal area begin.

Ventral head scales—Mental partly divided, in contact with 4 postmentals between the infralabials, 2 medial gulars between the very large first sublabials. Three additional sublabials in series with the first on each side are in contact with the infralabials.

Central gulars smooth, juxtaposed or subimbricate. Some of the posterior gulars next to the sublabials markedly enlarged, nearly as large as the last sublabial. Lateral gulars intervene between the posterior sublabials and the infralabials.

Trunk: A dorsal crest begins on the nape, seven scales behind the enlarged scales of the parietal area, as raised, still relatively small protuberant scales in 1 or 2 rows, rising to 3 broad-based triangular typically blade-like crest scales in sequence, behind which the crest is only indicated by a series of enlarged smooth oval scales, interrupted at intervals by paravertebrals joined over the midline. Flank scales heterogeneous with large round flat class 1 scales, largest dorsally and there often in contact, on lower flanks smaller and most often separated by class 2 and 3 scales and granules. Axilla and groin granular. Ventrals smooth, flat, irregular in size and shape, imbricate or subimbricate.

Limbs: Anterior face of fore- and hindlimbs with imbricate or subimbricate flat smooth scales. Posterior face of upper arm and thigh with granules, of lower arm and lower leg with small scales. Supradigitals smooth. All subdigitals lamellar. Lamellae under phalanges ii and iii of fourth toe 25.

Tail: Compressed, without a crest or a continuous middorsal row, smooth or with an occasional hint of keeling dorsally, none below, but the latter scales more convex. Postanals much enlarged (male).

Dewlap: *There is no trace of a dewlap.*

Food. Stomach contents from MECN 0327 were examined by James Carpenter (then at the Museum of Comparative Zoology). He reported:

At least four taxa are present in the sample as follows:

Order Lepidoptera, family Geometridae—an intact larva (“looper” or “inchworm”).

Order Coleoptera, family Buprestidae—elytra (forewings).

Order Hymenoptera, Halictidae, tribe Augoclorini—head capsule, thorax, wing, parts of legs.

Order Homoptera, Cicadidae—most of the large fragments, including a head capsule.

In addition there are a number of eggs. These could be from the cicada.

Ecology. The holotype was collected by Robert Bleiweiss. He here provides an expanded version of his field notes:

Collected during the early afternoon along a road cut. The animal was moving slowly and deliberately down the stem of a large vine belonging to the family Gesneraceae that was overhanging the road bank along a forested section of the road.

The weather was sunny and warm. It was probably between 1 and 2:30 in the afternoon. The collection site was a few minutes drive down from La Alegría near a stream gorge and on the shady side of the road.

Juan Carlos Matheus collected the second (damaged) specimen dead in the road near the same site.

Ana Almendáriz has reported on the times and sites of collection of the remaining specimens that have exact data. All were collected between 10:00 and 12:30 A.M., and all were collected along roads. The days of collection were humid, but at the moments of collection there was never rain but, instead, a bit of sun—"un poco de sol."

Ana Almendáriz has also provided a description of the general region where she collected (translated):

While the region is within the 'cloud forest zone', it has been heavily cultivated, removing the trees that were of commercial value, then clearing the forest for field crops. Original forest is therefore confined to slopes and ravines difficult of access. The margins of the roads are covered with secondary vegetation, mostly Asteraceae.

She reported also that the local people say that the "camaleon o camelion" is common in the fields of maize. Bleiweiss and Matheus collected at La Alegría at higher elevations with steep terrain. This area, the type locality, was still heavily forested in 1985.

The ecology reflected by these experiences accord wells with the observations of Williams collecting *heterodermus* in the Sabana de Bogota and with the more extended observations made by Kenneth Miyata on 2 full days of study in August 1973 (Miyata, 1983).

Comparisons. *Phenacosaurus vanzolinii* requires comparison

primarily with *P. inderenae*. The species are both giant, with *P. inderenae* significantly the larger, given the small series of both that are available. Both have rather similar coloration and both have highly differentiated flank scales—the three classes of scales described above—seen also in *P. heterodermus*. Both differ from *P. heterodermus* not only in size and the associated development of the casque but also in color pattern and details of squamation.

For the comparison of the two giant species, we have available the whole of the type series of *P. inderenae*, three females and one male, generously loaned by Hernández–Camacho and Rueda. For better comparison, we describe these specimens in the same detail as we have previously done for the type series of *P. vanzolinii*: one female, Inderena (IND)-R 2999, has already been quite accurately illustrated (fig. 1 in Rueda and Hernández–Camacho, 1988). The single male, IND-R 3381, is illustrated in our Figures 6–9.

Head: The head is casqued as massively and the posterolateral bosses of the casque are about as high as in any *P. vanzolinii*.

Dorsal head scales (Fig. 7)—Antorbital area: There appear to be larger scales behind the circumnasals and between the canthals and the median larger scales and no small scales in the frontal depression. The scales between the circumnasals appear to be larger than in *P. vanzolinii*. Postrostrals vary from 3 to 5, 3 in the holotype female IND-R 3213, 4 in IND-R 3744 and 3381, and 5 in IND-R 2999, in the latter case including the circumnasals, which are in broad contact with the first supralabials but only narrowly in contact with the rostral. In the 3 other specimens, the circumnasals are again broadly in contact with the first supralabials but separated on each side from the rostral by one of the postrostrals.

In the frontal depression in all specimens the scales are smooth and large. There is no rosette surrounding a central small scale. Instead, there is a symmetrical arrangement of 4 large scales, 1:2:1, and there are always 2 scales (3 or 4 scales in *vanzolinii*) between the second canthals across the frontal depression.

The canthals are smooth or very bluntly keeled. There are 4 asymmetrically in IND-R 2999, 4 left side, 5 right side, or 5 in all the others. On both sides of all specimens the anteriormost canthal is in contact with the circumnasals (separated by 2 superimposed small scales in *vanzolinii*).

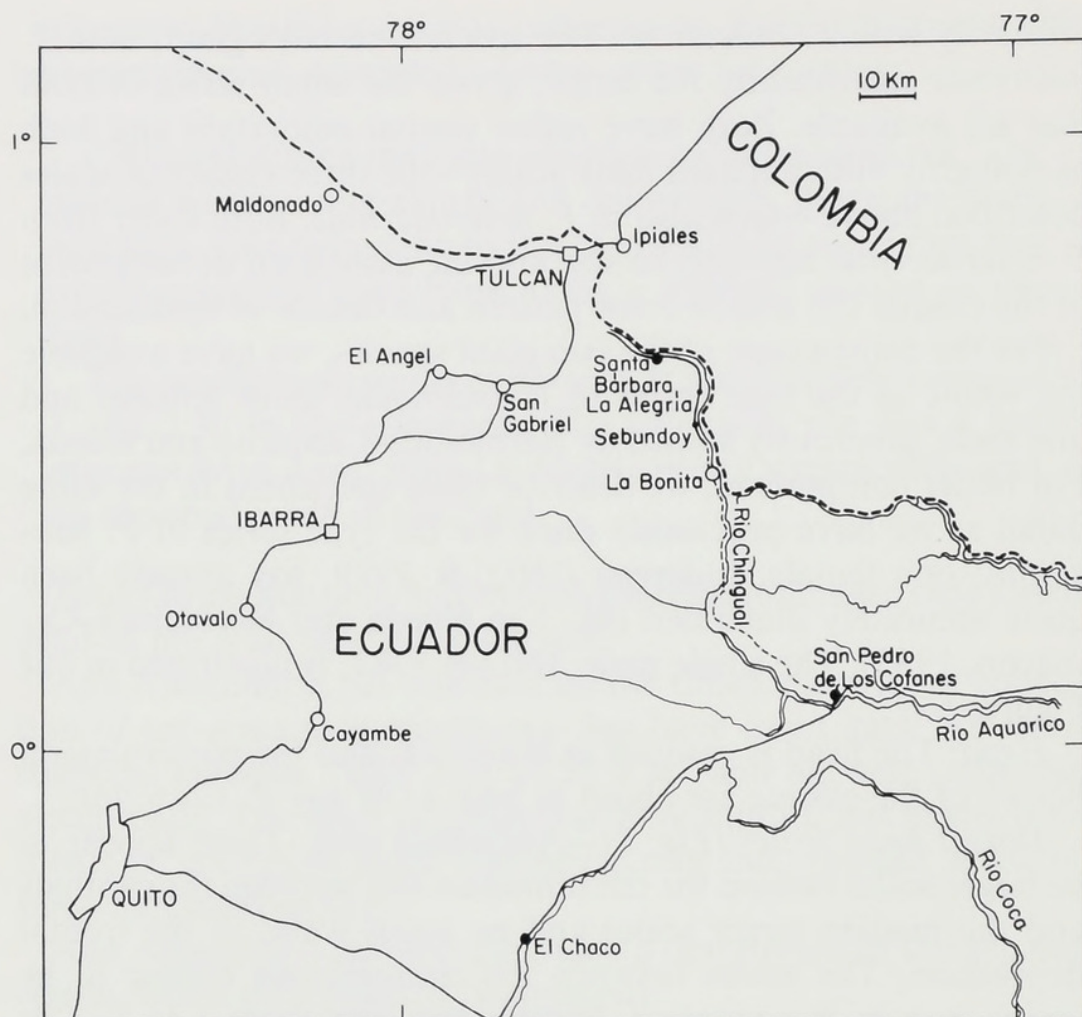
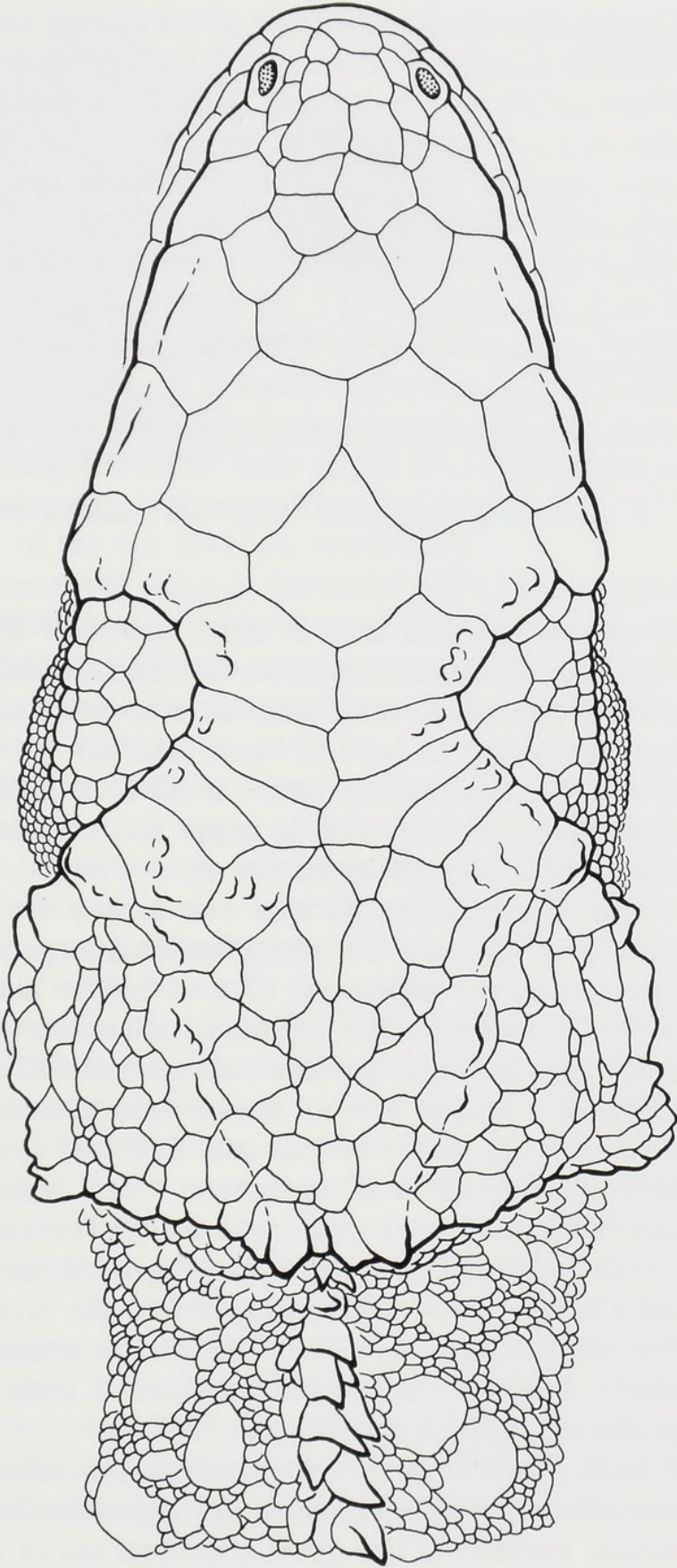


Figure 6. The known localities for *P. vanzolinii*.

Orbital area: In all 4 *inderenae*, the scales of the semicircles are wrinkled and vary from not to moderately pustulate, with 2 or 3 pairs in contact medially (1 or none in *vanzolinii*). The supraoculars (as in *vanzolinii*) are smooth or very finely shagreened. On both sides of all specimens the 2–3 largest scales are in contact with the semicircles, the 4 scales in the second row are in contact with the superciliaries, and a central scale is interposed between the first and second rows. As in 2 of the 6 paratypes of *P. van-*

Figure 7. *Phenacosaurus inderenae*, paratype male, IND-R 3381, Dorsal view of head.



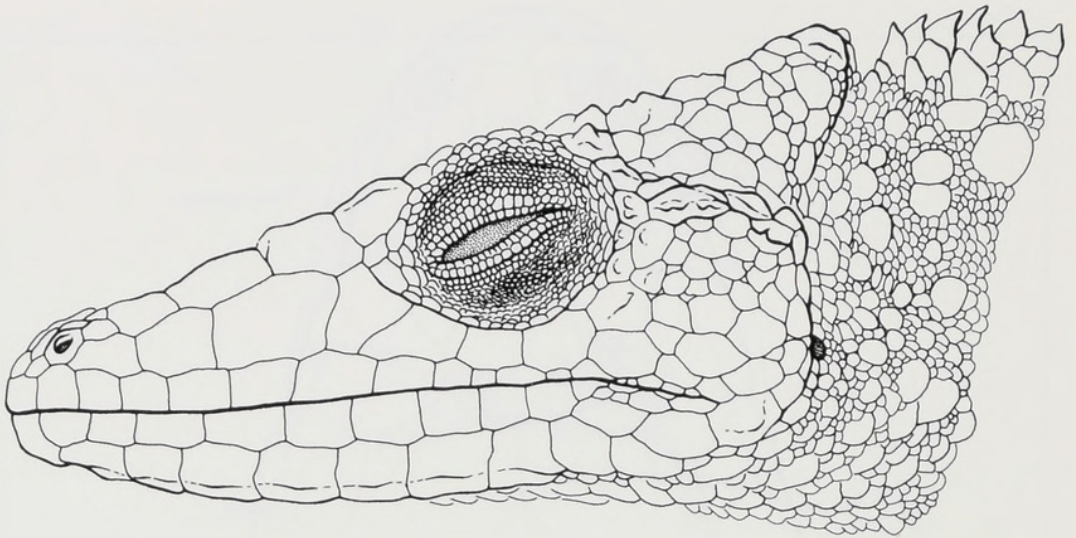


Figure 8. *P. inderenae*, paratype male, IND-R 3381, Lateral view of head.

zolinii, the superciliaries in IND-R 3381 and IND-R 2999 are fully exposed dorsally. In the holotype, the largest specimen, and IND-R 3744, the smallest, only the 2 or 3 largest superciliaries are visible dorsally, but in both of these the eyes are somewhat sunken in, and this feature may be an artifact. As in *vanzolinii*, the first superciliary on each side is larger and trapezoidal, and there are about 7–8 subequal posterior superciliaries.

Parietal area: There is no parietal eye in any specimen. In contrast to *vanzolinii*, there is a recognizable interparietal in all cases, diamond-shaped, variable in size, in narrow contact with at least 1 of the 2 scales of the last conjoined pair of the semicircles. Two pairs of scales lateral to the inferred interparietal are always relatively large and regular but not always symmetrical in shape or size. However, the posterolateral pair does not meet behind the interparietal. Instead, in all specimens 1 or 2 smaller scales, narrow and triangular, intervene posteriorly. The lateral crest scales are wrinkled and slope rather gently upward (more steeply in the male IND-R 3381) posteriorly toward the posterolateral bosses, which are separated by a notch, deep in the male, shallower in the females. Five to 7 scales can be counted from the interparietal to and including a notch scale.

Lateral head scales (Fig. 8)—As in *vanzolinii*, all the lateral head scales, other than the canthals, are smooth. The canthals may be weakly rugose but are never pustulate (as in some *van-*

zolinii). The loreals are in all specimens in only 1 row (usually 2 rows in *vanzolinii*, but 1 row on both sides in USNM 293683). The total number of loreals varies from 3 to 5 (7 to 9 in *vanzolinii*) (5 on both sides in the holotype of *inderenae*; 5 on the left side, 4 on the right in IND-R 3381; 4 on the left side, 3 on the right in IND-R 2999; 3 on both sides in IND-R 3744). There is one very large preocular in series with the loreals and in contact with the second canthal. There are 3 or 4 suboculars, 4 on both sides in the holotype of *inderenae*, 4 on the left side in IND-R 33821 (3–5 in *vanzolinii*), all broadly in contact with the supralabials. The postoculars are in 2 rows, 5 in the anterior row, 2 in the posterior row, the latter large scales that dorsally are in contact with the intertemporal ridge. The supralabials are 6 or 7 to below the center of the eye (7–10 in *vanzolinii*).

The intemporal ridge is distinctly shelf-like in *inderenae* but less regular than in *vanzolinii*, varying in shape and squamation.

The supratemporals are moderate, subequal, except on the posterolateral edge of the casque where they are smaller, narrower and vertically elongate.

The infratemporals tend to be smaller in the pigmented area of the infratemporal region and are distinctly smaller ventrally at the corner of the mouth. However, the distinction between the 2 zones of infratemporals—a smaller upper pigmented zone and a larger lower unpigmented zone—is decidedly blurred in *inderenae* as compared with the sharp distinction seen in *vanzolinii*.

Ventral head scales (Fig. 9)—The mental is wider than deep, almost completely divided (semidivided in *vanzolinii*), and indented posteromedially (not or only slightly indented in *vanzolinii*). The first sublabials vary as much or more in size as in *vanzolinii* and, again as in *vanzolinii*, may vary impressively on the 2 sides of 1 animal. In a unique instance (IND-R 2999), the left median gular (a gular in contact with the mental) is more than $\frac{1}{4}$ the size of the left first sublabial. In all other cases in both species, despite the striking variation in sublabial size the first sublabials (and most of the succeeding sublabials) are much more to very much more than $4 \times$ the size of any median gulars.

The number of sublabials in contact with the infralabials compared for *inderenae* and *vanzolinii*, shown in Table 1, barely overlaps.

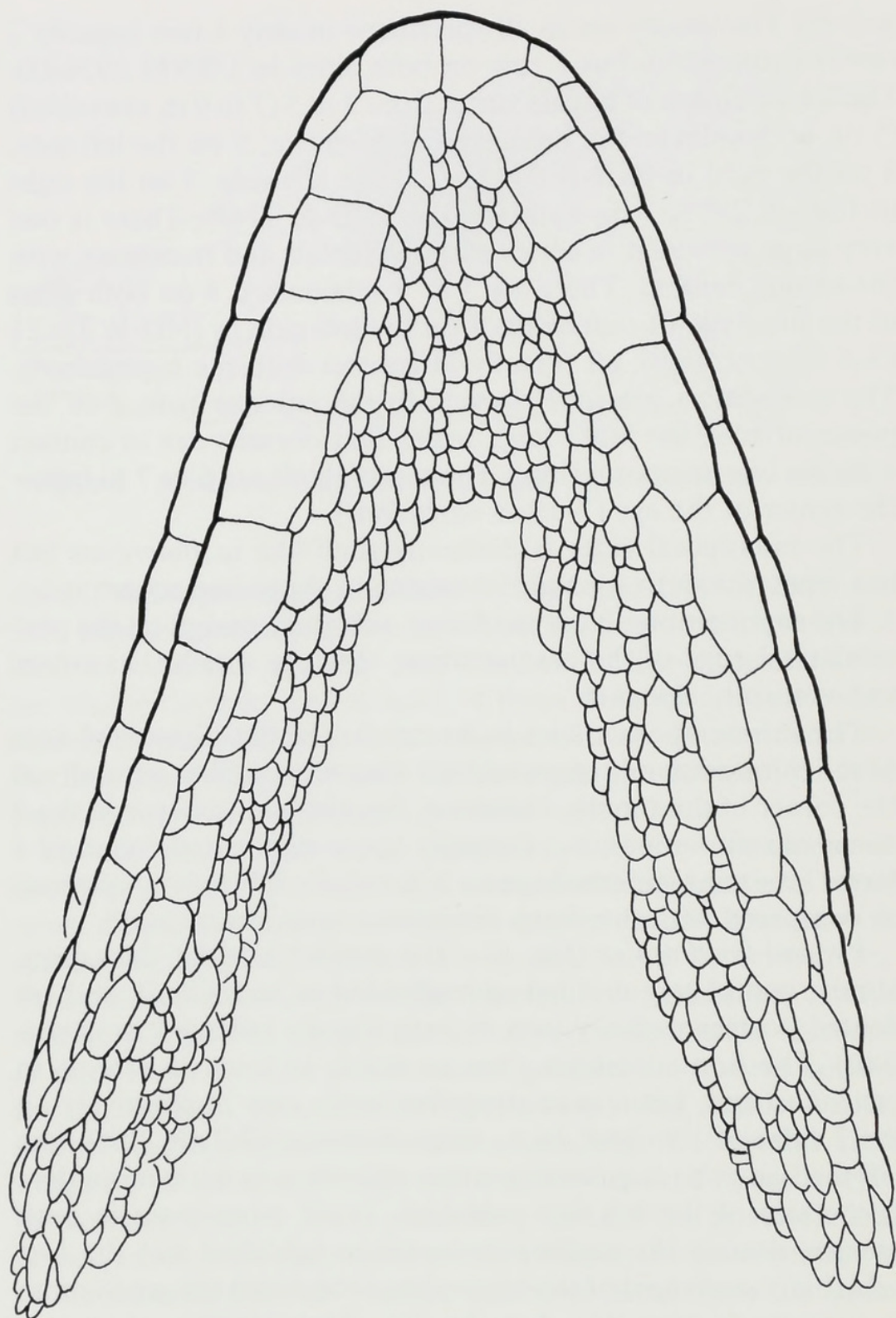


Figure 9. *P. inderenae*, paratype male, IND-R 3381, Ventral view of the head.

TABLE 1. SUBLABIALS IN CONTACT WITH INFRALABIALS.

Inderenae		Vanzolinii	
2999	8/6	2221	6/7
3381	8/7	175160	4/4
3744	7/8	2219	5/4
3213	7/9	309	5/5
		293683	5/6
		2220	5/6

The lateral gulars of *inderenae* are much like those of *vanzolinii*, tiny anteriorly between the sublabials and infralabials, larger to much larger behind the sublabials, from which, as in *vanzolinii*, they are distinguished by orientation. However, while in *vanzolinii* the lateral gulars may be large to quite large as they approach the insertion of the dewlap, the similar scales of *inderenae* are of 2 sizes only, moderate and small, well intermixed.

Dewlap (Fig. 10): As in *vanzolinii*, the dewlap of *inderenae* is moderate, not reaching much beyond the level of the insertion of the arms. There appears to be no appreciable sexual difference in this character, the dewlap of the single male of *inderenae* known, IND-R 3381, extending little or no farther back than that of the 3 females. The scales of the edge are smooth, imbricate, smaller than ventrals in both sexes. The lateral scales, while in rows, are, unlike *vanzolinii*, not separated by wrinkled naked skin but by numerous small scales, variable in size with larger scales next to the row scales, often making it difficult to determine whether the rows are single, double, or indeed multiple. Some rows are incomplete.

Trunk (Fig. 10): There is a single dorsal crest as in *vanzolinii* and, as in *vanzolinii*, it is interrupted at irregular intervals by 2 paravertebral scales that abut across the midline. As in *vanzolinii*, it is highest on the nape. There are 3 classes of flank scales as in *vanzolinii* and *heterodermus*. However, unlike the other two species, the class 1 scales are often more than twice as high and wide as the crest scales are high.

Ventrals in *inderenae* are smooth and imbricate, as in all phenacosaur, but in this species substantially larger than class 2 flank scales.

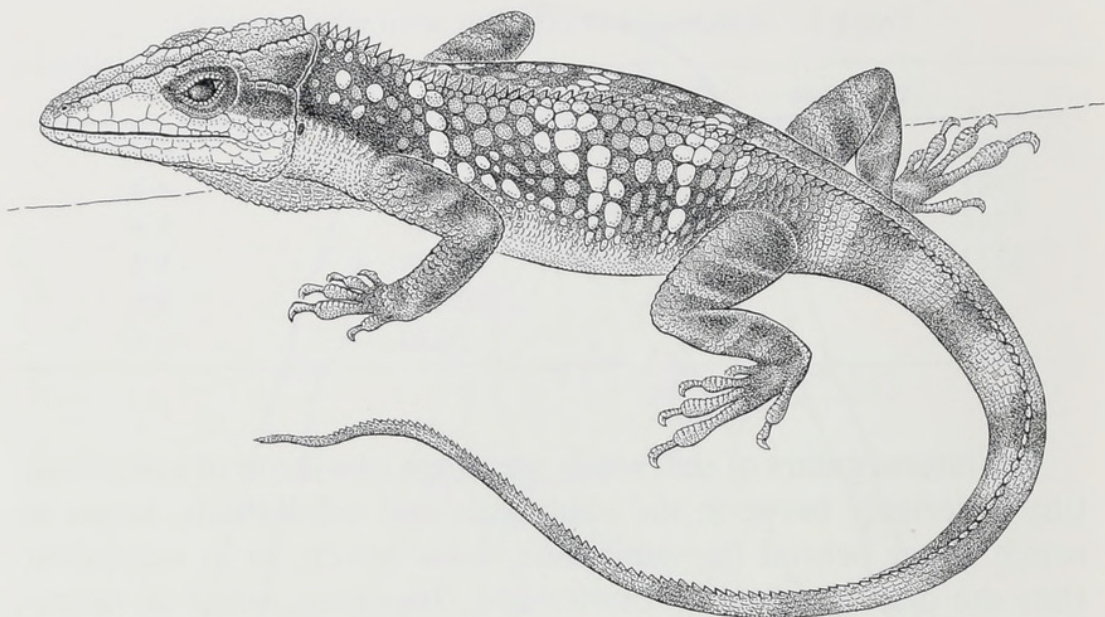


Figure 10. *P. inderenae*, paratype male, IND-R 3381, Lateral view of entire animal.

Limbs (Fig. 10): Anterior upper arm scales smooth, strongly imbricate to subimbricate, some larger than ventrals. Posterior upper arm scales granular, separated.

Anterior lower arm scales smooth, variable in size, smooth, subimbricate. Posterior lower arm scales granular subimbricate.

Manus with smooth scales, imbricate dorsally and on palm. Supradigitals smooth, all subdigitals lamellar.

Thigh scales anteriorly smooth, not as large as some upper arm scales, about as large as ventrals, imbricate proximally, subimbricate at knee, posteriorly smooth, swollen, smaller but variable in size, partly imbricate, partly separated. Tibial scales smooth, imbricate to subimbricate.

Pes with supradigitals smooth or very weakly carinate. All subdigitals lamellar. Lamellae under phalanges ii and iii of fourth toe 23–31.

Tail (Fig. 10): Strongly compressed with a dentate crest. Distal caudals keeled.

Color in life: There is an elaborate description of the color in life of the holotype. Two slides of color in life also exhibit color change. There is also the slide of the Houston Zoo animal taken by Harry Greene. The impression is that of a dorsally red brown animal that can change the vague dorsal banding to black.



Figure 11. Photo in life of the holotype of *Phenacosaurus vanzolinii*. Robert Bleiweiss, photographer.

DISCUSSION

Comparative Ecology and Behavior

Only Hellmich (1949) of those who have seen *Phenacosaurus* in the field has even the appearance of considering the genus as limited to páramo. In his case, his characterization of *Phenacosaurus* as a “Paramo-echse” may refer only to the species, named from a single specimen, found on the ground among the Espeletia in the Páramo de Sumapaz (a páramo that overlaps the borders of Cundinamarca, Meta, and Huila). He was, as appears from the text of his discussion, quite aware of the considerable range of elevations and habitats in which the genus has been found. Although, on the evidence of Hellmich’s single specimen, the genus is found in typical páramo, it is, in fact, known from a surprisingly broad range of elevations below those that support páramo under natural conditions.

All specimens of *P. vanzolinii*, for example, were collected between 1,950 and 2,630 m. These elevations, all on the eastern



Figure 12. Photo in life of the no locality *Phenacosaurus inderenae*. Harry Greene, photographer.

slope of the Andes, are in the forested zones corresponding to the humid premontane and montane formations of Holdridge (1967). The forests are typically tall and often bathed in clouds for much of the day. The trees, including many tree ferns, are heavily laden with epiphytes and mosses. Although human activities have destroyed much of the natural forest vegetation along the road between Santa Bárbara and La Bonita, large patches still exist along the steep slopes above the road and in the steeper stream gorges.

The scanty data from Bleiweiss's and Almendáriz's field notes are surprisingly consistent on a number of points. Bleiweiss collected the type on a sunny afternoon around 1:00 P.M., after the clouds had lifted: "The animal was moving slowly and deliberately down the stem of an unidentified (herbaceous) Gesneraceae overhanging the [upper] bank along a forested section of the road." Similarly, Ana Almendáriz reported that her specimens were collected along roads between 10:00 and 12:30 A.M. in humid but sunny weather.

These observations are congruent with those of a group led by Williams that collected *P. heterodermus* north of Bogota and with Miyata's (1983) more detailed account of the same species in the same area. It may well be characteristic of *P. vanzolinii* and its close relatives of the *heterodermus* species group within *Phenacosaurus* to be most active at midday and/or in relatively sunny weather.

Zoogeography

ROBERT BLEIWEISS

The discovery of a new species of *Phenacosaurus* is not surprising given that the remarkably diverse Andean herpetofauna remains poorly known (Lynch, 1986). We are nevertheless impressed by its discovery in the Santa Bárbara region. There is nothing about the physical relief or general climate of this section of the Andes to suggest that it might harbor endemic lizard species. Moreover, a large collection of forest frogs made by Bleiweiss and Matheus at the same time that they obtained the new *Phenacosaurus*, although containing new *Eleutherodactylus* and *Colostethus* species, appears no more distinctive than similar collections from other high-elevation sites in the northern Andes (W. R. Heyer, personal communication).

The discovery is, in fact, interesting primarily in showing how little we know about the Andean herpetofauna. The original impetus for Bleiweiss's exploration of the Santa Bárbara area was provided by his previous studies of geographic variation in the Andean hummingbird *Helianthus exortis*, a common resident of humid montane forests throughout Colombia and eastern Ecuador. The highly variable female plumage of *H. exortis* resolves into a striking dimorphism of male-like and female-like individuals in southern Colombia and northernmost Ecuador around Santa Bárbara (Bleiweiss, 1985a,b, 1991). Thus, avian patterns already suggest that the Santa Bárbara fauna was distinctive and had some zoogeographic connection with southern Colombia. In the absence of data from other vertebrate groups, birds provide the only available context for evaluating the new giant phenacosaur.

Indeed, several characteristics of Santa Bárbara's avifauna are noteworthy and parallel what is obtained in *Phenacosaurus*. A number of sources indicate that the avifauna is a mix of northern, southern, and even more typically western (Pacific slope) elements. Van Sneider's recent collection of birds from the Andes of extreme southern Colombia, near the border between Putumayo and Nariño (0°31'N, 0°49'N), and thus close to Santa Bárbara (0°23'N), documented northern range extensions for seven species (Fitzpatrick and Willard, 1982). All were previously known no farther north than the Napo drainage in Ecuador (about 0°20'S) (Meyer de Schauensee, 1971). Moreover, Bleiweiss and Matheus (in preparation) collected two White-faced Nunbirds (*Hapiloptila castanea*), the first east slope records for a species known previously only from scattered localities on the Pacific slope. Bleiweiss and Matheus's own observations also indicate that at least two rare birds endemic to the east slope were actually common around Santa Bárbara and La Alegría, the Collared Jay (*Cyanolyca viridicyana*) and Red-hooded Tanager (*Piranga rubriceps*), which appears true also for their populations just across the Colombian frontier in Nariño (Hilty and Brown, 1986). The phenacosaurus show the same ecological phenomena: The sympatric occurrence in the Santa Bárbara area (at La Bonita) of a northern (*heterodermus*—see earlier) and one from a southern (*orcesi*) species group of *Phenacosaurus* suggests a faunal mixing zone.

Admittedly, these patterns are inferred from few data and can only be regarded as provisional. They do, however, suggest that future collecting along this poorly known section of the Andes will prove fruitful. One distinctive feature of the Eastern Cordillera of the Andes south from Bogota to around Santa Bárbara may bear on the patterns described earlier. Nowhere along this stretch are there peaks higher than 3,000 m (Vuilleumier, 1970). If high-elevation habitats are too limited in extent to support viable populations, then animals found just below in the forested zones may enjoy ecological release (Terborgh and Weske, 1975). This could explain this unusual mix and greater abundances of species along this segment.

The significance of the new *Phenacosaurus* for our understanding of Andean speciation patterns must await further phylogenetic studies. Present evidence cannot distinguish whether the taxon is

a recently derived species or a relictual population of a once more widespread taxon. It is worth noting the Puffbird population of the Santa Bárbara region is morphologically distinguishable from populations on the Pacific slope (Bleiweiss and Matheus, unpublished observations). The possibility therefore remains that the lizard and the bird have differentiated in situ. This unprepossessing section of the Andes may turn out to be an ecological and evolutionary "hot spot."

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We are specially indebted to Ana Almendáriz and Alicia Arias for collecting five of the type series of *P. vanzolinii* and to Janira Regelado for providing two additional specimens. Without these specimens, the description of *Phenacosaurus vanzolinii* would have been extremely difficult or impossible. Without the drawings provided by Laszlo Meszoly, comprehension of the text would have been equally difficult or impossible. Brigitte Poulin assisted in proofreading the text. Publication costs were covered in part by a grant from the Wetmore-Colles Fund.

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