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THE GENUS *PHENACOSAURUS* (SAURIA: IGUANIDAE)

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> *The members of this order are the animals the Lord of the Hebrews did not create to grace his Eden; they are not among the products of the six days' labor. These are the sports, the offthrows, of the universe. . . . These are the weird children of the lust of the spheres.*
>
> *Charles Finney*

ABSTRACT: A complete revision of the Andean genus *Phenacosaurus,* using all available museum specimens, is presented. The genus is separated from *Anolis* on the bases of pelvic osteology and digital pad structure. Of four previously described species, two are retained: *heterodermus* (including *"richteri"* and *"paramoensis"*) and *nicefori.* A new species, *P. orcesi,* is described from Ecuador.

Among the strange and varied productions of the high Andes is a small assemblage of grotesque, big-headed, short-legged, prehensile-tailed lizards: the genus *Phenacosaurus.* Since Dunn's (1944) work on this genus in Colombia, it has not been re-examined as a whole. Through the efforts of E. E. Williams, Museum of Comparative Zoology (MCZ), it has now been possible to amass at one time and place the majority of specimens of all the species of this genus and thus attempt a complete review. Without the cooperation of the curators of many institutions, of course, this would not have been possible. I express here my gratitude to the curators of the following institutions: Instituto de La Salle, Bogota (ILS), British Museum (Natural History) (BMNH), Museum of Vertebrate Zoology (MVZ), University of Michigan Museum of Zoology (UMMZ), Stanford University Museum of Natural History (SU), Field Museum of Natural History (FMNH), Philadelphia Academy of Natural Sciences (PANS), Fundación La Salle

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de Ciencias Naturales, Caracas (FCN), United States National Museum (USNM), American Museum of Natural History (AMNH), Vienna Museum (WIEN), Munich Museum (MUN), Senckenberg Museum (SMF), Berlin Museum (ZMB), Museum National d'Histoire Naturelle de Paris (MHNP), and Universidad Nacional de Colombia (UNC).

Professor Gustavo Orces-V, Esquela Politécnica Nacional, Quito, Ecuador, has very kindly donated the first phenacosaur recorded from Ecuador, which I take great pleasure in designating as the type of a new species named in his honor (see below).

Dr. Fred Medem, Cartagena, Colombia, has made available an excellent collection of Colombian phenacosaurs, including the type and paratypes of *P. richteri* Dunn. Those specimens actually collected by him are fresh alcoholics and combine color retention with very accurate data — including elevations. Dr. George Gorman, Museum of Vertebrate Zoology, Berkeley, has recently collected series in the Bogota area.

The Orsono-Mesas (1946) have provided an informative treatment of several aspects of phenacosaur ecology and behavior.

Color photographs of living phenacosaurs taken around Bogota have been provided by Fred Medem and Jose Muñoz, Hans Zenke, and Victor Hutchison.

In addition to the problems posed by the species-group level taxonomy of *Phenacosaurus,* it seems necessary to re-examine the status and validity of the genus. *Anolis heterodermus* Duméril (1851) was included by Boulenger (1885) in his concept of *Xiphocercus* Fitzinger (1843). *"Xiphocercus"* was then separated from *Anolis* (and *Chamaeleolis*) on the character combination of tricuspid lateral teeth plus a prehensile tail, and from *"Norops"* on the character of a raised terminal phalanx. Barbour (1920) separated *heterodermus* from the West Indian form (*"Xiphocercus" [= Anolis] valencienni*) on the basis of body squamation, dorsonuchal crest, elevated rim of head plates (= circumoccipital swelling or casque of Dunn, 1944), digital dilations, and tail structure. *"Xiphocercus" heterodermus* thus became the type of the new genus *Phenacosaurus* Barbour (1920). However, Williams (1962) has shown *"Xiphocercus"* to be a synonym of *Anolis;* the validity of *Phenacosaurus* may be questioned also. Certainly neither body squamation nor dorsonuchal crest is useful in separating *Phenacosaurus* from *Anolis.* Caudal vertebrae that lack autotomy septa are found in such distantly related *Anolis* as *darlingtoni* and *latifrons;* though no *Anolis* has yet been demonstrated

definitively to use its tail in a prehensile manner, it seems reasonable to infer from structure that some, like *darlingtoni,* do.

The "circumoccipital swellings," or "casque," referred to is indeed a striking feature of adult male *heterodermus.* Actually posterolaterally directed flanges of the parietals, this "casque" is but weakly developed in juveniles and females of *heterodermus,* or in most specimens of *P. nicefori,* regardless of sex, and is reduced in the new form from Ecuador. In addition, some species of *Anolis* (e.g. *richardi* of the Lesser Antilles) develop similar parietal flanges; there is, admittedly, still a definite degree of difference between the condition in some *Phenacosaurus* and that shown even by adult male *Anolis richardi,* but one would hesitate to accept a genus wholly based on such a degree of difference.

The digital dilations of *Phenacosaurus* are distinctive. The toes are comparatively shorter than the toes of *Anolis* of similar size; the digital pad is expanded not only beneath the second and third phalanges of the fourth toe, but beneath the first phalanx as well; proximal continuation of the expanded digital pad is the rule with all the toes, and produces a rather gecko-like appearance of the foot. Although this condition is not matched by any species of *Anolis,* the variation in structure and dilation of the digital pad in *Anolis* is sufficiently great (see Williams, 1963) so that any degree of difference shown by the phenacosaur condition is surely of diminished importance.

After examination of skeletal material of more than 70 species of *Anolis* in the MCZ, I have discovered that not only is the structure of the ilium remarkably constant in that genus, but that it is strikingly different from the condition seen in all forms of *Phenacosaurus.* I therefore propose a redefinition of the genus *Phenacosaurus* and provide the following definition of *Anolis* for comparative purposes:

Anolis is a genus of iguanid lizards without femoral pores; subdigital lamellae bear cuticular hairs; pre- and post-zygopopheses of trunk vertebrae not expanded to form great lateral flanges; angular absent; lateral teeth cusped; ilial shaft subcylindrical, dorsal border forming an obtuse angle with the acute or nodular, elongate, anterior iliac process (see Figure 6).

PHENACOSAURUS Barbour

Anolis (part), Duméril, 1851, Cat. Meth. Rept., p. 59.
Xiphocercus (part), Boulenger, 1885, Cat. Lizards Brit. Mus. II, p. 10.
Phenacosaurus Barbour, 1920, Proc. New England Zool. Club 7, p. 62.

Type species. Anolis heterodermus Duméril, 1851.

Definition. Iguanid lizards without femoral pores; subdigital lamellae bear cuticular hairs; pre- and post-zygopopheses of trunk vertebrae not expanded to form great lateral flanges; angular absent; lateral teeth cusped; ilial shaft compressed and bladelike, inclining smoothly into a blunt, subrectangular anterior iliac process (see Fig. 6).

The condition of the ilium can be readily checked without undue damage to the specimen by merely lifting the skin above one hind limb and separating the muscle attachments from the bone. This has been done for all of *P. nicefori* and the new species, as well as many *P. heterodermus.* The only dry skeletons of *Phenacosaurus* examined are ILS 55d and MCZ 17111, both *heterodermus.*

Polychrus have femoral pores present in males and lack an anterior iliac process.

Anisolepis and *Aptycholaemus* (nearly or quite synonymous, *fide* Etheridge, *pers. comm.*) have an ilium basically similar to that of *Phenacosaurus,* but possess a "fairly large" angular, *fide* Etheridge (*in litt.*). *Anolis* and *Phenacosaurus* lack an angular bone.

The remaining anoline genera (*sensu* Etheridge, 1959) have an ilium like that of *Anolis.* In addition, *Tropidodactylus* is unique in lacking cuticular hairs on the lamellae; *Chamaeleolis* has simple, peglike lateral teeth and a small angular; *Chamaelinorops* has trunk vertebrae bizarrely modified by expansion and amalgamation of the pre- and postzygopophases to form great lateral flanges.

The usefulness of separating *Phenacosaurus* from *Anolis* may be questioned, and Dr. R. A. Etheridge (*in litt.*) has questioned the separation in principle. This, certainly, is the place to make a case for the genus, especially as I regard it as valid. Etheridge notes that phenacosaurs are an early offshoot of "alpha *Anolis* stock in South America that have developed some peculiar behavioral specializations and assorted anatomical specializations." In that, we concur; what alarms Etheridge, however, is that "*Phenacosaurus heterodermus* (for example) is much more closely related to *Anolis jacare* than *Anolis jacare* is to *Anolis nebulosus* (for example)." That is also true, but it in no way invalidates the genus *Phenacosaurus.* The difficulty, and the principle at stake, is the old bugbear of relationship. It is perfectly true that birds are, in a very real sense, more closely related to crocodilians than crocodilians are to lizards, and far more closely than crocodilians are to therapsids (for example). Yet, birds are not included within the Reptilia; they belong to a distinct class of their own. Simpson

(1961, pp. 129-132 and 140-145) has given detailed consideration to this problem. Its solution lies in defining taxa in higher categories in a way that best expresses their evolutionary position and adaptive similarities. In the present case, *Anolis jacare* and *A. nebulosus* are members of a presumably monophyletic group that have so much in common, from an adaptive and evolutionary point of view, that they are best regarded as congeneric despite obvious differences. Also, a plethora of other *Anolis* species spans the gap between them, and thus helps to unite them. The species of *Phenacosaurus,* on the other hand, are sharply distinct, in important adaptations, from any *Anolis;* the gap is not spanned by living intermediates. Of course, intermediates must once have lived, and this leads us to recognize a compelling truth: Any taxon at the level of a higher category (genus or above) must — either now or in the past — contain some member more closely related to members of some other taxon than that member may be to some members of its own taxon. I draw a line by defining the genus *Anolis:* the species of *Phenacosaurus* are outside that line.

It is only my opinion that *Phenacosaurus* — an apparently natural group of species — qualifies for the rank of genus; no definition of the category genus exists to tell me whether *Phenacosaurus* is one or not. I rest my case, therefore, on the evolutionary and adaptive significance of the characters that separate the groups: the structure of the ilium and the digital dilations. These seem to me to be quite as important as the distinctions, noted above, which separate the other anoline genera.

PHENACOSAURUS HETERODERMUS (*Duméril*)

Anolis heterodermus Duméril, 1851, Cat. Meth. Rept., p. 59. Syntypes: MHNP 1664, A1664, B1664, 6798, A6798.

Xiphocercus heterodermus, — Boulenger, 1885, Cat. Lizards Brit. Mus. II, p. 10.

Phenacosaurus heterodermus, — Barbour, 1920, Proc. New England Zool. Club 7, 61-63.

Phenacosaurus richteri Dunn, 1944, Caldasia 3, p. 60. Type: MCZ 69120.

Phenacosaurus paramoensis Hellmich, 1949, Dtsch. Aquar.-u. Terrar.-Ztschr. 2, p. 91. Type: MUN 118/37.

Diagnosis. A *Phenacosaurus* with large dorsal scales: 8-19 dorsals contained in the standard distance[1] (not counting interstitial

[1] Defined as the distance from the center of the eye to the tip of the snout.

granules); head plates large: interparietal sometimes as long as distance across head between orbits, but often shorter; subdigital lamellae under second and third phalanges of fourth toe 18-24.

Lectotype. MHNP 1664, an adult male with 14 dorsals in the standard distance and 19 subdigital lamellae.

Type locality. "Nouvelle Grenade" (= Colombia), here restricted to the vicinity of Bogotá, Colombia.

Discussion. The extreme variability of this species has led to taxonomic difficulties and confusions, and to the naming, therefore, of two additional species — *richteri* Dunn (1944) and *paramoensis* Hellmich (1949).

Dunn, in his 1944 review, used the following characters to separate *"richteri"* and *heterodermus:*

Dorsal crest squamation. Dunn separated *"richteri"* (and *nicefori*) from *heterodermus* on the basis of single, rather than double, dorsal crest scale row. In attempting to make sense out of the remarkable variation I found in this character, I assigned numbers, from one to ten, to the various sorts of crest scale arrangements noted. In Table 1 each specimen is graded according to the sort of crest scale variant it possesses. Where specimens showed more than one sort of arrangement, the two or more grades are indicated. The following ten grades of variation were noted:

1. Undifferentiated middorsal scales; *i.e.,* no dorsal crest at all, except sometimes a median series of single, enlarged scales on the nape or tail.
2. Some enlarged scales along the middorsum, but not arranged in a particular pattern.
3. Enlarged, tectiform to carinate scales along the middorsum, but separated from each other by undifferentiated smaller scales.
4. Single row of enlarged, tectiform to carinate scales in contact with each other along the middorsum.
5. Single row of spike-like scales in contact with each other along the middorsum.
6. Staggered series of tectiform to carinate scales, every other one separated by undifferentiated smaller dorsals, but each usually contacting the scale immediately adjacent at the dorsal midline.
7. Alternating series of tectiform to carinate scales, continuously in contact with each other.
8. Double row of spike-like scales on anterior body combined with alternating tectiform to carinate scales posteriorly.
9. Alternating series of spike-like scales.
10. Double row of spike-like scales.

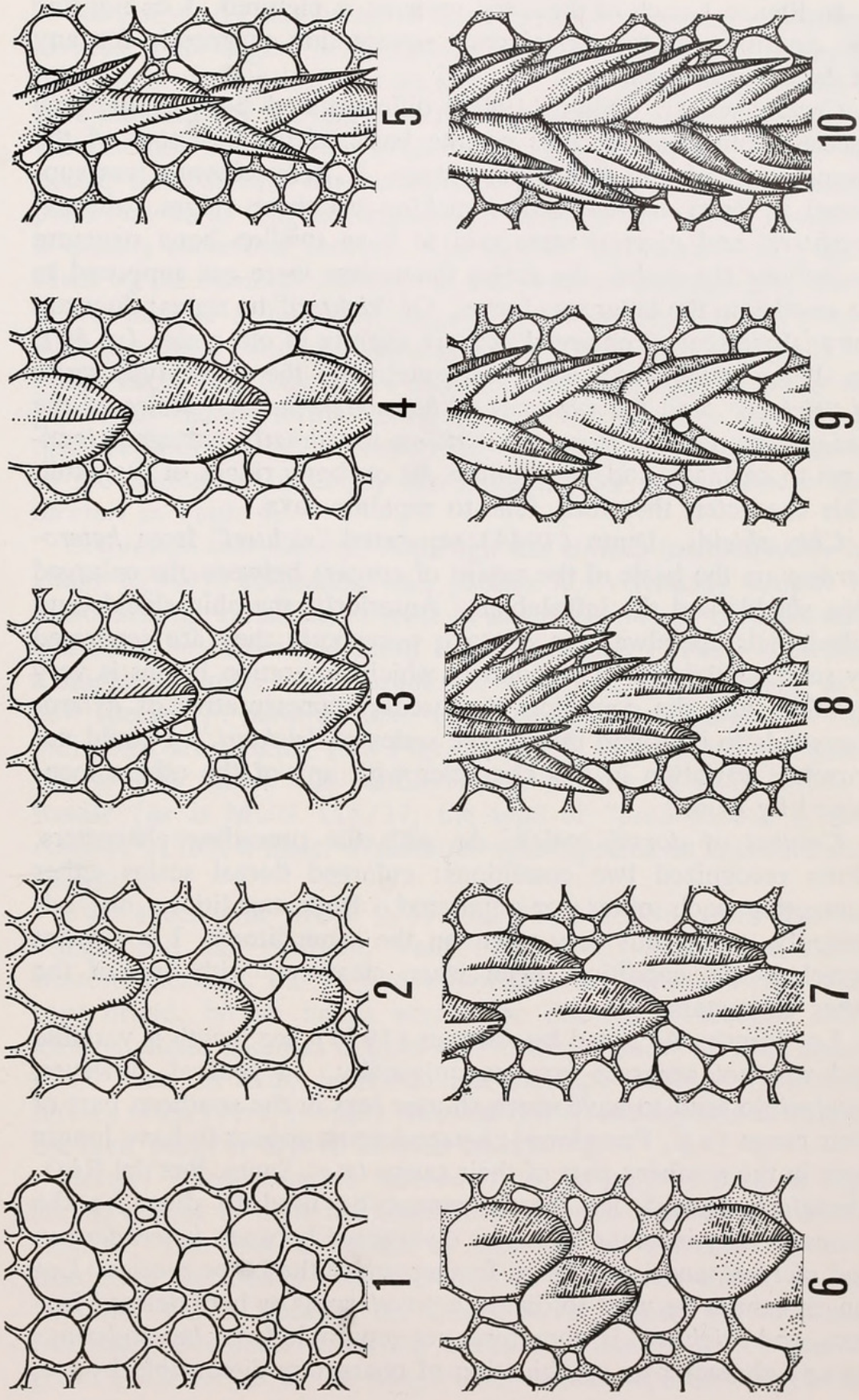

Figure 1. Variations in middorsal crest squamation in *Phenacosaurus*. See text for explanation.

In Figure 1 each of these ten variants is pictured. I do not find the condition of the dorsal crest squamation diagnostic for any of the named forms.

Cranial ridges. Dunn (1944) differentiated both of his new species from *heterodermus* on the basis of the structure of the circumoccipital and postocular ridges. *P. heterodermus* was supposed to have swollen scales making up these ridges, whereas *"richteri"* and *nicefori* were said to have swollen bone structure underlying the scales; the scales themselves were not supposed to be swollen in the latter two forms. Of *"richteri"* he states: "nor are they [these scales] enlarged" except slightly in old males (p. 60). In all the specimens I have seen, including the entire type series of *"richteri"* and the syntypes of *heterodermus,* the scales of the circumoccipital and postocular ridges are greatly enlarged, tectiform to carinate, and, in addition, lie on bony ridges of the skull. This character, therefore, fails to separate taxa.

Chin shields. Dunn (1944) separated *"richteri"* from *heterodermus* on the basis of the extent of contact between the enlarged chin shields and the infralabials. Anteriorly, the chin shields and infralabials are always in contact, posteriorly they are separated by small sublabials. The point at which separation begins is very variable, and the condition supposedly representative of *heterodermus* is to be found in the type series of *"richteri."* I could not correlate variation in this character with any of the others mentioned by Dunn.

Contact of dorsal scales. As with the preceding characters, Dunn recognized two conditions: enlarged dorsal scales either contacting each other, or separated. Both conditions do, admittedly, occur, but very often on the same lizard. I could not correlate this condition, even when clear-cut, with any of the other characters.

Leg length. As noted by Aleman (1953), leg length is variable and will not separate taxa unequivocally. In general, however, *nicefori* do tend to have much shorter legs in the southern part of their range (*e.g.,* Pamplona); *heterodermus* appear to have longer legs; in the northern part of their range (*e.g.,* Saota, Paz del Río). Therefore, though leg length cannot be used to diagnose the forms, it may indicate character divergence between *heterodermus* and *nicefori,* and is discussed further under the latter species. Leg length cannot be used to divide *heterodermus* as here defined into taxa, and *"richteri"* is, therefore, not separable from *heterodermus* on any character or combination of characters discernible by me.

Scale size. As may be noted from the above diagnosis of *heterodermus,* I do regard scale size as useful in separating forms. I have used two indices to scale size: the size of the head plates is here indicated by the length of the interparietal plate compared to the distance between the orbits across the top of the head. As noted, *heterodermus* has rather large head plates; the interparietal plate may be as long as the distance between the orbits, though it is usually somewhat shorter. The size of the dorsal scales, indicated by the number contained in the standard distance just lateral to the midline at midbody, separates *nicefori* and *heterodermus.* The new form from Ecuador combines scale size measured by both indices in a way that is radically different from either of the previously named forms. Both *nicefori* and the new species are discussed fully below. Dorsals in the standard distance just lateral to the midline at midbody are tabulated for *heterodermus* and *nicefori* in Table 1.

Coloration and pattern. Although not utilized taxonomically by Dunn (1944), coloration and pattern are obviously subject to some striking variation, at least in *heterodermus* as here defined, and must be considered more fully. Hellmich (1949) described a single specimen from Paramo de Sumapaz, 3750 meters, as a new species, *P. paramoensis.* The coloration and pattern of this individual are striking (see Figs. 2 and 3). Two other specimens I have seen match this condition: the smaller of ZMB 4256, a female (as is MUN 118/37, the type of *"paramoensis"*), and AMNH 91752, a male. Numerous other specimens approach this condition.

Two specimens, MUN 9/49 and MVZ 68686, from Tambo, Cauca, and San Antonio, Valle, respectively (the most southwestern localities for *P. heterodermus*), are pale ash-grey with very broad, brown bands across the dorsum. Excellent color transparencies taken at Bogotá by Hutchison show that the colors noted occur in living individuals at the type locality. Hutchison further notes (*pers. comm.*) that individuals are capable of changing their patterns as well as their colors.

Range. Phenacosaurus heterodermus, as may be seen in Figure 4, occurs in both the Cordillera Oriental and the Cordillera Central. The species occurs at least in the extreme southern Cordillera Occidental near the head of the Cauca River, at San Antonio, Valle. Because the Cauca River, which separates the Cordillera Occidental from the Cordillera Central, is nowhere as great a barrier as is the Magdelena, which separates the latter

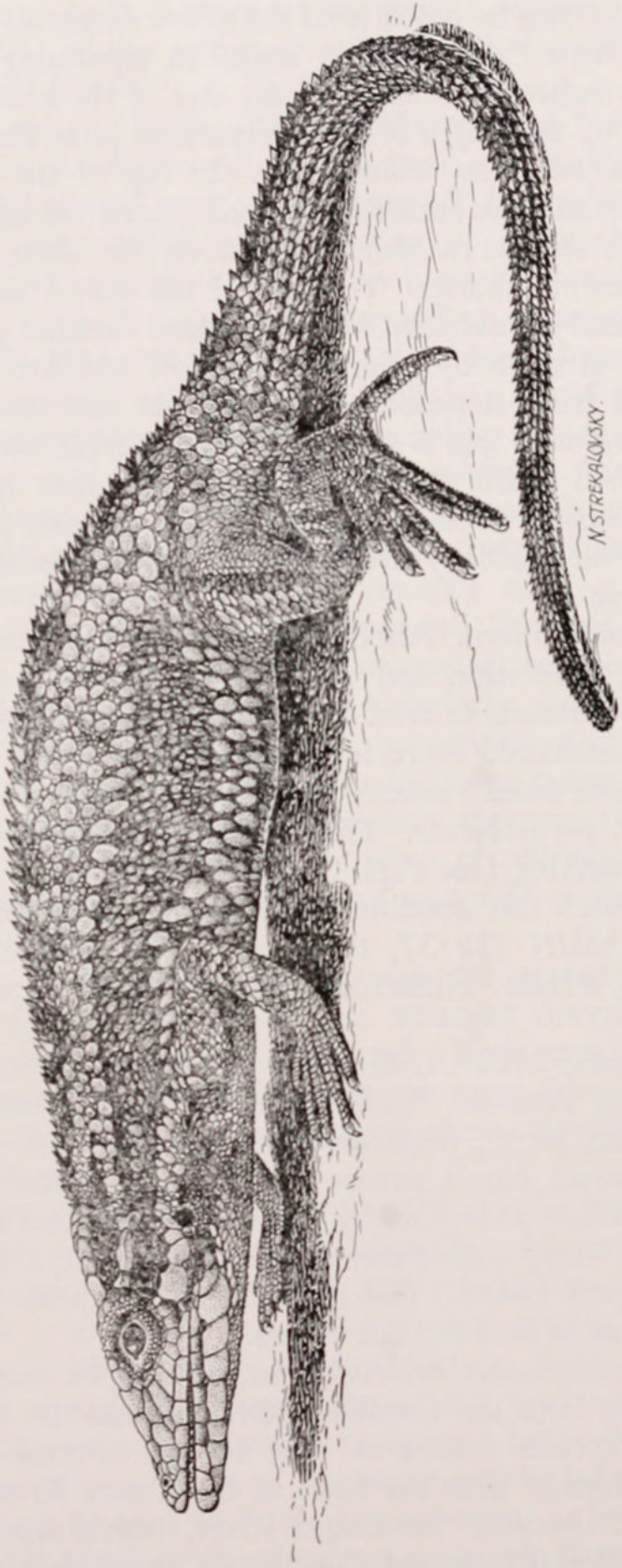

Figure 2. *Phenacosaurus heterodermus*. Specimen MUN 118/37, the type of "*paramoensis*" Hellmich.

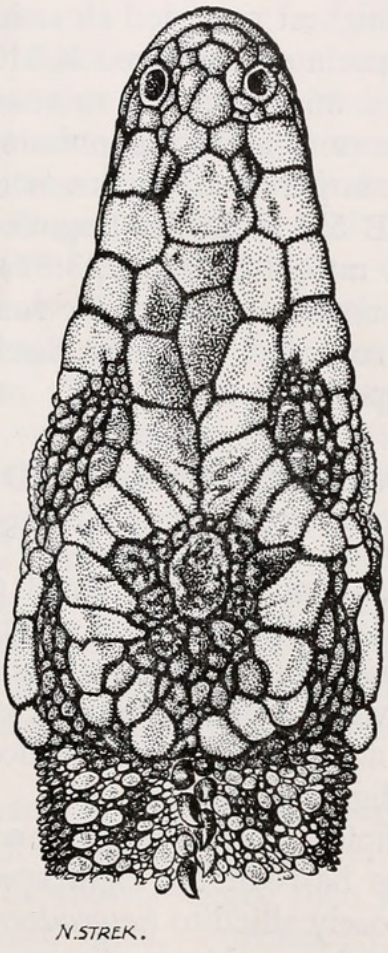

Figure 3. *Phenacosaurus heterodermus,* top of head. Specimen MUN 118/37, the top of *"paramoensis"* Hellmich.

from the Cordillera Oriental, and because all three Cordilleras merge in southern Colombia (*e.g.*, vicinity of Tambo, Cauca), I expect the total distribution of the species, at least in the western range, to be greater than is presently known. Dunn (1944) gives the altitudinal range as from 1800 m to 3500 m. Hellmich (1949) cites the elevation for *"paramoensis"* (= *heterodermus*) as 3750 m. This is the highest recorded elevation for the species.

Size. The largest specimen measured is MCZ 78531, from Paz del Río, Boyaca. It is 86 mm snout to vent. Remarkably, it is a female. In the more southern populations of *heterodermus* males seem to average larger than females, and reach 83 mm snout to vent (male of ZMB 5211) in the Bogotá area; females in the Bogotá area reach 80 mm (MHNP 1923.55). I therefore expect some males from the northern part of the range to be larger than any specimen here recorded. Size is discussed comparatively under the following species:

PHENACOSAURUS NICEFORI Dunn

Phenacosaurus nicefori Dunn, 1944. Caldasia 3, p. 59. Type: ILS 64.

Diagnosis. A *Phenacosaurus* with small dorsal scales: 21-34 contained in the standard distance (not counting interstitial granules); head plates small, interparietal much shorter than the distance across head between orbits; subdigital lamellae 16-20.

Type. ILS 64, an adult female with 24 dorsals in the standard distance and 17 subdigital lamellae.

Type locality. Pamplona, Norte de Santander, Colombia.

Discussion. On the basis of the eight specimens I have seen, this species is quite closely allied to *heterodermus.* The only definitive difference I have been able to discern is dorsal scale size. With respect to this character, it must be noted that for both *nicefori* and *heterodermus* the range of variation within the species, respectively, is greater by far than the gap which separates them. I have indicated in my discussion of *heterodermus* that I believe there is some evidence for character divergence between these two forms as they approach the area of potential sympatry. Though *heterodermus* and *nicefori* have not yet been demonstrated to be sym- or parapatric at any point (see Fig. 4), what evidence for character divergence we do have should be considered in full. Specimens of both forms have been arranged in Table 1 in a north-south sequence from Cerro Tetari (northernmost locality for *nicefori,* and the genus) to Tambo (the southernmost locality for

heterodermus). Thereafter, in Table 1, the sequence is northward through the more western *heterodermus* localities in the Cordilleras Occidental and Central. Characteristics of dorsal scale size, dorsal crest type, and subdigital lamellae are tabulated; these, with the exception of dorsal crest type (which I do not regard as indicative of either taxon or character displacement), are included in the discussion below:

Dorsal scale size. Although the numbers of specimens in the samples do not permit any meaningful statistical analysis, *nicefori* and *heterodermus* do seem to become more different as they approach one another. The smallest dorsals in *heterodermus* (19 in the standard distance) are in FMNH 69673, from San Antonio, Huila, one of the southernmost examples. Similarly, the largest dorsals in *nicefori* (only 21 in the standard distance) are in FCN 664, from Cerro Tetari, Venezuela — the northernmost representative of that form. The differences between the more nearly adjacent populations — Pamplona (with one specimen of *nicefori* with 22) and Saota (*heterodermus* with 14) — are not spectacular, but with more evidence might prove meaningful.

Subdigital lamellae. In this case the situation is not indicative; assuredly, the Cerro Tetari *nicefori* has the highest number of lamellae found in that species, but the highest counts in *heterodermus* come from the southern part of that range. The more nearly adjacent populations hardly differ with respect to this character.

Leg length. As mentioned previously, leg length does seem to provide an example of character divergence. However, females of both forms seem to be shorter-legged than males, and I can find little difference between them. Fortunately, the three southernmost *heterodermus* localities (San Antonio, Huila; Tambo; and San Antonio, Valle) are represented by males. In all of these the appressed hind limb barely reaches the axilla. In most males from around Bogotá, the one male from Paz del Río, and in the Saota specimen, the appressed hind limb extends beyond the axilla. In Pamplona males of *nicefori* (2) the hind limb is, as in females, shorter than the distance to the axilla, whereas in the Cerro Tetari male, as noted by Aleman (1953), the hind limb is quite as long as this distance. Even in a case like this, however, where the evidence seems clear cut on the face of it, the number of individuals involved is much too small for any sort of surety.

Size. Here again there is but little evidence. The largest *heterodermus* examined, as noted, was from a northern locality, one of

the two closest to a *nicefori* population. Similarly, the largest *nicefori,* FCN 664, is 86 mm snout to vent, and from the northernmost locality, farthest removed from the known range of *heterodermus.* Because all phenacosaurs begin life small, and because I have such a paucity of specimens and information about living animals, I cannot claim that this is necessarily meaningful.

Coloration and pattern. Most of the specimens of *nicefori* are formalin specimens, and show nothing in the way of coloration or pattern. FCN 664, however, is well preserved and appears to have been rather uniform green with a white stripe from the supralabials to the shoulder, as in many *heterodermus.* There is nothing about any of the other specimens of *nicefori* that could contradict the assumption that this is how they all look.

In the foregoing discussion I have tacitly assumed that FCN 664 actually represents a *nicefori.* If it does, it is by far the largest representative seen; those from around Pamplona are all less than 65 mm snout to vent. Also, it has the largest dorsals, the highest number of subdigital lamellae, and the longest legs of any *nicefori* seen. I have suggested that these differences may be attributable to character divergence in two species. On the basis of present information I see no alternative; if FCN 664 is not a *nicefori,* then a great deal of additional material will be required to demonstrate its true relationships. Certainly *heterodermus* and *nicefori,* whether they are distinct species or geographic representatives of the same species, are closely related.

Extreme with respect to major characters, the relationships of the new form from Ecuador are in no way so clear. I describe it as:

Phenacosaurus orcesi sp. nov.

Type. MCZ 38937, collected iv. 1957 by Jorge Olalla.

Type locality. Mt. Sumaco, Napo Pastaza Province, Ecuador.

Paratype. USNM 16533, collected by James Peters between L'Alegría and La Bonita, Ecuador.

Diagnosis. A *Phenacosaurus* with very small dorsals, 38-48 contained in the standard distance (no interstitial granules present); head plates very large, interparietal much longer than the distance across the head between the orbits; subdigital lamellae under second and third phalanges of fourth toe 16-18.

Description of the type. MCZ 38937 is a female measuring 58 mm snout to vent, with a 61 mm tail. Both the foot structure and the ilium (dissected on left side) are typically phenacosauran.

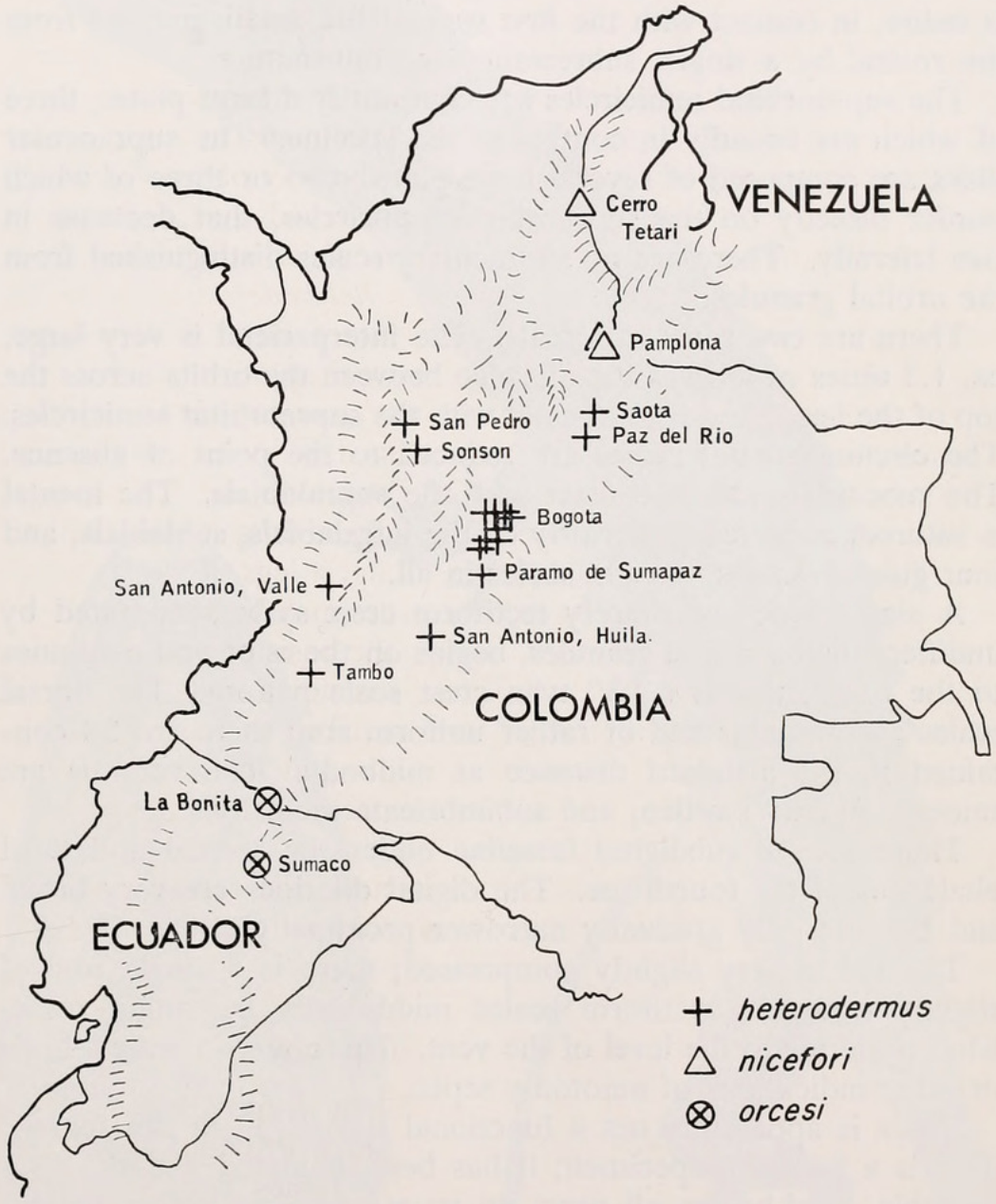

Figure 4. Localities for three species of *Phenacosaurus*. Names are not cited here for localities in the immediate vicinity of Bogotá but are tabulated in north-south order in Table 1.

There are three large plates across the snout at the level of the second canthals. Two scales, the right one of which appears to be two smaller scales anastamosed, border the rostral. The nasal is entire, in contact with the first supralabial, and separated from the rostral by a single, subrectangular prenasal.

The supraorbital semicircles are composed of large plates, three of which are broadly in contact at the midline. The supraocular disks are composed of several large plates, two or three of which border directly on the supraorbital semicircles, that decrease in size laterally. There are no supraciliary scales distinguished from the orbital granules.

There are two rows of loreals. The interparietal is very large, ca. 1.3 times as long as the distance between the orbits across the top of the head, and is in contact with the supraorbital semicircles. The circumoccipital ridges are reduced to the point of absence. The suboculars are in contact with the supralabials. The mental is sutured, bordered posteriorly by the infralabials, sublabials, and four gular granules — eight scales in all.

A single series of sharply tectiform crest scales, separated by undifferentiated dorsal granules, begins on the nape and continues to the rump; this is a "3" type crest scale pattern. The dorsal scales are granular and of rather uniform size; there are 38 contained in the standard distance at midbody. The ventrals are smooth, slightly swollen, and subimbricate medially.

There are 18 subdigital lamellae under the second and third phalanges of the fourth toe. The digital dilations are very broad and become only gradually narrower proximally.

The tail is very slightly compressed; there is a single row of slightly enlarged, tectiform scales middorsally beginning somewhat posterior to the level of the vent. There are no scale whorls or other indications of autotomy septa.

There is apparently not a functional throat fan in this female. This is a formalin specimen; it has been rendered a dark, disagreeable, mud-brown all over; no trace of coloration or pattern remains.

The type is illustrated in Figure 5.

The paratype. The only other specimen of *P. orcesi* currently available is a male 60 mm, snout to vent, with a 67 mm tail. The digital pads of both fourth toes on the hind feet taper more abruptly proximally than is usual in *Phenacosaurus,* but are broader under the first phalanx than in *Anolis* of similar size. The ilium (dissected on the left) is typical of the genus: blade-like, with a blunt, obtuse anterior prominence.

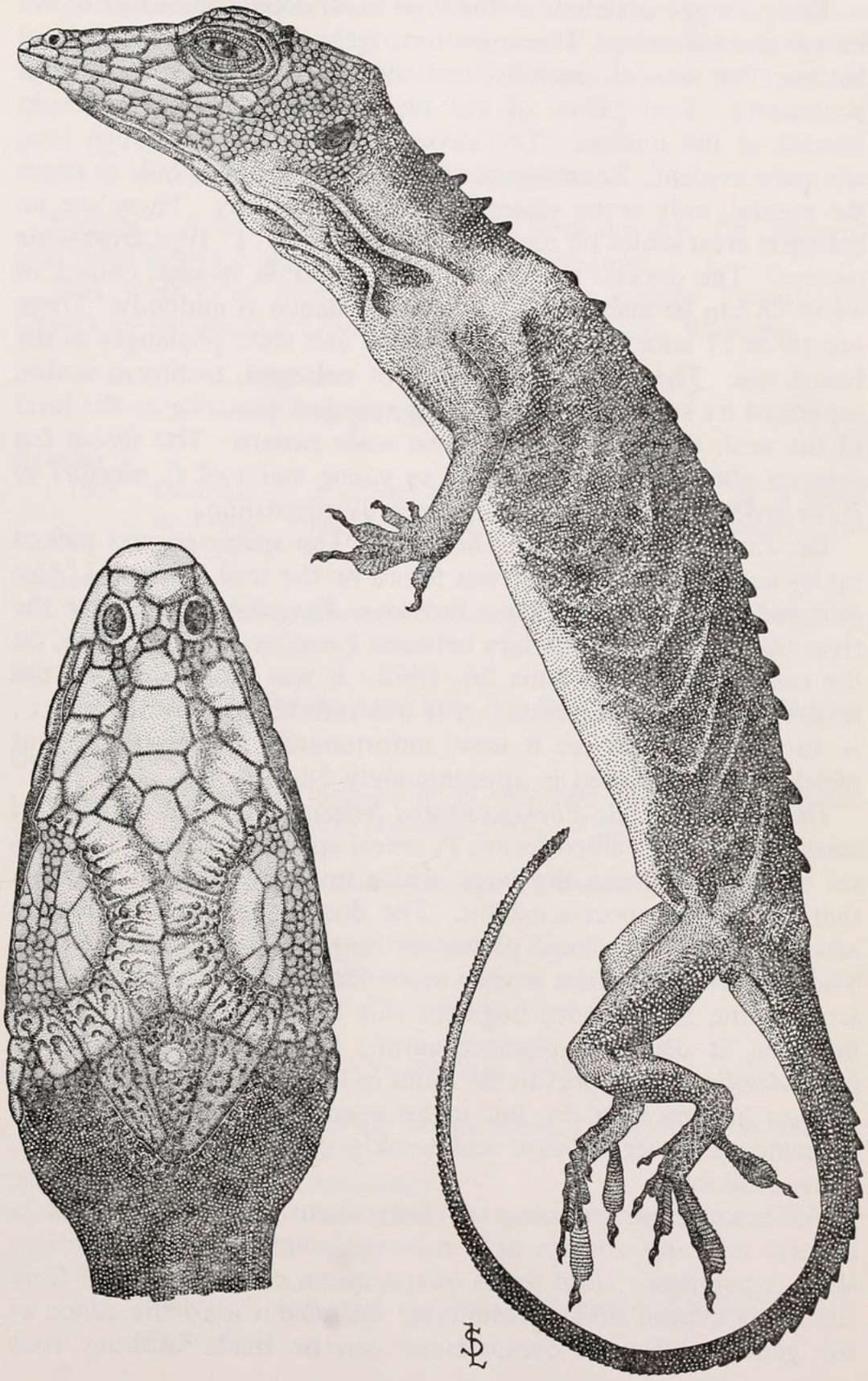

Figure 5. *Phenacosaurus orcesi* sp. nov., type, MCZ 38937, from Mt. Sumaco, Ecuador.

The paratype is similar to the type in all details described above except the following: There are four large plates across the head between the second canthals, and three scales border the rostral posteriorly. Two plates of the supraorbital semi-circles are in contact at the midline. The circumoccipital ridges, though low, are quite evident. Because one row of gular granules fails to reach the mental, only seven scales border it posteriorly. There are no enlarged crest scales on nape or back; this is a "1" type crest scale pattern. The dorsals are granular but variable in size; counts of 46 to 48 can be made in the standard distance at midbody. There are 16 or 17 lamellae under the second and third phalanges of the fourth toe. The tail bears a series of enlarged, tectiform scales, separated by smaller granules, beginning just posterior to the level of the vent; this is a "3" type crest scale pattern. The throat fan appears about as well developed as young males of *P. nicefori* or *P. heterodermus:* not apparently greatly extensible.

Dr. James Peters reports (*in litt.*): "The specimen was picked up by me personally. . . . It was found on the trail between L'Alegría and La Bonita, in Napo Province, Ecuador, high above the river that forms the boundary between Ecuador and Colombia, on the eastern slopes, on June 26, 1962. It was found dead on the trail, in a horse's hoofprint. . . . It was rather badly beaten up . . . — in the state you see it now, unfortunately. The elevation at which it was collected is approximately 5800 feet."

Discussion. While *Phenacosaurus heterodermus* and *P. nicefori* seem quite closely allied forms, *P. orcesi* appears remote. The dorsal squamation lacks the large scales interspersed with granules that both other species exhibit. The dorsals are smaller than in *nicefori,* though the head plates are larger than in *heterodermus.* The general appearance is very much like some *Anolis* (e.g., *solitarius*); the small scales augment this effect. The pelvic girdle, however, is distinctly phenacosauran; *P. orcesi,* in fact, differs from *Anolis* with respect to the ilium in the same ways that *heterodermus* and *nicefori* do, but to an even greater extent; the ilial prominence is very obtuse and weakly developed in both specimens available.

All considered, we know so little about the phenacosaurs in general that any attempt at a reasonable assessment of relationships is pointless. Until series of specimens can be collected from the many crucial areas presumably included within the range of the genus, and until comparisons can be made utilizing such

characteristics as coloration in life and behavior in the field — features demonstrably of great importance in the systematics of anoline lizards — our knowledge of *Phenacosaurus* will remain reprehensibly elementary.

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Figures 2 and 3 were prepared by N. Strekalovsky. Dr. Richard Etheridge has provided data on anoline osteology.

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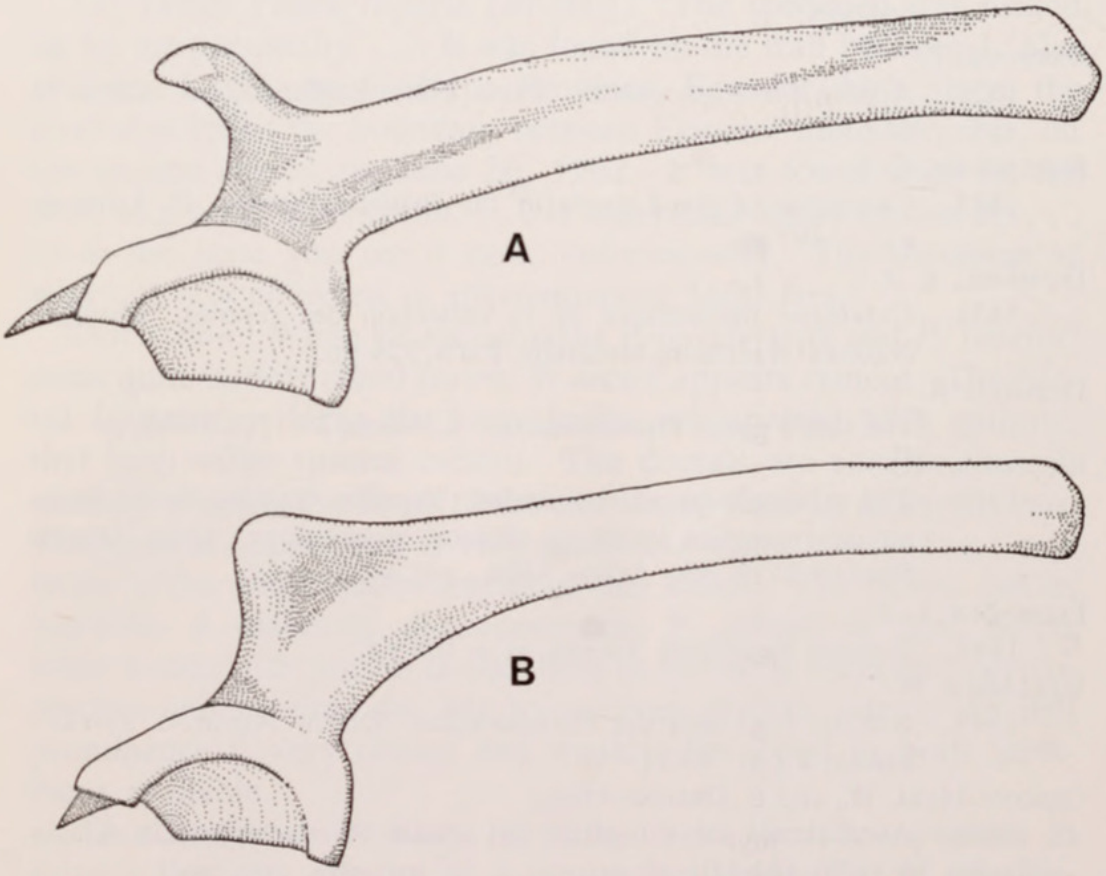

Figure 6. Ilia of two anoline lizard genera: A. *Anolis* (specimen MCZ 61027, *A. richardi*, Tobago, West Indies); B. *Phenacosaurus* (specimen MCZ 17111, *P. heterodermus*, Guasca, Colombia).

TABLE 1: SPECIMENS EXAMINED

Specimens of the three species of *Phenacosaurus* and three of their characters: dorsal scales counted in the standard distance, type of dorsal crest, and number of subdigital lamellae. See text and map (Fig. 5). The locality "Bogotá" is of highly variable precision.

PHENACOSAURUS NICEFORI

Specimen	*Sex*	*Locality*	*Dorsals*	*Crest*	*Lamellae*
FCN 644	♂	Cerro Tetari	21	3	20
FMNH 5684	♀	Paramo de Tana	28	6	17
FMNH 56443	juv.	Pamplona	31	3	18
PANS 25865	♂	"	27	3	17
ILS 64	♀	"	24	3	17
ILS 64a	♀	"	22	3	16
MCZ 6729	♂	"	34	3, 4	17
USNM 72745	♀	Tapatá	33	3	16

PHENACOSAURUS HETERODERMUS

ILS 63	♂	Saota	14	9	18
UNC 692	♀	Paz del Río	10	2, 9	21
UNC 693	♂	" " "	14	5, 7	20
MCZ 78520	♂	Cogua	11	3, 5	20
MCZ 78521	♂	"	12	4	20
ILS 62	♂	Subachoque	13	8	18
ILS 62a	♂	"	15	9	19
MCZ 78524	♂	Cajica	13	5, 4	21
MCZ 78525	♂	"	10	5, 4	21
MCZ 78526	♀	"	9	5	20
MCZ 78527	♂	"	11	5, 3	20
MCZ 78528	♂	"	12	5	20
MCZ 78529	♂	"	14	5, 3	19
MCZ 78534	juv.	"	12	4	20
UNC 705	♀	"	10	5, 4	21
MCZ 104409	♂	Chia	10	4	19
MCZ 110133	♂	"	10	7	10
MCZ 110134	♀	"	12	4	18
MCZ 110135	juv.	"	17	2	20
MCZ 110136	♀	"	8	2	22
MCZ 110137	♀	"	14	2	22
MCZ 110138	♂	"	11	2	20
MCZ 110139	♂	"	11	7	19
MCZ 78522	♀	Usaquen	10	8	19
MCZ 78523	♂	Bosque Popular	16	6	20

Specimen	*Sex*	*Locality*	*Dorsals*	*Crest*	*Lamellae*
MCZ 78519	♂	Tena	12	4, 7	19
MCZ 69120	♂	Tabio	10	4	20
MCZ 69121	♀	"	9	5, 7	19
MCZ 69122	♂	"	12	4	21
MCZ 69123	♂	"	10	5	23
PANS 25074	juv.	"	12	8	19
PANS 25192	♂	"	10	8	20
PANS 25193	♂	"	11	8	18
PANS 25194	♂	"	9	5	19
PANS 25195	♂	"	11	5	20
PANS 25196	♀	"	10	5	19
PANS 25197	♂	"	12	3	20
ILS 55	♂	Sopo	8	5	20
ILS 55a	♀	"	12	5, 6	18
ILS 55b	♂	"	12	5	20
ILS 55c	♀	"	10	5, 6	19
ILS 55e	♂	Sopo	10	5	20
ILS 55f	♀	"	13	5, 6	20
UMMZ 56755	♀	Guasca	10	5, 6	20
MCZ 117111	♀	"	10	10	19
MCZ 117112	♂	"	11	9, 5	20
MCZ 14164	♂	Bogotá	14	4	19
MCZ 14165	juv.	"	14	9, 5	21
BMNH 68.3.3.9	♂	"	13	9, 6	20
BMNH 68.3.3.10	juv.	"	14	9	19
BMNH 1919.3.6.1	♂	"	12	9, 5	19
BMNH 1919.3.6.2	♀	"	10	6	21
BMNH 1919.3.6.3	♂	"	12	5	20
BMNH 1919.3.6.4	♀	"	11	5, 6	20
BMNH 1919.3.6.5	♂	"	13	9, 10	20
BMNH 1919.3.6.6	♂	"	13	9, 6, 4	21
SU 8275	♀	"	12	9	20
SU 8276	♀	"	15	5	20
SU 8277	♂	"	14	5	19
PANS 21058	♂	"	12	1	21
PANS 21059	♂	"	11	8	21
PANS 21060	♀	"	13	1	19
ILS 61	♂	"	13	5, 6, 3	20
ILS 61a	♂	"	11	8, 6	20
ILS 61b	♂	"	12	8	21
ILS 61d	♀	"	14	9, 5	20
ILS 61e	♀	"	11	8	21
ILS 61g	♂	"	14	8	20
ILS 61h	♂	"	13	8	20

PHENACOSAURUS HETERODERMUS

Specimen	*Sex*	*Locality*	*Dorsals*	*Crest*	*Lamellae*
ILS 61i	♀	"	8	9, 5	19
ILS 61j	♂	"	15	9	20
ILS 56	♀	"	10	5, 1	20
ILS 56a	♂	"	11	5, 3	19
ILS 56b	♀	"	9	5, 3	20
ILS 56c	♀	"	10	5	21
ILS 56d	♂	"	15	5, 3	21
ILS 56e	♀	"	14	5, 1	20
MCZ 74314	♀	"	10	8, 5	20
MCZ 74315	♂	"	11	8	20
UNC 687	juv.	"	11	5	20
MUN 119/37	♂	"	13	5	21
MUN 119/37	♀	"	11	5	20
WIEN 72	♂	"	16	9, 4	21
WIEN 72	♂	"	14	9, 4	21
WIEN 72	♂	"	16	6, 9, 4	19
WEIN 72	♂	"	15	6, 9, 4	22
WEIN 72	♂	"	14	9, 5	20
WEIN 72	♂	"	15	9, 6	20
WEIN 72	♂	"	10	5, 7, 2	20
WEIN 72	♂	"	10	5, 7, 6	21
WEIN 72	♀	"	14	9, 7, 6	19
WEIN 72	♀	"	14	8	20
WEIN 72	juv.	"	12	9, 4	20
MHNP 1923-55	♀	"	12	8	21
ZMB 4255	♂	"	12	5, 2	20
ZMB 4255	♂	Bogotá	13	9	19
ZMB 4256	♂	"	10	8	21
ZMB 4256	♀	"	10	9	19
ZMB 5211	♂	"	14	5	19
ZMB 5211	♂	"	13	5, 9, 2	19
UMMZ 56258	♂	"	13	9	23
SMF 10789	♂	"	18	8, 4	22
AMNH 91752	♂	"	14	6, 3	19
AMNH 91753	♂	"	14	7	20
AMNH 91754	♂	"	15	4, 7	18
AMNH 14024	♂	"	9	5	19
AMNH 14023	♂	"	13	9	22
AMNH 27567	♀	"	9	9	22
AMNH 7641	♂	"	17	5, 9	20
AMNH 24215	♂	"	13	9, 10	20
USNM 93225	♂	"	13	9	24
USNM 95923	♂	"	13	9, 10	21
USNM 92495	♂	"	13	9	19

Specimen	*Sex*	*Locality*	*Dorsals*	*Crest*	*Lamellae*
USNM 95922	♀	"	11	9	18
AMNH 44987	♀	no locality	15(?)	8, 6	21
AMNH 44986	♂	"	12	7, 6	19
MHNP 1664	♂	"Nouvelle Grenade"	14	9, 7	19
MHNP A.1664	♂	" "	13	5, 7	20
MHNP B.1664	♂	" "	12	5, 8	19
MHNP 6798	♀	" "	10	10, 7, 2	18
MHNP A.6798	♂	" "	12	5, 7	18
WIEN 12662	♂	" "	17	5	21
WIEN 451	♂	"Alto de los Cruces"	15	9, 6	20
WIEN 12660	♀	Paramo de Cruz Verde	10	6, 4	21
WIEN 12661	♂	" " " "	15	9, 4	20
UNC 680	♂	" " " "	16	5, 7	21
UNC 681	♀	" " " "	16	5, 7	19
UNC 686	♀	" " " "	11	8, 6	19
MCZ 78514	♂	Arracachal	13	5, 2	21
MCZ 78515	♂	"	16	5, 2	21
PANS 24150	♂	Aguadeta	11	5	19
PANS 24151	♀	"	13	9	22
PANS 24152	♂	"	17	8, 6	21
ILS 57	♀	Fusagasuga	11	5	19
USNM 127099	♂	"	13	3	19
USNM 127100	♂	"	16	3	20
USNM 127101	♀	"	8	3, 2	20
MUN 118/37	♀	Paramo de Sumapaz	10	8	20
AMNH 32680	♂	Gutierrez	12	5, 9	19
AMNH 32681	♀	"	9	5, 9	20
FMNH 69673	♂	San Antonio, Huila	19	3, 5	21
MUN 9/49	♂	W. Tambo	16	3, 5	24
MVZ 68686	♀	San Antonio, Valle	16	3, 5	21
PANS 25285	♂	"Laguneta" (?), Caldas	16	5, 2	19
SMF 10443	♂	Río Samana	13	2	22
UMMZ 65209	♀	Sonson	15	5, 4	20
AMNH 35303	♀	"	9	5, 4	21
AMNH 35304	♀	"	14	5	19
AMNH 35305	♂	"	12	5	20
AMNH 35306	♀	Sonson	13	3, 1	21
AMNH 32673	♂	Medellin	14	5	19
ILS 58	♂	San Pedro	17	5	19
ILS 59	♂	" "	9	8, 4	21
ILS 60	♂	" "	14	8, 6, 4	22
		PHENACOSAURUS ORCESI			
MCZ 38937	♀	Mt. Sumaco	38	3	18
USNM 166533	♂	btwn. L'Alegría and La Bonita	48	1	16