

A REVIEW OF THE SOUTH AMERICAN LIZARD GENERA *UROSTROPHUS* AND *ANISOLEPIS* (SQUAMATA: IGUANIA: POLYCHRIDAE)

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ABSTRACT. Lizards of the genera *Urostrophus* and *Anisolepis* represent a small, apparently monophyletic group of southern South American Iguania, placed in the family Polychridae by Frost and Etheridge (1989), and referred to informally as the "para-anoles." Para-anoles are small (70–108 mm maximum snout–vent), with a slender, moderately compressed body, and a long tail (60–77% total length). Females reach a greater maximum adult size than males, and have a slightly shorter tail, but apparently there is no sexual dichromatism. The tail is non-autotomic and has been reported to be prehensile in both species of *Urostrophus* and in *Anisolepis grilli*.

Two species of *Urostrophus* are recognized, *U. vautieri* from the Atlantic Forest of southeastern Brazil, and *U. gallardoi*, described here as new, from Misiones Province in northeastern Argentina, from the Chacoan Region of northern Argentina, and from southeastern Bolivia. Both species have smooth, flat, juxtaposed dorsal and ventral body scales, and smooth, flat subdigital scales, but the head and body scales of *U. gallardoi* are smaller and more numerous overall, and it has a larger external ear, a color pattern of greater contrast, and a smaller maximum adult size: female snout–vent length 78 mm rather than 108 mm.

Anisolepis differs from *Urostrophus* in having sharply keeled and strongly imbricate ventral body scales, a longer tail and higher number of caudal vertebrae, caudal transverse processes angled forward rather than laterally, and a higher total number of inscriptional ribs. *Anisolepis* contains three apparently allopatric species: *A. grilli*, *A. undulatus*, and *A. longicauda*, the latter formerly recognized as the only species of the genus *Aptycholaemus*, here synonymized with *Anisolepis*. The most obvious differences among the species are: the absence of a transverse gular fold and presence of a very small external ear in *A. longicauda*, distinctly heterogeneous scalation on the dorsal body and neck in *A. undulatus*, and the alternatives to these characters in *A. grilli*—

a large ear, transverse gular fold, and less heterogeneous scalation.

Anisolepis grilli occurs in eastern Brazil in the Atlantic Forest and in the cultural steppe in the state of São Paulo, and in Misiones, Argentina. *Anisolepis undulatus* occurs in extreme southeastern Brazil, Uruguay, and on the south shore of the Río de La Plata in Argentina; the Uruguayan and Argentinian specimens are larger and have a different pattern than those from Brazil, but the status of the southern populations is uncertain. *Anisolepis longicauda* occurs in Paraguay and in Argentina near the western bank of the Río Paraguay and in Misiones Province, where it may be sympatric with *A. grilli*.

Published and unpublished information on various aspects of para-anole biology are included. Accounts of *Urostrophus* and *A. grilli* indicate they live in trees and bushes and are slow in their movements. There are no records of the ecology or behavior of *A. longicauda* or *A. undulatus*, but all of their known localities appear to be in a habitat of seasonally flooded grasslands (*esteros* or *bañados*), adjacent or close to a large river or lake.

One of us (RE) summarizes the long and complex history of hypotheses of para-anole relationships. There is a strong consensus that Polychridae is a monophyletic family and that *Urostrophus* and *Anisolepis* (including *Aptycholaemus*) are among its member genera, but the historical relationships of these genera to one another and to other members of the family are yet to be resolved.

INTRODUCTION

Etheridge and de Queiroz (1988), in an analysis of the phylogenetic relationships of "Iguanidae," and Frost and Etheridge (1989) tentatively recognized as monophyletic a small group of subtropical South American genera: *Urostrophus*, *Anisolepis*, and *Aptycholaemus*, and called them the "para-anoles." As the informal name implies, they show a number of resemblances to the anoles proper, a distinctive

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and clearly monophyletic group containing *Anolis*, *Chamaeolis*, *Phenacosaurus*, and *Chamaelinorops*. The para-anole genera were first linked by Etheridge in a dendrogram published by Paull, Williams, and Hall (1976), reproduced, in part, by Peterson (1983a, fig. 1b; 1983b, fig. 1), who used the term "para-anoline" for a group consisting of *Urostrophus*, *Anisolepis*, *Aptycholaemus*, and *Enyalius*. However, Etheridge and de Queiroz (1988) specifically exclude *Enyalius* from the para-anoles, placing it instead with the austral South American genera *Pristidactylus*, *Diplolaemus*, *Leiosaurus*, and *Aperopristsis*, in a group termed the "leiosaurs," an action followed by Frost and Etheridge (1989). Williams (1988) included para-anoles within the leiosaurs.

Para-anoles, as we here define them, are small lizards, with a maximum snout-vent length from 70 to 108 mm. The body is slender and moderately compressed, and the slender tail represents 60 to 77% of the total length. Females attain greater maximum size than males, and have a slightly shorter tail, but there is otherwise no sexual dimorphism or dichromatism. The tail is non-autotomic and has been reported to be prehensile in some species.

Para-anoles share with other Polychridae (*sensu* Frost and Etheridge, 1989) the presence of nuchal endolymphatic sacs and midventrally continuous postxiphisternal inscriptional ribs ("chevrons"). They share with other polychrids, except *Polychrus*, the loss of femoral pores and the presence of a spinulate oberhautchen in which the spinules of the epidermal sense organs and of the subdigital scales are longer than the background spinules. With leiosaurs, para-anoles share clavicles with an angular and hooked lateral margin, and a small posterior coracoid fenestra. With anoles the para-anoles share the presence of three (rather than four) sternal ribs.

At this time, the relationships of the para-anole genera to one another (whether *Urostrophus* is monophyletic, whether the para-anoles form a monophyletic group)

and their relationships with other polychrids are still in doubt; we ourselves do not agree on how to resolve these questions. Nevertheless one of us (RE) provides a summary and discussion of earlier speculations, below.

NOMENCLATURAL HISTORY

The nomenclatural history of *Urostrophus* and *Anisolepis* has been exceedingly complex, with as many synonyms as valid names. Virtually all of the descriptions, diagnoses, and accounts of distributions date from the last century and earliest part of this century, and we have found the available material to be widely scattered, frequently misidentified, mostly in South American museums, and three of the five species must still be counted as rare. Because the history of these forms has been so complex, even though published accounts are few, old, and widely scattered, we provide, below, descriptions somewhat more detailed than is usual in a work of this sort, together with what little information we have been able to accumulate on other aspects of their biology. In anticipation of our diagnosis of the genus *Anisolepis*, we point out here that the recognition of *Aptycholaemus* cannot be supported and we consider *longicauda* to be a species of *Anisolepis*.

Wiegmann (*Herpetologia Mexicana*, 1834) described the first species of para-anoles. He referred them to his new genus *Laemanctus*, describing three specimens in the Berlin Museum under the three names *Fitzingeri*, *undulatus*, and *obtusirostris*, differentiating them by details of color and head shape. For each of the three, the locality was "Brasilia." A fourth species, *Laemanctus longipes*, which Wiegmann described much more fully, was later made the type of that genus by Fitzinger (1843).

A further nominal species was described by Duméril and Bibron (1837) in the fourth volume of the "*Erpétologie Générale*," in the new genus *Urostrophus*, monotypic with the single species *vautieri*. The two

type specimens, one collected by Vautier, the other by Gaudichaud, were reported by Duméril and Bibron (1837) as having only the locality "Brasil." However, as Vanzolini (1977, p. 49) has already commented, C. Duméril (Duméril and Bibron, 1834, p. xv), in the *Discours préliminaire* to the first volume of the "Erpétologie Générale," reported that Vautier's collection was made in "Rio de Janeiro ou aux environs." One of the two syntypes in Paris is labelled "Rio de Janeiro," and this is the locality accepted for the types by Duméril and Duméril (1851, p. 55).

There was early recognition that three of the taxa named by Wiegmann were close to *U. vautieri* and distant from the fourth species, *longipes*, that Wiegmann had placed in *Laemanctus*. Fitzinger (1843) placed *undulatus* and *Fitzingeri*, along with *vautieri*, under his concept of *Urostrophus* and indeed cited *obtusirostris* only in the synonymy of *vautieri*. Gray (1845), who on page iv of his "Catalogue of Specimens of Lizards in the British Museum" mentions that he visited Berlin, among other museums, in an effort to verify species identities, placed the three Wiegmann taxa, not in *Urostrophus*, which he kept monotypic, but in his next listed genus, *Ecphymotes* Fitzinger, 1826. He distinguished *Ecphymotes* from *Urostrophus* on the basis of keeled dorsal and tail scales. This character, like the round rather than compressed tail by which he keyed out the three Wiegmann species from the fourth taxon that he referred to *Ecphymotes*, *E. acutirostris*, could only have been obtained by direct observation of the Berlin specimens. Gray is therefore the first to cite a character by which the Wiegmann types differed from *U. vautieri*, the type by monotypy of *Urostrophus*. His referral of the Berlin types to *Ecphymotes* cannot be upheld. *Ecphymotes* Fitzinger, 1826, was published as a *nomen nudum* (p. 49). In 1843 Fitzinger emended *Ecphymotes* to *Ecphymatotes* and provided a description of it as a subgenus of *Laemanctus* (p. 62). He had already on page

16 designated *Polychrus acutirostris* as the type of the genus. *Ecphymotes* thus became a strict synonym of *Polychrus* Cuvier, 1817, a phyletically distant genus. Thus, if the Wiegmann types were not referable to either *Urostrophus* or *Laemanctus*, as a result of Gray's (1845) action, they were left without a valid generic name.

Cope (1864), who had visited Berlin, and Peters (1877), who was in charge of the Berlin collection, both preferred to refer the Wiegmann species to *Urostrophus*, although Peters stressed the keeled scales of the Wiegmann types as a difference at the species level from *U. vautieri*. Boettger (1882) used the name *Laemanctus undulatus* Wiegmann for a specimen from São Paulo Province, Brasil, about which he said (translated): "A rare species. Head scales smooth but ventral scales strongly keeled, larger and more strongly keeled than those of the back." The color description, which Boettger appends, could be that of one of the specimens named by Wiegmann. On distributional grounds we believe Boettger's specimen to be the taxon that Boulenger (1891a) described as *Anisolepis grilli*.

The genus *Anisolepis* was described by Boulenger (1885a), with the sole species *A. iheringi*, on the basis of two specimens sent to the British Museum by Dr. H. von Ihering from Rio Grande do Sul, Brazil. His description was repeated and a figure published (plate IX, fig. 3, reproduced here as Fig. 7) in the second volume of Boulenger's "Catalogue of the Lizards of the British Museum (Natural History)" (Boulenger, 1885b).

In the same volume of the Catalogue, without having visited Berlin, Boulenger interpreted Gray's referral of Wiegmann's types to *Ecphymotes* and Peters' (1877) comment on keeled scales as a difference from *Urostrophus vautieri* to imply that the three names belonged in the genus *Enyalius*. He believed that he had two specimens of one of them, *Fitzingeri*, at the British Museum. He therefore based his

concept of the latter species on these, under the name *Enyalius fitzingeri*, in the process erroneously synonymizing *Enyalius undulatus* Duméril and Bibron, 1837—a mistake not corrected until noticed by Etheridge (1969). Boulenger provisionally recognized *Enyalius undulatus* Wiegmann, with *obtusirostris* as a synonym, commenting: "Although never properly characterized, this species is introduced on the authority of Peters."

In 1886, after personally examining the Berlin types, Boulenger realized that his *iheringi* was a synonym of *undulatus*, reporting the species thereafter as *Anisolepis undulatus* (Wiegmann) (Boulenger, 1886, 1887). He did not retract his reference of *Fitzingeri* to *Enyalius* and continued to synonymize *obtusirostris* with *undulatus*.

By the courtesy of Günther Peters and Rainer Günther, we have ourselves examined the Berlin types. We agree with Boulenger (1886, 1887) that *undulatus* is, indeed, the prior name of *iheringi*, but if the genus *Anisolepis* is recognized, then *Fitzingeri* and *obtusirostris*, as Etheridge indicated in 1969, are also members of that genus. Our new study shows, however, that, contrary to the opinion of Etheridge (1969), the two latter types are identical with the species which Boulenger did not describe until 1891 as *A. grilli*. We shall discuss the nomenclatural problem involved, below, under the latter name.

Having excluded Wiegmann's taxa from his concept of *Urostrophus* (relying on the character of keeled ventrals), Boulenger (1885c) in his Catalogue, on the other hand, expanded that concept to include the Chilean species *Leiosaurus torquatus* Philippi, 1861, in Philippi and Landbeck (1861). In so doing, as we shall show below, he was committing an error, but one at that time plausible, since he was relying on external characters that are in fact very similar in *torquatus* and *vautieri*.

Boulenger continued his error when in 1889, in redescribing Burmeister's (1861) types of *Leiosaurus scapulatus*, *L. multipunctatus*, and *L. marmoratus* in the

Museum at Halle, he synonymized the latter two with the first under the name *Urostrophus scapulatus*. The first two Burmeister taxa are indeed close relatives of the Chilean *torquatus*, but not of *U. vautieri*, the type of the genus; the third is now regarded as a *Liolaemus*. (See Müller, 1928, 1940, for discussion of the Burmeister types.)

On the point of confusion of *Leiosaurus* (*partim*) and *Urostrophus*, Boulenger's high authority for a long period carried the day. (Confusion had in fact begun before Boulenger, but in the reverse direction: Reinhardt and Lütken in 1861 had reported Duméril and Bibron's species from Rio de Janeiro and Lagoa Santo in Brazil as *Leiosaurus vautieri*.)

No additional species of para-anoles were described until Boulenger (1891a) described *Anisolepis grilli* from Palmeira in the state of Paraná, Brazil, and, in the same year (Boulenger, 1891b), the closely related new genus and species, *Aptycholaemus longicauda* from "Riacho del Oro, Argentina" = mouth of the Río de Oro into the Río Paraguay.

A. longicauda was the first para-anole to be discovered outside Brazil, but soon additional material turned up. In 1895 Koslowsky, of the Museo de La Plata in Argentina, referred two new species to the genus *Anisolepis*: *A. Bruchi* from Punta Lara on the south bank of the Río de La Plata in northern Buenos Aires Province, and *A. argentinus* for which the type locality was said to be "Sierra de la Ventana, cerca de Bahía Blanca," also in the Buenos Aires Province, but which Koslowsky himself, after failing to find the animal during a visit to the Sierra de la Ventana (Koslowsky, 1896), corrected to the Province of Misiones (Koslowsky, 1898).

Both Koslowsky's names were soon synonymized, *A. bruchi* with *A. undulatus* by Werner (1896) (perhaps incorrectly, see below under *A. undulatus*) and *A. argentinus* with *Aptycholaemus longicauda* by Berg (1898).

Werner himself (1896) created a syn-

onym, *A. lionotus* = *A. grilli*, from Blumenau, Santa Catarina, in Brazil, but this synonymy went long unrecognized. The name was still considered valid by Burt and Burt in 1933, and was only synonymized by Peters and Donoso-Barros (1970) on the advice of Paulo Vanzolini (confirmed by Vanzolini himself, 1977, p. 175).

The first authentic record of *Urostrophus* from Argentina was provided by Boulenger in 1902, who reported "*U. vautieri*" from Cruz del Eje, Córdoba, Argentina. Liebermann (1939) added a second locality, "Santa Fé," but without comment or mention of the museum in which the specimen was to be found.

Confusion between *Urostrophus* and the Argentinian species related to *torquatus* was at last resolved when Gallardo (1964) separated the two generic units correctly, creating for the Argentinian species *scapulatus*, mistakenly referred to *Urostrophus*, a new genus *Cupriguanus*, describing at the same time two new species in the genus, *C. achalensis* and *C. araucanus*, the latter now considered a synonym of *scapulatus* (see Etheridge and Williams, 1985). He cited in the same paper a number of records for true Argentinian *Urostrophus* as *Urostrophus vautieri*. He left, however, the position of *torquatus* uncertain, saying that it might be either *Cupriguanus* or *Leiosaurus*.

Gallardo's conclusions, although an important advance, were not entirely correct. *Cupriguanus* Gallardo, 1964, is a synonym of *Pristidactylus* Fitzinger, 1843. We report the tangled history of these two names elsewhere (Etheridge and Williams, 1985).

Gallardo was, however, quite right in recognizing *torquatus* as possibly part of the leiosaur assemblage. Peters and Donoso-Barros (1970) were, on the contrary, somewhat regressive, copying Donoso-Barros (1966) in continuing Boulenger's erroneous association of *torquatus* with *U. vautieri* and adding *U. valeriae*, a species related to *torquatus* and described by Donoso-Barros (1966) in his "Reptiles de Chile."

Prior to the present paper, then, *Urostrophus* was monotypic, all species referred to it, save *vautieri*, having been placed in *Pristidactylus* (Etheridge and Williams, 1985). Two very distinct species of *Anisolepis* are currently cited as *A. undulatus* and *A. grilli*, although there are two senior synonyms of the latter (as mentioned above). *Aptycholaemus* remains monotypic, including only *longicauda*.

In the present paper we describe and diagnose *Urostrophus* and *Anisolepis*, describing a new species of the first and synonymizing *Aptycholaemus* with the latter. Included under each species is a full diagnosis and description, with such information as we have been able to find about para-anole biology from the literature and personal correspondence. Measurements, scale counts, and skeletal characteristics are presented in tables, scale definitions are supplied in the appendix, a key is provided, and a list of specimens examined is included.

Urostrophus Duméril and Bibron 1837

1837 *Urostrophus* Duméril and Bibron, *Erpét. gén.*, Paris, 4: 74.—Type species (by monotypy): *Urostrophus vautieri* Duméril and Bibron 1837.

Diagnosis. *Urostrophus* is an iguanian lizard of the family Polychridae diagnosed by the acquisition of endolymphatic sacs that extend back between the supraoccipital and parietal bones into the dorsal neck musculature, and other synapomorphies (Frost and Etheridge, 1989). *Urostrophus* differs from *Polychrus* in having lost femoral pores, from the leiosaurs (*Enyalius*, *Pristidactylus*, *Diplolaemus*, *Leiosaurus*, *Aperopristsis*) in having reduced the number of sternal rib pairs from four to three and in lacking longitudinally divided distal subdigital scales, and from the anoles (*Anolis*, *Chamaeolis*, *Phenacosaurus*, *Chamaelinorops*) in having acquired a small posterior coracoid fenestra and in lacking elongate second ceratobranchials and the anole type digital pad. *Urostrophus* differs from *Anisolepis* (including *Ap-*

tycholaemus, see below) in having smooth ventral scales, and posterior marginal tooth crowns with straight sides and moderate secondary cusps. The characters that distinguish *Urostrophus* from *Anisolepis* may be primitive, and the genus may be paraphyletic.

Etymology. From the Greek words *oura* meaning tail and *strophos* meaning a twisted cord, in allusion to the prehensile tail in this genus.

Characteristics. Head flat and wide.

General squamation moderately heterogeneous.

Head scales small, polygonal, juxtaposed, smooth and flat or convex, or bluntly keeled and convex.

Nasal ovoid, the nostril posterior within it or almost filling the scale, separated from the rostral by 1 postrostral, in contact with the first supralabial or separated by 1 lorilabial.

Supraorbital semicircles in contact with or separated by from 1 to 3 scales.

Supraoculars somewhat enlarged medially, in contact with the supraorbital series or not; a circumorbital series complete or not.

Interparietal suboval, larger than the other scales of the area, which are usually not differentiated, separated from the semicircles by 1 to 3 scales and from the nape granules by 5 to 8 scales. Parietal eye present.

Canthals 3 to 4, oriented toward the nasal, the anteriormost separated from it by 1 to 2 scales.

Superciliaries 11 to 16, squarish, or the first or first 3 elongate and oblique.

Loreals 8 to 27, varying much in size.

Lorilabials in 1 to 2 rows, partly or completely separating the subocular scale or scales from the supralabials. One or 2 rows continue forward on a labial shelf to below the nasal.

Supralabials 6 to 10, the fifth to eighth below the center of the eye.

Preoculars 1 to 3, the uppermost usually in contact with the first canthal.

Subocular single, elongate or broken into 2 to 4 scales, rarely in contact with su-

pralabials, usually separated by 1 to 2 rows of lorilabials.

Postoculars variable, not well differentiated.

Lower temporals larger or smaller, smooth, flat or convex. An intertemporal line or zone of enlarged scales not or weakly indicated.

Ear variable, from subround to vertically oval, from slightly smaller than interparietal to as much as three times larger. Anterior margin of ear beaded or not, posterior margin granular.

Mental triangular to pentagonal, in contact with 2 postmentals (=first sublabials) between infralabials. One to 5 sublabials on each side in sequence with the first sublabials.

Central gulars smooth, convex, separated by minute granules, grading posteriorly into large imbricate smooth scales.

Transverse gular-antehumeral fold present. A pregular fold present or not.

Nape folds ill-defined. A longitudinal fold sometimes distinguishable.

Middorsals smooth, flat or slightly convex, partly separated by minute granules, none enlarged into a median row, but variable in size.

Nape scales smaller than dorsals, granular, smooth.

Body slightly to noticeably depressed.

Flank scales smooth or very bluntly keeled, separated by minute granules, variable in size.

Ventrals much larger than any dorsal or flank scales, smooth, imbricate or subimbricate, in transverse rows. Scales at anterior border of vent granular.

Tail somewhat compressed, without verticils.

Caudal scales granular at base and smooth, becoming larger, hexagonal, keeled, and imbricate distally.

Tail less than 76% of total length.

Limb scales smooth, largest in front of thigh, varying from granular to imbricate and separated by minute granules or not.

Supradigitals of hand smooth, imbricate, often wide, lamella-like. Supradigitals of foot smooth, imbricate, narrower

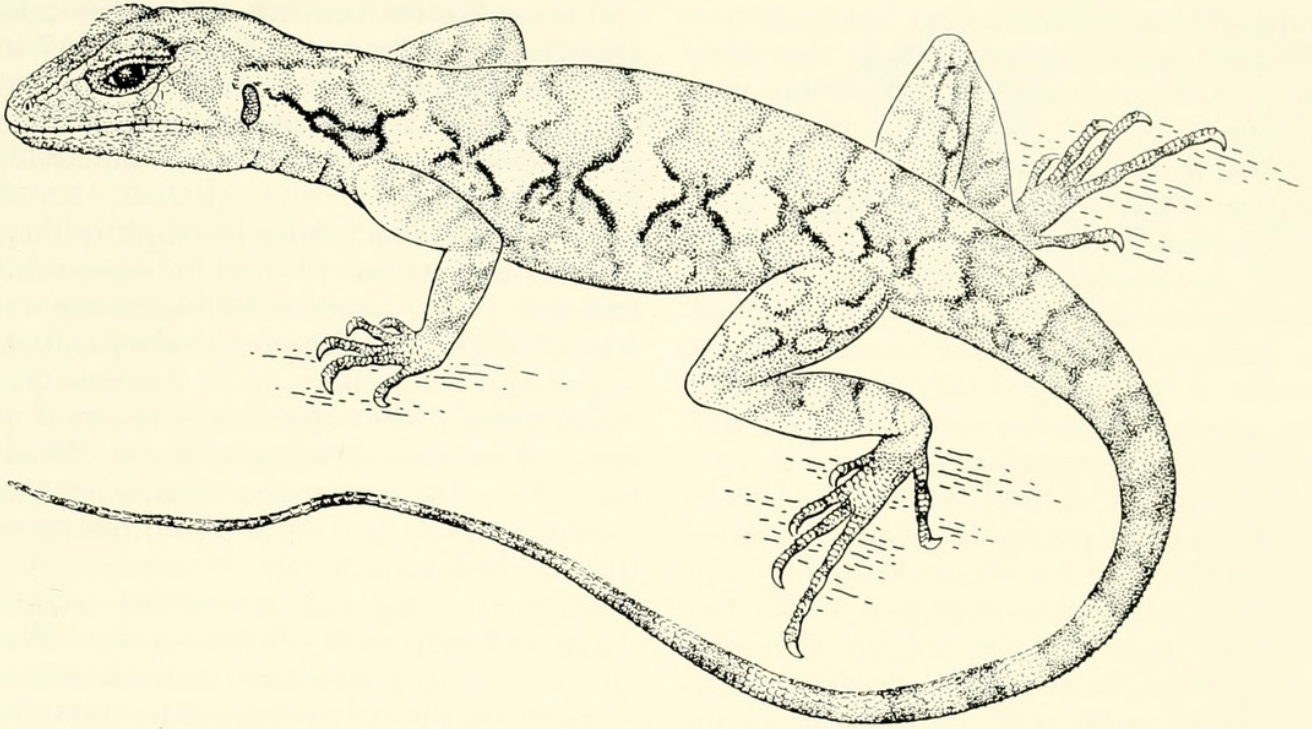


Figure 1. *Urostrophus gallardoi*, MACN 4311.24, adult male 70 mm snout-vent length, from Rosario de la Frontera, Argentina.

than those of hand. Infradigitals of both hand and foot smooth, imbricate, wide, lamellar.

No femoral or preanal pores.

Axillary pocket distinct to obscure. An inguinal pocket never present.

Urostrophus gallardoi new species

Figures 1 and 2; Tables 1–4

1902 *Urostrophus vautieri*—Boulenger, Ann. Mag. Nat. Hist., London, (7)9: 337.

1939 *Urostrophus vautieri*—Liebermann, Physis, Buenos Aires, 16: 66.

1960 *Urostrophus vautieri*—Hellmich, Abh. Bayer, Akad. Wiss. (N.F.), 101: 48.

1964 *Urostrophus vautieri*—Gallardo, Neotropica, Buenos Aires, 10(33): 126.

1979 *Pristidactylus vautieri*—Gallardo, Monogr. Mus. Nat. Hist. Univ. Kansas, Lawrence, 7: 302.

1981 *Urostrophus vautieri*—Laurent and Teran, Misc. Inst. M. Lillo, Tucumán, 71: 11.

1984 *Urostrophus vautieri*—Bee de Speroni and Cabrera, Rev. Mus. Argent. Cien. Nat. "Bernardino Rivadavia," Zool., 8(10): 115.

1985 *Urostrophus gallardoi* (*nomen nudum*)—Laurent, Nat. Geogr. Soc. Research Rept., 1977 projects, p. 422.

1986 *Urostrophus vautieri*—Cabrera and Bee de Speroni, Historia Natural, 6, p. 8.

1986 *Urostrophus vautieri*—Ceï, Monographie IV, Mus. Reg. Sci. Nat. Torino, p. 175, footnote.

Holotype. Mus. Argent. Cien. Nat. No. 11043, Urundel, Dept. Oran. Prov. Salta, Argentina (23°43'S-64°47'W). J. Crespo, collector.

Paratypes. ARGENTINA: *Córdoba*: Cruz del Eje, BMNH 1902.5.22.4. *La Rioja*: Aimogasta (possibly in error fide R. Laurent in litt.), MZUSP 45908. *Salta*: El Quebrachal, ABarrio 746; Quebrada Río Las Conchas, FML 01266; Río Chuña Pampa (=Chuñapampa), about 10 km WNW La Viña, FML 01296; Puesto San Borja, Sierra de Metán, 15 km W Metán, FML 00847; Rosario de la Frontera (city), MCZ 162922, MACN 4311-24 (1 specimen); 35 km N Cafayate, MCZ 162920, MACN 12016. *Santa Fé*: no additional data, MACN 19740. *Santiago del Estero*: Santiago del Estero (city), MACN 8019-21; outskirts of Santiago del Estero, ABarrio 121; Bandera, ABarrio 345. *Tucumán*: no additional data, MACN 4318-25 (1 specimen); Dept. Burruyacú, no additional data, FML 00483. *BOLIVIA*: *Santa Cruz*: Santa Cruz de la Sierra, MACN 2786-88.

Etymology. Named in honor of José Maria Gallardo, who first correctly distin-

guished *Urostrophus* from *Cupriganus* = *Pristidactylus*, and also briefly described the characteristics of the Argentine population.

Diagnosis. Differs from *U. vautieri* in having smaller scales (i.e., higher scale counts, see Tables 2 and 3), a larger external ear opening, much larger than the interparietal scale, and a more distinct color pattern, with regular crossbands and usually a fully ringed tail. In large adults the upper head scales and underlying dermal skull roof rugosities are more convex.

Description. *Head* (Fig. 2). Head scales small, smooth, polygonal, convex, becoming swollen and sometimes keeled in large adults. Rostral subpentagonal, about two or three times as wide as high. Five or 6 postrostrals. Nasal ovoid, nostril in posterior dorsal position or almost filling scale, in contact with the first supralabial, separated from the rostral by the lateral postrostral or in very narrow contact. Five to 8 scales between the nasals dorsally. Frontonasal scales small, smooth (or swollen), polygonal, varying greatly in size, 7 to 11 between the posterior canthals. Eight to 13 supraorbitals in an arc on each side, the semicircles separated medially by 2, rarely 1 or 3 scales that are only slightly smaller than the scales of the semicircles themselves. Supraoculars enlarged medially (the largest may be transversely oriented), usually separated from the semicircles by a complete circumorbital series. Six or 7 scales across the supraocular area from the supraorbitals to the superciliaries. Scales of parietal region small, smooth (or swollen), varying greatly in size. Interparietal nearly oval, separated from the semicircles by 1 to 2 scales on each side, separated from the nape scales by about 5 scales. Canthals 3 to 4, the anteriormost separated from the nasal by a much smaller scale. Superciliaries 11 or 12, all squarish except the first, or first 2 which may be elongate; none overlapping. Loreals varying much in size, 11 to 18. Two rows of lorilabials, only 1 extending beneath the subocular. One preocular on each side. Subocular single,

elongate. Postoculars not well differentiated from the temporals. Supralabials 7 to 10, separated from the subocular by one row of lorilabials or rarely in contact, the sixth, seventh, or eighth below the center of the eye.

Temporals small, smooth, slightly convex, variable in size, 11 to 14 between orbit and ear. A very indistinct intertemporal area of slightly enlarged scales separating upper and lower temporals. Anterior auriculars like lower temporals but more convex, hence anterior margin of ear "beaded." Posterior auriculars granular. Ear vertically oval, usually two to three times the size of interparietal.

Mental pentagonal, in contact with 2 polygonal postmentals between the infralabials. One to 4 sublabials on each side in sequence with the postmentals; only the postmentals in contact with the infralabials. Infralabials 8 to 13. Central gulars granular, smooth, convex, subimbricate, often partially separated by minute granules, grading posteriorly into larger distinctly imbricate smooth scales just in front of the gular fold. Antehumeral-transverse gular fold distinct. A pregular fold at best vaguely indicated. Lateral nape folds not well defined.

Body. Middorsals subgranular, smooth, convex, subimbricate, or partially separated by minute granules, irregular in size. No trace of a vertebral scale row. Nape scales smaller than middorsals, granular, smooth, separated by minute granules. Flank scales granular, smooth, separated by minute granules, varying in size. Ventrals much larger, smooth, imbricate, subhexagonal, in transverse rows. Scales at anterior margin of vent subgranular.

Limbs. Brachials: all upper forelimb scales smooth, convex, and separated by minute granules, some as large as dorsals but infrabrachials and axillary scales granular. Antebrachials: all lower forearm scales smooth, convex, but the more distal become larger and more imbricate and only the more proximal retain minute granules between them. Carpals: supra-

carpals smooth, strongly imbricate. Infracarpals smooth, not as large or as strongly imbricate. Digitals of hand: supradigitals weakly tectiform, imbricate distally, wider than long or not. Infradigitals smooth, imbricate distally, wider than long proximally, narrower on the distal part of the toe except for the 3 most distal scales, which are again wider than long. Axilla granular with minute granules interspersed. No axillary pit.

Femorals: suprafemorals larger than dorsals, smooth. Prefemorals larger to much larger than dorsals, largest near knee and subimbricate to imbricate. Infracarapals like prefemorals but smaller and less distinctly imbricate. Postfemorals granular with minute granules between. Tibials: supratibials like dorsal scales but sometimes subimbricate. Pretibials and infratibials enlarged, imbricate. A granular zone at the ankle joint dorsally. Tarsals: supratarsals smooth, imbricate like pre- and infratibials. Infratarsals swollen, smooth, imbricate. Digitals of foot: supradigitals smooth, imbricate distally, not wider than long. Infradigitals smooth, imbricate distally, wider than long proximally or not wider than long, narrower distally. Lamellae under fourth toe 22 to 29.

Groin granular. No inguinal pit.

Tail. Base of tail scaled like body, the more distal scales becoming larger both above and below, and 4 to 7 ventral rows always distinctly keeled, and the dorsal and lateral scales becoming keeled after the proximal third of tail length.

Color and Pattern. (Fig. 1). The color pattern of *Urostrophus gallardoi*, at least in preservative, appears to be quite uniform, and that of a paratype (MCZ 162922) is typical: Ground color pale yellowish gray brown. On dorsum and nape a pattern of brown darker edged rhombs, two dorso-lateral, two on midflanks. These connected transversely by broad bridges into cross-bands that have boldly undulant borders anteriorly and posteriorly. Continuing onto the distal tail these bands become paler and with straighter edges and extend

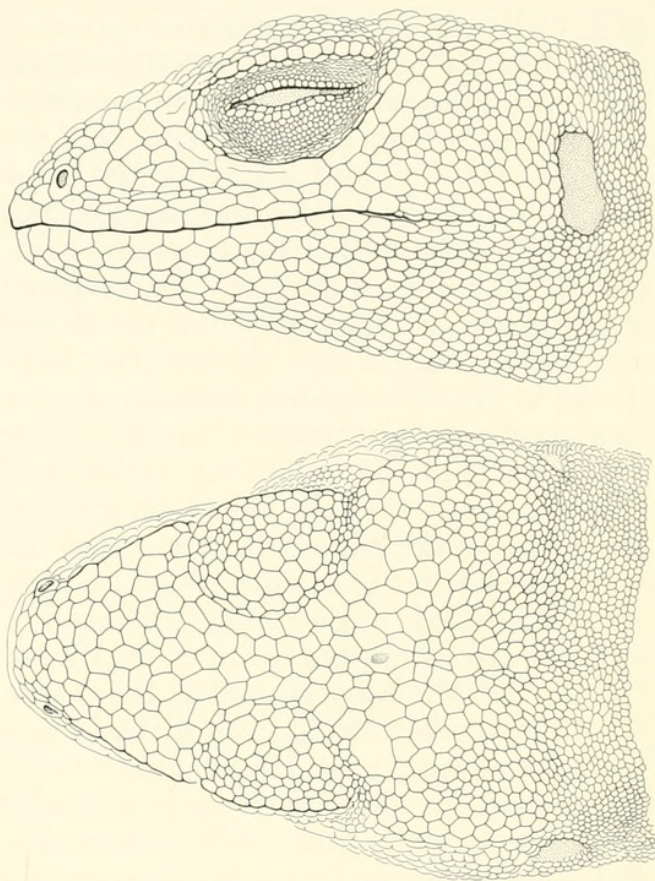


Figure 2. Head scales of *Urostrophus gallardoi*, MACN 4311.24, adult male, from Rosario de la Frontera, Argentina: Top, left lateral. Bottom, dorsal.

around the tail as full rings. Limbs above more vaguely patterned in brown and yellow gray. Belly, throat and undersides of limbs very vaguely and weakly patterned.

According to Gallardo (1964, translated): "Its coloration is light brown with seven darker transverse bands with rhomboidal figures on the dorsum of the trunk; the tail is ringed with dark." Bee de Speroni and Cabrera (1984, translated) describe a specimen from northern Córdoba Province as follows: "Dorsally yellowish gray with markings of dark gray almost black, arranged transversely in the form of irregular rhombs, six from neck to anus, and 20 on the tail, there continuing ventrally as rings. On the arms and legs the dark color predominates over the white like diffuse spotting. . . . Ventrally the color is pale yellowish gray sprinkled with black dots on the throat, arms and legs. The coloration coincides with previous descriptions

(e.g., Gallardo, 1964), except that this specimen does not possess a black but a whitish palate, and the axillae and the internal border of the mouth are yellow, a fact not reported by other authors." That the latter description is from a live specimen is confirmed by Cabrera (in litt.). He states, comparing coloration of the Córdoba specimen in life with our Figure 1, that the dorsal and limb patterns are darker, the light spaces in between having scattered brown spots, and emphasizes again that the axillae and borders of the mouth are yellow and brighter than the pale yellowish gray of the background. He further describes the ventral color in life as pale yellowish gray with small dark brown spots, scattered or sometimes forming a network on the throat. Under the throat and under the arms, where the scales are granular, the brown spots are almost central and many times larger than the scale itself, while ventrally under both body and limbs, where the scales are larger and smooth, the spots are scattered, fewer, and situated at the edges of the scales.

Gallardo's (1964) report of a black palate and throat in *U. gallardoi* is in agreement with Duméril and Bibron's (1837) description of the palate of *U. vautieri*, which Rand (in litt.) has confirmed (see below). However, Cabrera (in litt.) restates and amplifies the description in Bee de Speroni and Cabrera (above), remarking that in *U. gallardoi* the oral mucosa that covers the vomer, palatines, and more anterior part of the pterygoid bones is white, and only becomes black in the throat. He comments that when the lizard opens its mouth it is hard to see the black surface. (The anterior palate of the MCZ paratype of *U. gallardoi* from Salta, Argentina, has been compared with the anterior palate of an MCZ specimen of *U. vautieri* from São Paulo, Brazil. The first is unpigmented, the second is black.)

Distribution. (Map 1). Known in Argentina from the provinces of Córdoba, Misiones, Santa Fé, Tucumán, Santiago del Estero, and Salta, and in Bolivia from Santa Cruz de la Sierra. A record from Aimosgasta, La Rioja Province, Argentina, is

questionable (R. Laurent, in litt.). The specimen from Misiones (Universidad Nacional de Córdoba AC 079) is widely separated from the localities in the Chacoan Region of northern Argentina and Bolivia, but Cabrera (in litt.) has compared it with specimens from Córdoba and confirms its identification as *U. gallardoi*.

Reproduction. Gallardo (1964) states that a female from Salta collected in December contained seven eggs; another contained five eggs, 16×8 mm, with a yellowish-white membranous shell.

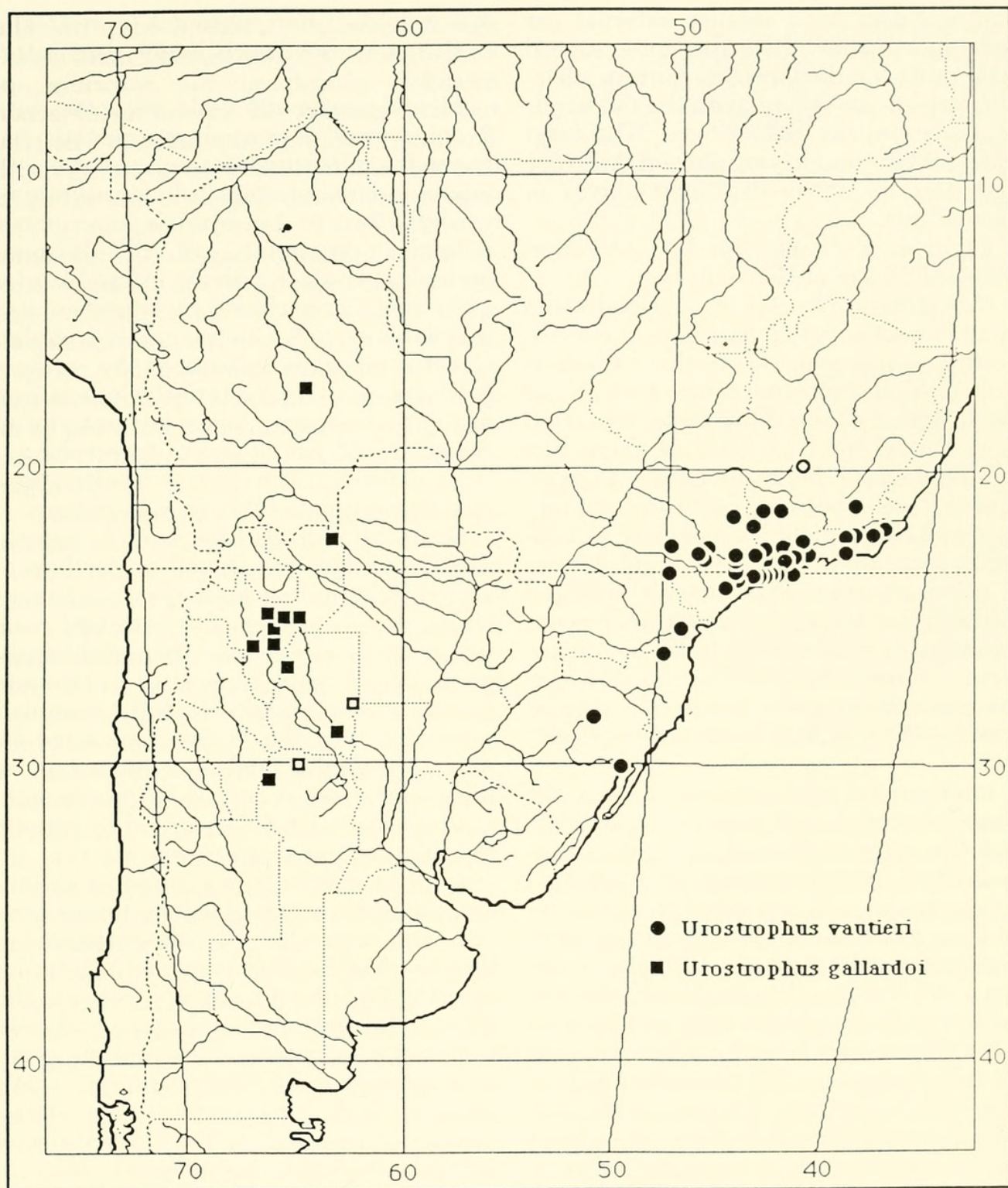
Behavior. The tail is partly prehensile according to Bee de Speroni and Cabrera (1984).

Ecology. Gallardo (1979) lists this species, under the name *Pristidactylus vautieri*, as an endemic of the Argentinian Chaco, and in figure 12 of the same work, which diagrams the "structural habitat" of lizards in an arid chacoan landscape, he places it on the trunk of a small, low tree, at the same height as *Aperoprists paronae* on an adjacent tree, and with *Tropidurus spinulosus* and *Tropidurus* sp. (= *T. etheridgei*) occurring both above and below the perch of *U. gallardoi*. Bee de Speroni and Cabrera (1984) say that the cryptic coloration of *U. gallardoi* imitates quite well the trunks of the trees with lichens (*Prosopis*, *Acacia*) that are common in the zone where the species is found, allowing them to pass unnoticed, an observation quite parallel to that of Gallardo (1977) for *Anisolepis grilli* that we record below. In a list of the herpetofauna of the province of Tucumán, Laurent and Terán (1981) indicate the occurrence of this species (as *U. vautieri*) in the eastern part of the province in "Bosques chaqueños . . . 250–500 (750) m" and "Bosque de transición . . . 350–700 m."

Urostrophus vautieri Duméril and Bibron 1837

Figure 3; Tables 1–4

1837 *Urostrophus vautieri* Duméril and Bibron, *Erpét. gén.*, Paris, 4: 78; 8: pl. 37, fig. 1.—Type locality: "Brésil."—Restricted type locality (Duméril and Duméril, 1851): "Rio-Janeiro." (Syntypes: Mus. Hist. Nat. Paris 6779, 6780.)



Map 1. The distribution of *Urostrophus gallardoi* (squares) and *Urostrophus vautieri* (circles). Solid symbols represent localities from which specimens were seen by us.

1843 *Laemactus (Urostrophus) Vautieri*—Fitzinger, Syst. Rept., Wien, 1: 62.

1845 *Urostrophus (lapsus) vautieri*—Gray, Cat. Liz. Coll. Brit. Mus., London, 184.

1851 *Urostrophus vautieri*—Duméril and Duméril, Cat. Méth. Coll. Rept. Mus. d'Hist. Nat. Paris, 55.

1862 *Leiosaurus vautieri*—Reinhardt and Lütken, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn, 1861: 223.

1868 *Urostrophus vautieri*—Hensel, Arch. f. Naturgesch., 34(1): 348.

1885 *Urostrophus vautieri*—Boulenger, Cat. Liz. Brit. Mus., London, 2: 122.

Diagnosis.—Differs from its only congener, described above, in having larger scales overall (i.e., lower scale counts, see

Tables 2 and 3), a smaller external ear opening, smaller than the interparietal scale, and a less distinct color pattern, characteristically lichenate, with the tail banded above but not fully ringed. The head scales and the underlying dermal skull roof rugosities are not as distinctly convex in large adults.

Etymology. Named for L. L. Vautier, collector of one of the syntypes.

Description. *Head* (Fig. 3). Head scales small, smooth, polygonal, flat or convex. Rostral pentagonal, two to three times as wide as high. Four to six postrostrals. Nasal ovoid, nostril almost filling scale, separated from rostral by 1 to 2 scales, from first supralabial by 1. Six scales between nasals. Five to 8 scales between posterior canthals. Supraorbital semicircles narrowly in contact or separated by 1 scale as large as those of the semicircles. Supraoculars enlarged medially, the largest oriented transversely, separated from the semicircles by a complete circumorbital series or this series incomplete. Four scales across supraocular area between supraorbitals and superciliaries.

Interparietal oval, separated from the semicircles by 1 to 2 scales on each side, from the nape scales by 3 to 7 scales. Canthals 2 to 4, the anteriormost often oriented obliquely upward, separated from the nasal by a much smaller scale or in contact. Superciliaries 10 to 14, the first largest, the first 1 to 3 oblique, the remainder squarish. Loreals very variable in size, 9 to 22. One row of lorilabials which extends beneath the suboculars. One to 2 preoculars. Suboculars 1 to 3, elongate. Postoculars not well differentiated from the temporals, except for the lowermost, which is distinctly larger. Eight to 9 supralabials, the fifth or sixth below the center of the eye, separated from the subocular by 1 row of lorilabials.

Temporals small, flat or slightly convex, variable in size, about 9 to 11 between orbit and ear. No distinct area of enlarged scales between upper and lower temporals. Anterior auriculars like temporals but smaller and slightly convex. Anterior margin of ear not distinctly "beaded." Posterior auricu-

lars granular. Ear subround to vertically oval, not or not much larger than interparietal.

Mental pentagonal, wide, in contact with 2 transversely oriented postmentals between the infralabials (sometimes also with lateral gulars, symmetrically or asymmetrically). Two to 4 sublabials in sequence with the postmentals, but only the postmentals in contact with the infralabials (or even the latter excluded by lateral gulars). Infralabials 6 to 8. Central gulars granular, smooth, partially separated by minute granules, grading posteriorly into larger, distinctly imbricate scales just anterior to the gular fold. Antehumeral-transverse gular fold distinct. A pregular fold often present. Lateral nape folds very ill-defined.

Body. Middorsals subgranular, smooth, slightly convex, juxtaposed or partly separated by minute granules, rather irregular in size. No trace of a vertebral scale row. Nape scales smaller than middorsals, granular, smooth, separated by minute granules. Flank scales smooth, granular, somewhat variable in size, separated by minute granules, and in almost regular transverse rows. Ventrals larger, smooth, not imbricate, partly separated by minute granules, in transverse rows.

Limbs. Brachials: all upper forelimb scales smooth, some as large as dorsals, convex, and separated by minute granules. Antebrachials: all lower forelimb scales smooth, and flat or slightly convex, the most distal distinctly imbricate and only the most proximal retaining minute granules between them. Carpals: supracarpals smooth, flat, imbricate. Infracarpals smooth, juxtaposed or weakly imbricate. Digitals of hand: supradigitals smooth, more or less wrapping around the digits, wider than long proximally, less so distally. Infradigitals smooth, wider than long and relatively flat proximally, the intermediate scales narrower and wrapping around the digit, the 3 distal scales again wider than long and wrapping around the digit. Axilla granular with minute granules interspersed. No axillary pit.

Femorals: suprafemorals larger than

dorsals, smooth, juxtaposed. Prefemorals larger than dorsals, smooth, subimbricate to imbricate, not significantly larger at knee. Infra-femorals like prefemorals but smaller. Postfemorals granular with minute granules between. Tibials: supratibials the size of dorsals, smooth with minute granules between. Pretibials and infratibials enlarged, smooth, subimbricate or imbricate. A granular zone at the ankle dorsally. Tarsals: supra- and infratarsals smooth, imbricate. Digitals of foot: supradigitals smooth, subimbricate, not wider than long. Infradigitals smooth, wider or not wider than long proximally, narrower distally. Lamellae under fourth toe 23 to 32.

Groin granular with minute granules interspersed. No inguinal pit.

Tail. Base of tail scaled like body, but more distal scales becoming slightly larger both above and below, and rectangular or trapezoidal. Six ventral rows becoming keeled just beyond the base of the tail and all caudal scales after about the proximal third of tail length.

Color and Pattern. The color pattern in preserved animals is variable but seems always to be weakly defined. Description of MZUSP 4462 from Garça, São Paulo, exchanged to San Diego State University, will serve for comparison with color in life as described below:

"Greyish, very vaguely mottled with brown above. Lines of dark pigment in the sutures of many head scales. On the side of the head two oblique dark rays across the orbit, one angled toward the ear, the other onto the posterior labials. Vague irregular brownish rhombs on the dorsum in front of hind limbs. More distinct rhombs on tail just posterior to hind limbs, continuations of these distally becoming fainter and assuming the character of dorsal bands. Below belly, throat, undersides of limbs and tail white without pattern."

A. S. Rand (notes taken in São Paulo in 1963 and 1964, generously provided) has the only description of *U. vautieri* in life, all from caged animals. He records one animal as having the general appearance

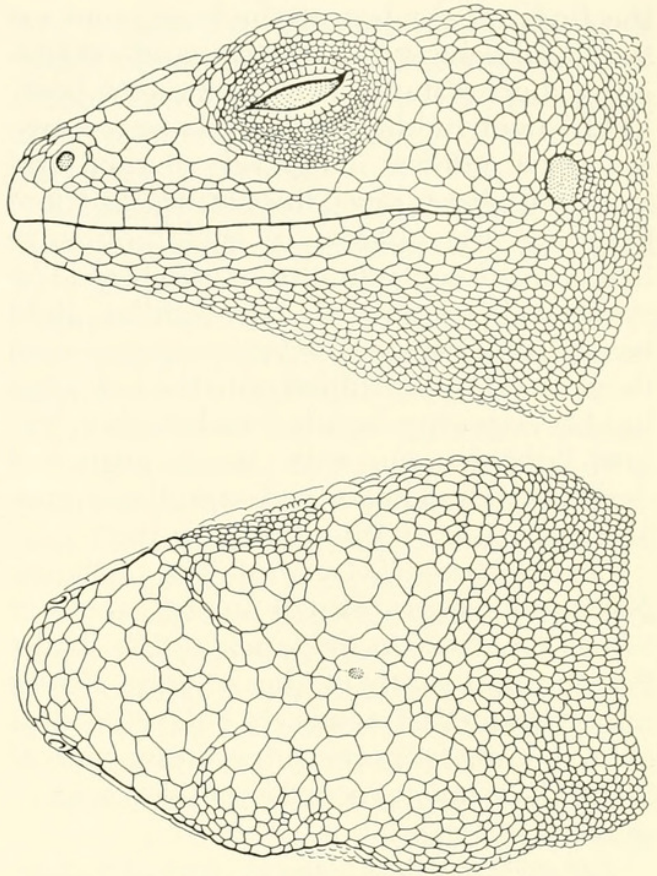


Figure 3. Head scales of *Urostrophus vautieri*, MCZ 84037 from Serra Negra, Brazil: Top, left lateral. Bottom, dorsal.

of a lichenate stick, the throat and roof of mouth black, tongue, lips, and mouth pink, and the body as "grey mottled with brown, sometimes taking a definite greenish tint. The mottling is heaviest on the neck and back and less on the sides. The tail is banded with brown (not ringed)."

Another lizard is described as "brown with dark brown markings dorsally. Head above light grey-brown with several narrow dark markings. A narrow dark brown line across head at anterior border of orbits. Another line behind this on each side running posterodorsally to meet its fellow at the interparietal scale. Posterior margin of head marked by a narrow transverse band broken at the midline and with several short anterior extensions. Some of the sutures between the head scales are also dark. The side of the head below and in front of the eye light grey-brown. Orbit brown with several dark markings radiating from it, two dorsally to connect with

the lines on the top of the head, one extending backward as a dark band extending a short distance toward the ear. Body light brown with a series of seven cross-bands or saddles, irregularly shaped and reaching down onto the sides and there breaking up, middorsally widening so as to connect longitudinally or nearly so. The middorsal centers of the saddles light brown like the areas between and around them. Saddles continued onto the tail. Legs light brown cross-banded with darker. Below light brown with many scattered darker scales. The animal sometimes grey and sometimes with a greenish cast."

Distribution. (Map 1). The Atlantic Forest of eastern Brazil in the states of Minas Gerais, Rio de Janeiro, São Paulo, Paraná, and south of the Atlantic Forest in northern Rio Grande do Sul; no records are available from the intervening state of Santa Catarina. A record from "Paraguay" may be in error.

Behavior. Rand's notes include comments on behavior, again on caged animals. We abstract them here:

U. vautieri is slow-moving, indeed moves less than *Polychrus acutirostris* and is immobile for long periods. Like *Polychrus* the head is held straight out from the body which is held close to and parallel to the supporting branch. The tail is definitely prehensile, and the animal can hang by the tail but does not do so unless compelled by being pushed off its perch. It can then turn around and pull itself up to the supporting branch. In climbing, the tail is used as a holdfast; in jumping, the tail is used upon landing. The tail coils slowly.

A brief display was seen by one animal in response to an *Enyalius* that shared its cage and which it chased about: A slow full up movement of the head, a slow movement down, then quick up and down. Body compressed, throat gorged.

Commenting on eye movement, Rand remarks: "The eye in this species has a light greyish iris with a pair of brownish areas on each side. These spots permit the observation that when the head is tilted

upward, the eye rotates in such a way that it retains its position relative to the horizontal."

Reproduction. Rand (1982) removed clutches of fully shelled eggs from the oviducts of five individuals measuring 68 to 86 mm snout-vent length. Clutch size varied from 6 to 13 ($M = 9.6$), egg volume from 0.5 to 0.7 ml ($M = 0.6$), and clutch volume from 3.1 to 8.3 ml ($M = 5.5$). One of us (RE) counted 5 eggs in the right oviduct and 7 in the left in a female (MZUSP 36114) measuring 78 mm snout-vent length.

Karyotype. M. L. Beçak *et al.* (1973) report a karyotype of $2n = 36$ (12 macrochromosomes and 24 microchromosomes). This pattern is regarded as primitive for lizards (Gorman, 1973; Paull, Williams, and Hall, 1976) and conveys no information about the species' affinities.

Miscellaneous. Pessôa and de Biasi (1973) report a plasmodium in the blood of *Urostrophus vautieri*.

Anisolepis Boulenger 1885

1885 *Anisolepis* Boulenger, Ann. Mag. Nat. Hist., London, (5)16: 85.—Type species (by monotypy): *Anisolepis iheringi* Boulenger 1885 = *Laemanctus undulatus* Wiegmann 1834.

1891 *Aptycholaemus* Boulenger, Ann. Mag. Nat. Hist., London, (6)8: 85.—Type species (by monotypy): *Aptycholaemus longicauda* Boulenger 1891.

Diagnosis. *Anisolepis* is a member of the iguanian family Polychridae, diagnosed by the acquisition of endolymphatic sacs that extend back between the supraoccipital and parietal bones into the dorsal neck musculature and other synapomorphies (Frost and Etheridge, 1989). It differs from *Polychrus* in having lost femoral pores, from the leiosaurs (*Enyalius*, *Pristidactylus*, *Diplolaemus*, *Leiosaurus*, *Aperoprists*) in having reduced the number of sternal rib pairs from 4 to 3 and in lacking longitudinally divided distal subdigital scales, and from the anoles (*Anolis*, *Chamaeolis*, *Phenacosaurus*, *Chamaelinorops*) in having acquired a small posterior coracoid fenestra, and in lacking

elongate second ceratobranchials and an anole type digital pad. *Anisolepis* differs from *Urostrophus* in having keeled ventral scales, and posterior marginal tooth crowns with tapered sides and reduced secondary cusps.

Etheridge and de Queiroz (1988) listed as derived characters shared by *Anisolepis undulatus*, *A. grilli*, and *Aptycholaemus longicauda* the reduction in secondary cusps of the marginal tooth crowns, loss of the posterolateral processes of the basisphenoid, and the acquisition of a ventrolateral row of enlarged scales and ventral body scales with sharp keels in parallel rows. *Aptycholaemus* was diagnosed by loss of the transverse gular fold, elongation of the tail, and reduction of the external ear. However, there are no derived features known to be shared by *undulatus* and *grilli* to the exclusion of *longicauda*, and therefore no evidence that *undulatus* and *grilli* share a more recent common ancestor with each other than with *longicauda*. Accordingly we here place *Aptycholaemus* Boulenger 1891 in the synonymy of *Anisolepis* Boulenger 1885. Thus constituted, *Anisolepis* is probably monophyletic.

Etymology. From the Greek *anisos* meaning unequal and *lepis* meaning scale, with reference to the heterogeneity of the squamation.

Characteristics. General squamation moderately to strongly heterogeneous.

Head scales small, polygonal, juxtaposed, smooth, flat or swollen.

Nasal round to flask-shaped, nostril posterodorsal or nearly filling scale, separated from the rostral by a postrostral, in contact with the first supralabial or separated by a lorilabial.

Supraorbital semicircles usually separated by 1 or 2 scales, rarely in contact or separated by 3.

Supraoculars rather weakly enlarged medially, in contact with supraorbitals or not, the circumorbital series differentiated or not.

Interparietal round or vertically oval,

larger than the other scales of the area, which are usually not differentiated, separated from the semicircles by 1 to 3 scales and from the nape granules by 5 to 8 scales. Parietal eye present.

Canthals 3, the anterior often angled above the nasal from which it is separated by a granule.

Superciliaries 7 to 10, the anterior 2 to 5 overlapping strongly posteriorly, the remainder with vertical sutures.

Loreals 11 to 31, varying much in size.

Lorilabials in 1 to 2 rows, completely or partly separating the subocular from supralabials. One to 2 rows continue forward on a labial shelf, to or below nasal.

Supralabials 6 to 10, the seventh to ninth below the center of the eye.

Preoculars 1 to 3, the uppermost in contact with the first supralabial and first canthal, or with first canthal only.

Subocular single, elongate, rarely in contact with the supralabials, usually separated by 1 to 2 rows of lorilabials.

Two to 4 differentiated postoculars or these indistinct.

Lower temporals smooth or weakly keeled. An intertemporal line or zone of enlarged scales present.

Ear subround, small and oblique, smaller than interparietal; or oval, equal to or larger than interparietal. Anterior margin like adjacent temporals, beaded, posterior margin granular.

Mental subpentagonal, wider than high, in contact with 2 postmentals (=first sublabials) between the infralabials or with these and a small median scale (=median gular). One to 7 sublabials in sequence on each side with the first sublabials.

Central gulars smooth and juxtaposed, rarely weakly keeled and subimbricate, becoming larger and imbricate, smooth or keeled just before the transverse gular fold or posteriorly always large, keeled and imbricate, continued without change into the keeled ventrals.

Transverse gular-antehumeral fold present or absent. Pregular fold present or absent.

Longitudinal nape fold present, well defined by the enlarged scales, or indistinct and without distinctly enlarged scales.

Middorsals irregular in size, weakly to strongly keeled, flat or swollen, in a distinct zone or not, the vertebral rows smaller than the paravertebrals or not. No middorsal row of aligned scales.

Nape scales granular or subgranular, grading into keeled dorsals. Two lines of enlarged scales on lateral nape or not.

Flank scales smaller but irregular in size, keeled or smooth, separated by minute granules or not, with 1, 2, or no longitudinal, partial or complete lines of enlarged scales that are keeled and imbricate. Granular areas in axilla and groin.

Ventrals much larger, strongly keeled, imbricate, mucronate or submucronate. Scales at anterior margin of vent smaller, less strongly keeled or subgranular.

Tail more or less compressed, all scales keeled, imbricate. Ventral scales of tail may be larger than body ventrals. Verticils not present.

Tail greater than 69% of total length.

Limb scales imbricate, keeled anteriorly, granular on posterior of humeri and femora, sometimes with minute granules grading into keeled scales dorsally. Ankle and inside of knee also granular.

Supradigitals of hand wide, imbricate, smooth, or uni- or multicarinate. Supradigitals of foot narrower, imbricate, weakly keeled or multicarinate.

Infradigitals of both hand and foot wide, smooth, imbricate, sublamellar.

No femoral or preanal pores.

Axillary pocket present or absent. No inguinal pocket.

Anisolepis grilli Boulenger 1891

Figures 4, 5, and 6; Tables 1–4

1834 *L. [aemactus] obtusirostris* Wiegmann, Herp. Mex., Saur. Spec., Berlin, 46.—Type locality: "Brasilia." (Holotype: Zool. Mus. Berlin No. 496).*

* Although these names have priority over the name *Anisolepis grilli* Boulenger 1891, neither have been used since Gray (1845). At least five authors in ten publications have used Boulenger's *A. grilli* to refer

1834 *L. [aemactus] Fitzingeri* Wiegmann, Herp. Mex., Saur. Spec., Berlin, 46.—Type locality: "Brasilia." (Holotype: Zool. Mus. Berlin No. 495).*

1837 *Laemactus Fitzingeri*—Duméril and Bibron, Erpét. gén., Paris, 4: 74.

1837 *Laemactus obtusirostris*—Duméril and Bibron, Erpét. gén., Paris, 4: 75.

1843 *Laemactus (Urostrophus) Fitzingeri*—Fitzinger, Syst. Rept., Wien, 1: 62.

1845 *Ecphymotes Fitzingeri*—Gray, Cat. Spec. Liz. Coll. Brit. Mus., London: 184.

1845 *Ecphymotes obtusirostris*—Gray, Cat. Spec. Liz. Coll. Brit. Mus., London: 185.

1882 *Laemactus undulatus*—Boettger, Ber. Senckenberg. Naturf. Ges., 130.

1891 *Anisolepis grilli* Boulenger, Ann. Mus. Civ. Stor. Nat. Genova, (2)10: 909.—Type locality: "Palmeira, Province of Paraná, Brazil." (Syntypes: Brit. Mus. Nat. Hist. Nos. 91.11.19.2 [RR 1946.8.12.38], 91.9.24.10 [RR 1946.8.5.58]).

1893 *Anisolepis undulatus*—Boettger, Kat. Rept.-Samm. Senckenberg, 1: 61.

1896 *Anisolepis lionotus* Werner, Verhandl. Zool. Bot. Ges. Wien, 46: 470.—Type locality: "Blumenau, Provinz Sta. Catarina, Brasilien." (Holotype: Naturhist. Mus. Wien No. 18904).

1896 *Anisolepis grilli*—Werner, Verhandl. Zool. Bot. Ges. Wien, 46: 471.

1905 *Anisolepis undulatus*—Boettger, Zool. Anz., 29(11): 373.

1930 *Aptycholaemus longicauda*—Burt and Burt, Proc. U.S. Nat. Mus., 78(6): 7.

1961 *Anisolepis grilli*—Capocaccia, Ann. Mus. Civ. Stor. Nat. Genova, 72: 92.

1965 *A. [nisolepis] iheringi*—Etheridge, Herpetologica, 21(3): 167.

1965 *A. [nisolepis] lionotus*—Etheridge, Herpetologica, 21(3): 167.

1970 *Anisolepis grilli*—Peters and Donoso-Barros, Bull. U.S. Nat. Mus., 297: 42. (*A. lionotus* synonymized.)

1976 *Anisolepis iheringi*—Gundy and Wurst, J. Herpet., 10(2): 116.

1982 *Anisolepis undulatus*—de Queiroz, Herpetologica, 38(2): 310.

Diagnosis. *A. grilli* differs from *A. undulatus* in having less distinctively heterogeneous scalation: enlarged dorsal body scales grading gradually into smaller flank

to this species during the past 50 years, which, according to Article 79c of the International Code of Zoological Nomenclature (1985) provides a prima facie case for suppression of the two Wiegmann names in favor of Boulenger's *A. grilli*. Accordingly we are applying to the International Commission on Zoological Nomenclature for suppression of *L. obtusirostris* and *L. Fitzingeri*.

scales rather than being abruptly larger, nape without enlarged, erect scales, no dorsolateral rows of enlarged, keeled scales, supradigital scales of hand smooth rather than indistinctly uni- or multicarinate, keeled ventral scales in more (17 to 25 versus 13 to 19) longitudinal rows, and a larger adult size (maximum snout-vent length of females 97 mm, males 79 mm, versus females 83 mm, males 70 mm). *A. grilli* differs from *A. longicauda* in having a larger external ear, larger than the interparietal scale rather than conspicuously smaller, in having an antehumeral-transverse gular fold, and a shorter tail (mean tail/total length in males 0.73, females 0.71, versus males 0.77, females 0.74).

Etymology. Named after Dr. G. Franco Grillo, collector of the syntypes.

Description. *Head* (Fig. 4). Head scales small to moderate, smooth, swollen, variable in size. Rostral subpentagonal, twice to about three times as wide as high. Postrostrals 6 or 7. Nasal ovoid, nostril slightly posterior in position, in contact with the first supralabial or separated from it by 1 scale, separated from the rostral by 1 post-

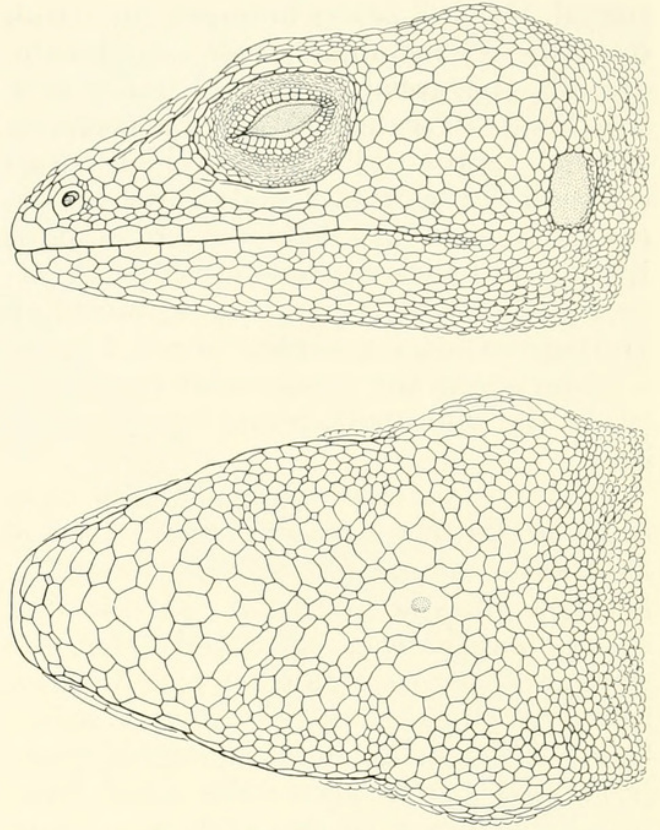


Figure 4. Head scales of *Anisolepis grilli*, MCZ 133190 from Dorizon, Paraná, Brazil: Top, left lateral. Bottom, dorsal.

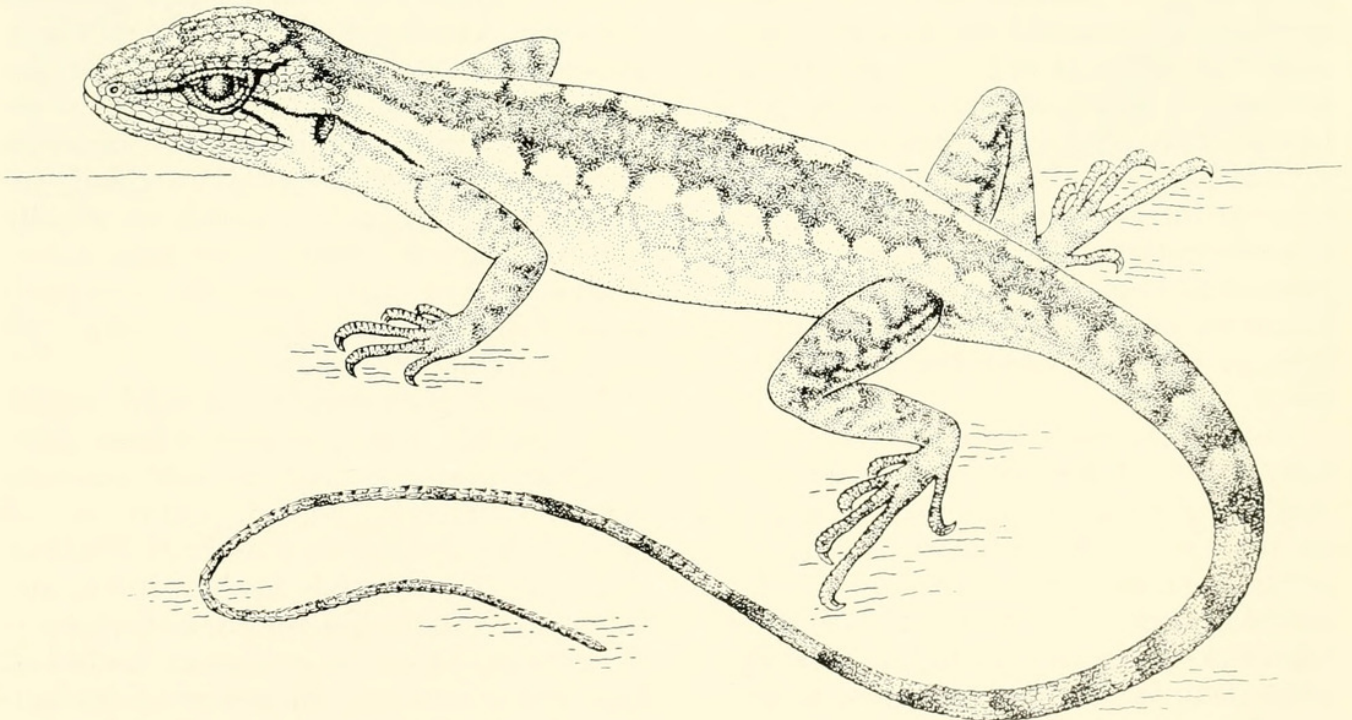


Figure 5. *Anisolepis grilli*, NMW 18904, holotype of *Anisolepis lionotus*, from Blumenau, Santa Catarina, Brazil.

rostral. Six to 7 scales between the nasals dorsally. Frontonasal scales moderate, smooth, polygonal, relatively uniform in size. Six to 10 scales between the posterior canthals. Supraorbital semicircles separated medially by 1 to 4 scale rows. Supraoculars enlarged medially, the largest scales tending to be transversely oriented. A circumorbital series separating supraorbitals and supraoculars, complete or not. Four to 6 scales across the supraocular region between the supraorbitals and the superciliaries.

Scales of parietal region smaller than those of the frontonasal region, smallest anteriorly and posteriorly, largest laterally. Interparietal larger than surrounding scales, nearly oval, separated from the semicircles on each side by 1 to 3 scales, from the nape granules by 5 to 7 scales. Canthals 2 to 4, the anteriormost obliquely positioned partly above the nasal from which it is separated by a scale or granule, or with which it is in contact. Eight to 11 superciliaries in 2 rows, the first largest, the first 3 to 5 slightly elongate, the remainder squarish or rectangular, those anterior in the lower row overlapping more strongly those in the upper row. One to 2 preoculars, in contact with the posterior canthal or separated from it by a polygonal scale. Suboculars 1 to 2. Two to 4 postoculars, not very distinct from the temporals. Loreals 25 to 39, very variable in size. Two rows of lorilabials below the loreals, a complete or incomplete row extending below the subocular, separating it from the supralabials. One anterior lorilabial inserted below the nasal. Ten to 11 supralabials, the sixth or seventh below the center of the eye.

Temporals small, somewhat variable in size, about 11 between orbit and ear. A single or double line of enlarged scales or no such line differentiated. Anterior auriculars smaller than temporals, and anterior margin of ear weakly "beaded." Posterior auriculars granular. Ear vertically oval, larger than or equal to interparietal.

Mental pentagonal, wide, in contact with 2 transversely positioned postmentals (=first sublabials), rarely also narrowly in contact with a lateral gular on one or both sides. Two to 3 sublabials in sequence with the first sublabials. Six to 9 infralabials. Central gulars smooth, juxtaposed or sometimes with granules between, becoming larger, keeled and imbricate in front of the transverse gular fold.

Antehumeral-transverse gular fold distinct. A pregular fold often present.

Body. About 6 to 9 middorsal rows of small, keeled scales, irregular in size, juxtaposed, tending to grade into flank scales, which are smaller but also irregular in size, keeled and partly separated by minute granules. A ventrolateral line of enlarged scales ca. 6 scales above the ventrals or this line absent. Nape scales, juxtaposed or separated by granules, smaller than middorsals, swollen, keeling weak or absent. No lines of enlarged scales on nape. Ventrals larger, keeled, the keels not in line, imbricate, mucronate, in about 21 to 25 transverse rows.

Limbs. Brachials: suprabrachials rather large, keeled, imbricate. Infra- and postbrachials subgranular, imbricate or granular, juxtaposed or with minute granules between. Antebrachials: keeled, imbricate above; below imbricate, generally smaller and only some scales keeled. Carpals: supracarpals imbricate, keeled. Infracarpals imbricate, smooth. Digitals of hand: supradigitals imbricate, smooth or weakly uni- or bicarinate, wider than long. Infradigitals imbricate, smooth, wrapped around digit. Axilla granular. Axillary pit present, deep or shallow.

Femorals: suprafemorals keeled, imbricate, variable in size, smaller at knee. Postfemorals granular with minute granules between. Tibials: keeled, imbricate all around. A granular zone dorsally at ankle.

Tarsals: supratarsals keeled, imbricate. Infratarsals smooth, swollen, imbricate.

Digitals of foot: supradigitals keeled, at least as wide as long, imbricate. Infradigitals smooth, wider than long, imbricate.



Figure 6. Sketch of *Anisolepis grilli* done by a São Paulo artist from the living animal and donated by A. S. Rand.

Twenty-nine to 33 lamellae under fourth toe. Groin granular. No inguinal pit.

Tail. All caudal scales keeled, the keels in line, ca. 4 ventral rows larger.

Color and Pattern. (Figs. 5, 6). The color pattern in preserved animals is highly variable; gray or brown may predominate. Boulenger's (1891a) color description ap-

pears to represent a decidedly reduced pattern, as Werner (1896) has already commented: "Purplish brown above, with some rusty spots, loreal region and lips bluish gray, the throat whitish, the rest of the lower parts pale brown."

More frequently the pattern, as again Werner (1896) commented, may be quite similar to that of *A. undulatus* as figured by Boulenger (1885c) for a syntype of *A. iheringi*. We describe such a pattern below from MZUSP 10142 from São Bernardo, São Paulo, exchanged to San Diego State University.

"Color composed of browns, light browns, dark browns, grey browns and grey. Head above dark brown. Laterally a light brown stripe with irregular margins extending from the posterior orbit onto nape above ear. Light brown on labials continued backward to lower edge of ear and flecked with darker scales. Body middorsally with a broad brown band continuous forward with the dark brown of the head, edged laterally with darker triangles, apices ventral, which are each continued ventrolaterally by narrow irregular dark lines that are bordered anteriorly by wider lines of grey and posteriorly by light brown oval areas. The grey and dark brown lines join on the lower flanks a ventrolateral band, grey mottled with dark brown. This ventrolateral band is itself continued ventrally by grey and dark brown lines like those above, but more vertical, and like the upper lines enclosing light brown spots, but these more random. Belly light brown vaguely streaked with grey. Throat light brown with sparse fine dark spotting. Underside of limbs light brown mottled and smudged with grey. Tail above like dorsum at base but dorsolateral band fading into the light lateral color of the distal tail which is very lightly smudged with darker."

Rand (1964 notes on São Paulo caged specimens) reports the color in life of a female *Anisolepis grilli*:

"Brown above with a definite darker dorsal pattern. Head above medium brown with indistinct dorsal mottling and scat-

tered lighter scales. Sides of head, loreal region, lips and lower jaw light brown or yellowish brown, with scattered dark brown scales. An indistinct dark line starting at the anterior border of the orbit, broken by the eye, continuing to the posterior margin of the orbit, there forking with a narrow branch going posteriorly to the upper half of the anterior border of the ear, broken by ear, then proceeding onto neck almost to the level of the shoulder. Iris golden.

"Body with a middorsal stripe, about 10 or 12 scales wide, of medium grey brown, margined by a series of dark triangles, apices lateral, bases merging into the dorsal stripe. The triangles start at the back of the head as irregular dark spots close together (or an interrupted dark band). These spots take on their triangular shape just behind the level of the shoulders, alternating from side to side, so close-set that their bases seem to touch, about 11 on each side from shoulder to base of tail. The tips of the most distinct triangles are surrounded by white or tan light spots and are extended posterolaterally by dark lines reaching about halfway down the flanks, to about the level of the ear and the upper face of the hindleg. The upper parts of these dark lines are the most distinct and are edged by the same light color that emphasizes the tips of the triangles. On the neck this light color is seen as a light line margining the dark nape band laterally. The areas between the dark triangles and the lines, as well as the lower flanks, are light brown, flecked with small dark markings.

"The dark triangles extend onto the proximal three-fourths of the tail, becoming saddles separated by light brown. The legs above are, like the lower flanks, light brown flecked with darker. The venter is light brown, becoming yellow midventrally on the belly and the chest and chin, the latter and the throat with black or dark brown scales not arranged in any pattern. The undersides of legs and tail are light brown. The tongue and the lip pale pink, the inside of mouth and throat black."

Another female specimen is described as "like the first in pattern but the brown areas darker, almost a slaty grey, and the light areas a pinkish or reddish brown. The belly is distinctly flecked with dark and like the light areas in ground color."

Still another specimen differs only slightly: "The lizard a grey brown, speckled or mottled with lighter. The top of the head is grey with lighter grey flecks; the side of the head has a light stripe from the eye, including the upper eyelid, back to the temple, light brown below this and then a dark grey band through the eye, above the ear and onto the neck. Underneath this the loreal region, the upper part of the eye, the lips and back through the ear are light brown like the throat.

"The back has a light grey brown dorsal stripe, edged with the bases of black triangles. These point laterally; their bases do not meet but are separated by about their own length. From the tip of each triangle a black streak with irregular margins extends down and back at about a 45° angle less than halfway down the side. The triangles and lines are edged behind by light tan patches. The ground color is a medium grey flecked with dark. There is an indistinct series of light spots in a line from the axilla to the groin. The black triangles alternate.

"The dorsal black markings continue on the tail, where they meet at midline and for the posterior two-thirds of the tail form irregular cross bands. The legs have irregular light and dark cross bands on a grey ground.

"The venter is light, lightest in the midline and flecked with black.

"The pupil is round, the iris light brown."

Distribution. (Map 2). Known in Brazil from the states of Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, where it occurs in the Atlantic Forest, but also in "cultural steppe" in the state of São Paulo (Vanzolini, 1983). Recorded in Argentina from the Misiones Province. Two specimens (Zool. Mus. Berlin 6246) are said to have

come from Montevideo, Uruguay. The locality seems doubtful, but if accurate, *A. grilli* may be sympatric with *A. undulatus* in Uruguay.

Behavior. Rand (notes of 1963 and 1964) reports that *A. grilli* like *U. vautieri* has a fully prehensile tail, can hang by it and pull itself back up to its perch, but, like *vautieri*, it does not do so willingly. The tail of *grilli* curls immediately on contact with a perch; it is used as a hook not a hand. Again, like *vautieri*, *grilli* may be immobile (in cages) for long periods.

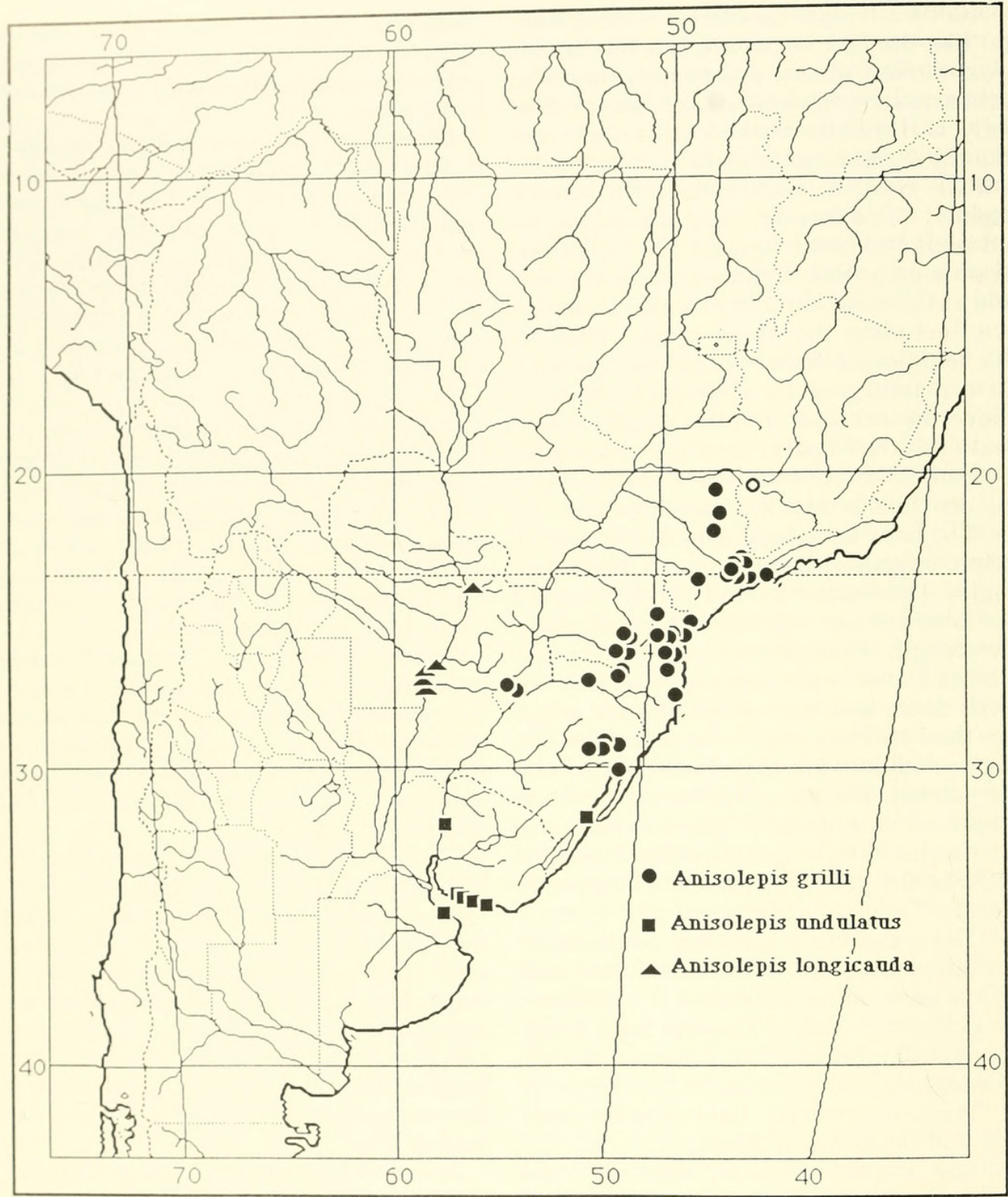
A field report on this species is that by W. W. Milstead for a specimen from Rio Grande do Sul, Brazil, misidentified by him as *A. undulatus* but confirmed by us as *A. grilli*. We have information on this specimen both from a letter from Milstead to one of us (RE) and from an oral report to Rand transcribed in the latter's notes. We quote both sources verbatim:

Rand: "Milstead reports that the only individual that he saw in the field was on the slender trunk of a spindly tree at the edge of a field in open second growth. It was head up several feet above the ground and had its tail wrapped in a long spiral around the tree."

Letter to Etheridge: "No. 429 [now FMNH 80115] W. W. Milstead, March 29, 1954, Brazil, R.G.S., Farroupilha, 18 km south . . . in a small tree about midafternoon. This was on a hill in an area of dense vegetation consisting of pampas grass, weeds and small weed-like trees. The area was probably forest land that had been burned off in the past. Typical succession: forest-arson-cultivated field-worn out field-weeds."

A second field report is that by Gallardo (1977, p. 125, translated) for two specimens taken in the Reserva de Paranapiacaba, São Paulo, Brazil: ". . . they cling to the branches of shrubs in the forest, passing easily unnoticed, aided by their immobility and the grayish-greenish coloration, which matches the bark and lichens."

Reproduction. Rand (1982) removed clutches of fully shelled eggs from the oviducts of 9 individuals measuring 73 to 93



Map 2. The distribution of *Anisolepis*: *A. grilli* (circles), *A. undulatus* (squares), and *A. longicauda* (triangles). Solid symbols represent localities from which specimens were seen by us.

mm (M = 82.8 mm) snout-vent length. Clutch size varied from 4 to 11 (M = 8.1), egg volume from 0.4 to 0.7 ml (M = 0.6 ml), and clutch volume from 2.6 to 8.0 ml (M = 4.8 ml).

Karyotype and DNA Content. The

karyotype is $2n = 36$ (12 macrochromosomes + 24 microchromosomes) (Gorman, Atkins, and Holzinger, 1967; Gorman, 1973; Beçak *et al.*, 1973; Soma, Beçak, and Beçak, 1974). DNA content is reported by Soma, Beçak, and Beçak (1975) as 3.8 pi-

cograms, the lowest of the 15 thus far reported in iguanians (Olmo, 1984).

Miscellaneous. De Queiroz (1982) reported (as *A. undulatus*) the presence of 14 scleral ossicles, with numbers 1, 6, and 8 positive, and numbers 4, 7, and 10 negative, a common pattern in pleurodont iguanians. Arnold (1984) states that this species has a distinctive, swollen insertion of the *m. retractor lateralis anterior* of the hemipenis, a condition it shares with *A. longicauda*.

Discussion. Capocaccia (1961) listed two specimens of *A. grilli* in the Museo Civico di Storia Naturale di Genova, from Palmeira and Curitiba (=Curitiba), Brazil, as syntypes. Through the kindness of Dr. Lilia Capocaccia we have been able to examine these specimens and find that their scale counts and other data are within the expected ranges of variation of *A. grilli*. However, the type description (Boulenger, 1891a) was based solely on the two British Museum specimens from Palmeira, and thus, under the provisions of Article 72(b) of the International Code of Zoological Nomenclature adopted in 1985, only these two specimens may be considered syntypes.

Anisolepis undulatus (Wiegmann, 1834)

Figures 7, 8, 9, and 10; Tables 1–4

1834 *L. [aemactus] undulatus* Wiegmann, Herp. Mex., Saur. Spec., Berlin, 46.—Type locality: "Brasil" (Holotype: Zool. Mus. Berlin No. 497).

1837 *Laemactus undulatus (lapsus)*—Duméril and Bibron, Erpét. gén., Paris, 4: 75.

1843 *Laemactus (Urostrophus) undulatus*—Fitzinger, Syst. Rep., Wien, 1: 62.

1845 *Ecphymotes undulatus*—Gray, Cat. Spec. Liz. Coll. Brit. Mus., London, 185.

1885 *Anisolepis Iheringii* Boulenger, Ann. Mag. Nat. Hist., London, (5)16: 86.—Type locality: "Province Rio Grande do Sul . . . S. Lorenzo, on the southern border of the Lagoa dos Patos." (Syntypes: Brit. Mus. Nat. Hist. No. 85.6.26.4–5 [RR 1946.8.5.90–1].)

1885 *Anisolepis iheringii*—Boulenger, Cat. Liz. Brit. Mus., London, 2: 122; pl. 9, fig. 3.

1887 *Anisolepis undulatus*—Boulenger, Cat. Liz. Brit. Mus., London, 3: 500 (*Anisolepis iheringi* synonymized).

1895 *Anisolepis Bruchi* Koslowsky, Rev. Mus. La Plata, 6: 417; pl. 1.—Type locality: "Punta Lara,"

Provincia de Buenos Aires, Argentina. (Holotype Museo de La Plata, not located).

1896 *Anisolepis undulatus*—Werner, Verhandl. Zool. Bot. Ges. Wien, 46: 471. (*Anisolepis bruchi* synonymized).

1960 *Anisolepis undulatus*—Vaz-Ferreira and Sierra de Soriano, Rev. Fac. Human. Cienc., 18: 20.

Diagnosis. *A. undulatus* differs from *A. grilli* and *A. longicauda* in having a more distinctively heterogeneous scalation: dorsal body scales abruptly larger than, rather than grading into lateral body scales, nape with enlarged erect scales, and a conspicuous dorsolateral row of large, keeled scales. It further differs from *A. grilli* in having uni- or multicarinate supradigital scales on the hand, the keeled ventral body scales in 13 to 19 rather than 17 to 25 rows, and a smaller maximum adult size (females 83 mm, males 70 mm, versus females 97 mm, males 79 mm). It further differs from *A. longicauda* in having an external ear opening larger than, rather than conspicuously smaller than, the interparietal scale, an antehumeral-transverse gular fold, and a shorter tail (mean tail/total in males 73, females 71, versus males 77, females 74).

Etymology. Named *undulatus* because of the zig-zag dorsal pattern.

Description. **Head** (Fig. 9). Head scales small, more or less swollen, smooth or bluntly keeled. Rostral subpentagonal, two to three times as wide as high. Five postrostrals. Nasal oval or round, nostril central or slightly posterior in position, in contact with the first supralabial, separated from the rostral by 1 postrostral. Five to 7 scales between the nasals dorsally. Frontonasal scales smooth, convex, relatively uniform in size. Six to 11 scales between the posterior canthals. Supraorbital semicircles separated by 1, rarely in contact or separated by 2 scale rows. Supraoculars enlarged medially, transverse or not, completely or incompletely separated from the semicircles by a circumorbital series. Scales of the interparietal region usually largest laterally, about the same size or some of them a little smaller than those of the frontonasal region. Interparietal larger than surrounding scales, oval, separated from

the semicircles by 1 to 2 scales on each side, from the nape granules by 4 to 8 scales of varying size. Canthals 2 to 4, the anteriormost oriented above the nasal and separated from the nasal by 1 scale, 1 or more granules, or in contact. Superciliaries 7 to 8, the first 2 or 3 elongate and strongly and obliquely overlapping posteriorly. The posterior superciliaries less elongate and tending to overlap anteriorly. One to 2 preoculars (usually 1), in contact with the posterior canthal or separated by a polygonal scale. One subocular. Postoculars not well differentiated. Loreals 11 to 26, varying very much in shape and size. A single row of lorilabials, extending anteriorly below the nasal, posteriorly between subocular and supralabials. (Rarely the subocular may be in contact with supralabials.) Supralabials 7 to 9, the sixth or seventh below the center of the eye.

Temporals small, rather uniform in size, smooth or weakly keeled, 8 to 12 between orbit and ear. An indistinct zone of larger scales separating upper and lower temporals. Anterior auriculars like lower temporals, not enlarged, but anterior margin of ear "beaded." Posterior auriculars granular. Ear round or vertically oval, not or not much larger than interparietal.

Mental subpentagonal, wider than high, in contact with 2 postmentals (=first sublabials) between the infralabials. Three to 5 sublabials in sequence with the first sublabial on each side. Only the first sublabials in contact with the infralabials. Eight to 10 infralabials, smaller than or only equal to the scales of the sublabial series. Central gulars smooth or keeled, sometimes swollen, juxtaposed, subimbricate or imbricate, becoming larger, pointed and very distinctly keeled and imbricate at the transverse gular fold (Fig. 10), which is continued laterally on the two sides as antehumeral folds. Pregular fold well defined or indistinct.

Body. A middorsal zone 6 to 9 rows wide, with enlarged keeled imbricate scales, the 2 largest rows separated by 2 to 3 rows of irregularly smaller keeled imbricate scales,

the scales anteriorly smaller and more pointed, posteriorly becoming larger and truncate. On the nape, erect middorsal scales behind the pileus grading into the much larger keeled, imbricate, often truncate scales of the middorsal zone. Laterally on the nape, often 2 rows of distinctly enlarged spinose scales, interrupted or not, 1, less frequent, beginning at the intertemporal area and continuing as swollen keeled scales above the ear to beyond the shoulder, the second, invariably present and almost always continuous, starting from the posterior lower corner of the ear, and perhaps tapering posteriorly, ending at the shoulder.

On the flanks, usually an area of smaller swollen keeled scales, very unequal in size, separating the middorsal zone from a dorsolateral line of 1 to 4 rows of enlarged keeled scales that continues forward, sometimes interrupted, to join the upper line of enlarged scales. Below this upper line of enlarged flank scales, if present, an area of mostly smaller swollen keeled scales but with irregular broken rows of larger scales. Still below this and 5 rows above the ventrals a single, usually regular, but sometimes interrupted, line of enlarged scales from the thigh to the zone of granular smooth scales that lies behind the shoulder and in the axilla.

Ventrals much larger, strongly keeled, mucronate or notched, the keels in line, in 13 to 19 longitudinal rows.

Limbs. Brachials: suprabrachials and prebrachials keeled, imbricate except at immediate insertion of arm. Infra- and postbrachials granular, swollen. Antebrachials: keeled and imbricate all around. Carpals: supracarpals keeled, imbricate. Infracarpals smooth, imbricate. Digitals of hand: supradigitals uni- or multicarinate, imbricate, wider than long, truncate or notched. Infradigitals smooth, imbricate. Axilla granular.

Femorals: supra-, pre-, and infra-femorals keeled, imbricate, truncate, as large as middorsals. Postfemorals granular. Scales at knee smaller. Tibials: keeled, imbricate

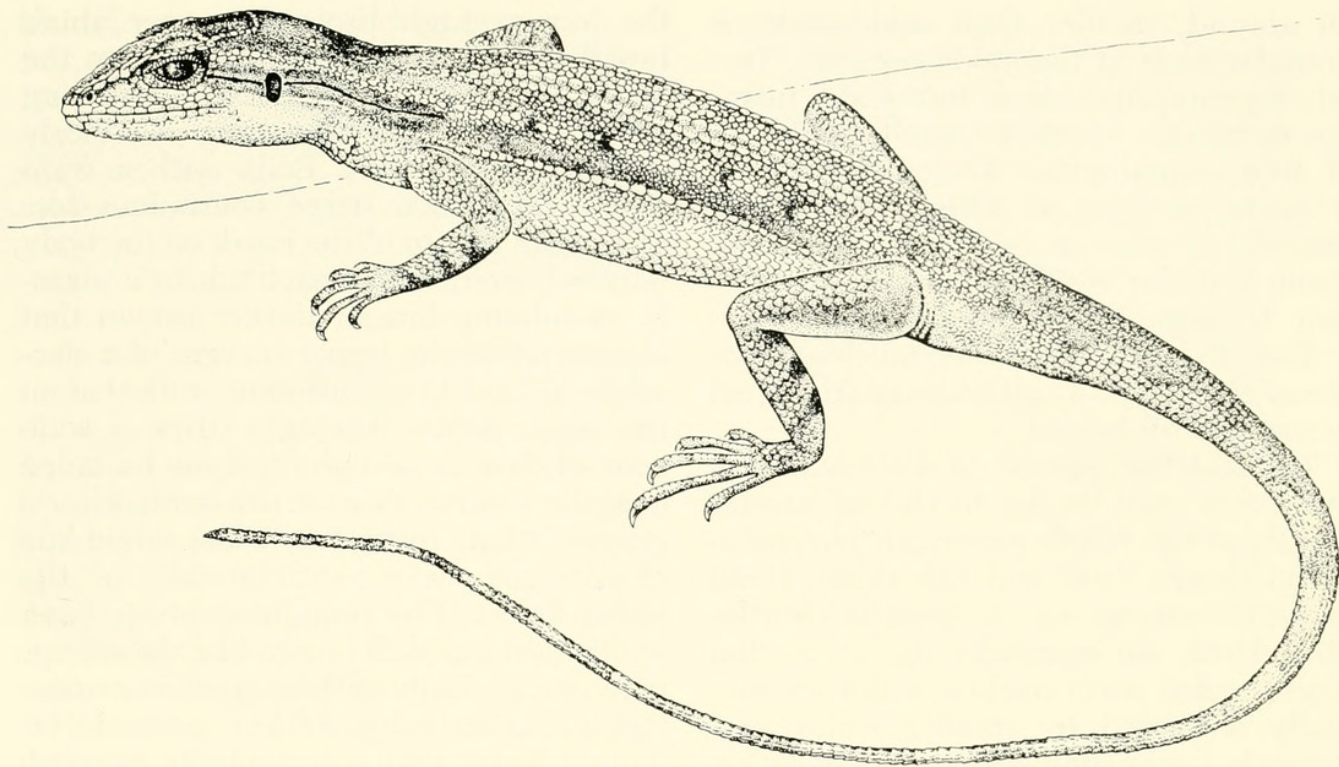


Figure 7. *Anisolepis undulatus*, USNM 65545, 75 mm snout-vent, adult female from Paysandú, Uruguay.

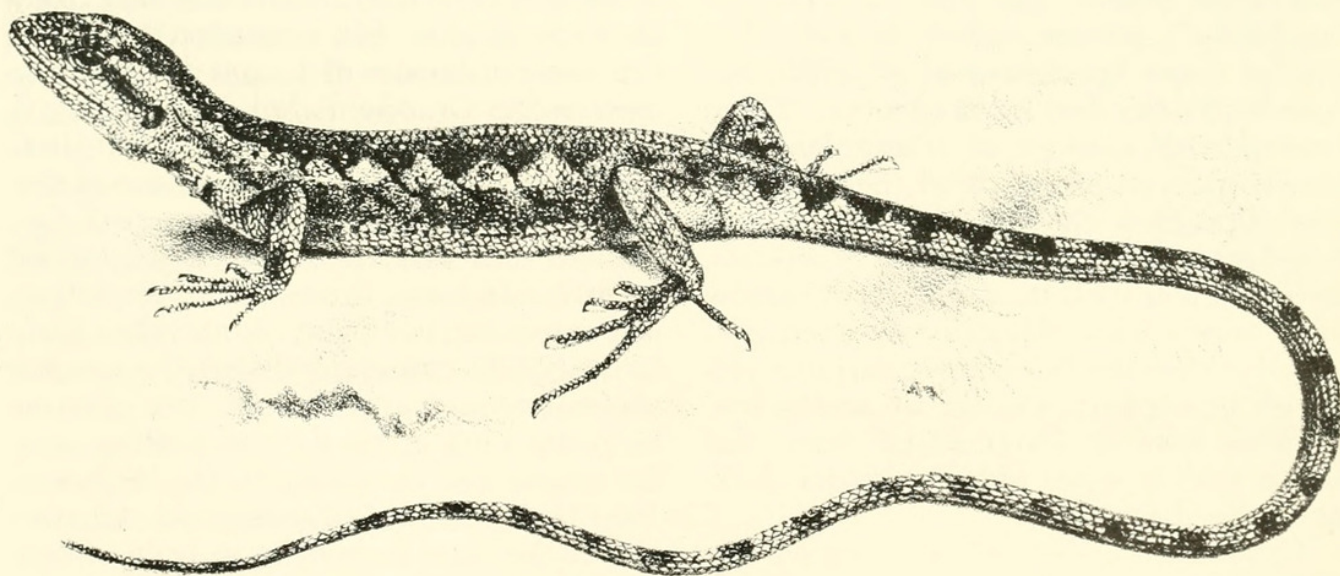


Figure 8. *Anisolepis undulatus*, reproduced from Boulenger (1885c), 2: pl. 9, fig. 3 (as *Anisolepis iheringi*).

all around, smaller than middorsals. A granular zone at the ankle dorsally. Tarsals: supratarsals keeled, imbricate. Infratarsals smooth, imbricate, swollen. Digitals of foot: supradigitals keeled, imbricate, truncate, as long as wide. Infradigitals smooth, as wide as or wider than long. Groin granular. Axillary pit shallow or absent. No inguinal pit.

Tail. Dorsum of base of tail like middorsal zone. Distally all scales nearly equal in size and all keeled.

The scalation pattern of *Anisolepis undulatus* is very similar to that of certain species of the North American phrynosomatid (*sensu* Frost and Etheridge, 1989) genus *Urosaurus*, e.g., *U. ornatus* (Mittleman, 1942, see especially fig. 3), in that large, keeled paravertebral scales are medially separated by smaller scales, and abruptly larger than adjacent flank scales, the flank scales with rows or patches of larger scales.

Color and Pattern. (Figs. 7 and 8). There appear to be two major color patterns—one that was figured by Boulenger (1885c) for the type of *A. iheringi*, another corresponding to Koslowsky's (1895) figure of *Anisolepis bruchi*. The first ("zig-zag" or "undulate") pattern, which is quite like that of many specimens of *A. grilli*, has been well described by Boulenger: "Olive brown, with a series of triangular dark brown spots on each side of the vertebral line, forming a zig-zag band; this is bordered externally with yellowish or reddish; the triangular spots may send forth narrow dark brown lines obliquely directed posteriorly down the sides; lower surfaces yellowish or coppery, the throat with a few blackish dots or longitudinal lines; tail above with a series of rhomboidal dark, light-edged spots."

The second ("lineate") pattern we describe from a Uruguayan specimen (DZVU 280: from near Carrasco, Canelones District, near Montevideo): Head above dark brown. On each side a light grayish band from the upper posterior border of the orbit, extending backward above the ear onto

the dorsum. Light brown on upper labials broadening backwards to encompass the lower two-thirds of the ear, narrowing again to a grayish line ending posteriorly in front of shoulder. Body with a wide middorsal brown stripe continuous forward with brown of the head, on the body narrowly bordered on each side by a slightly undulating line of darker brown that also serves as the upper margin of a dorsolateral light line continuous with that on the nape. Below this light stripe a wide zone of dark brown on the flank bounded near the ventrals by a narrow ventrolateral grayish streak restricted to the single line of enlarged scales ventrolaterally on the lower flanks. The remaining lower flank scales light purplish brown like the adjoining ventrals. Belly without spots or streaks, lighter anteriorly, darker posteriorly. Throat darker than anterior belly, purplish brown. Limbs below light like anterior belly. Tail above like dorsum at base but dorsolateral lines fading into the light, slightly smudged color of the sides of the tail. Tail below more smudged and mottled than the side of the tail but ground color light.

Distribution. (Map 2). In Brazil *A. undulatus* is known with certainty only from the type locality, São Lourenço do Sul on the western border of Lagoa dos Patos in eastern Rio Grande do Sul. In Uruguay it is known from Paysandú, on the Río Uruguay, and along the northern shore of the Rio de La Plata in the departments of Canelones and San José, and in Argentina from Punta Lara, Buenos Aires Province, just across the bay from Montevideo. Gallardo (1977) commented that the species was uncommon and had not been retaken in Punta Lara at his date of writing, and the more recent attempts (J. Williams, 1984, 1985, in litt.) to rediscover this species at the same locality have been unsuccessful. The specimen reported as *Anisolepis undulatus* from Santa Fé, Argentina, by Günther (1897) is an *A. longicauda* (BMNH 98.11.3.1), now a skeleton.

Behavior. Gallardo (1980, p. 334) states in a general review of the ecology of the

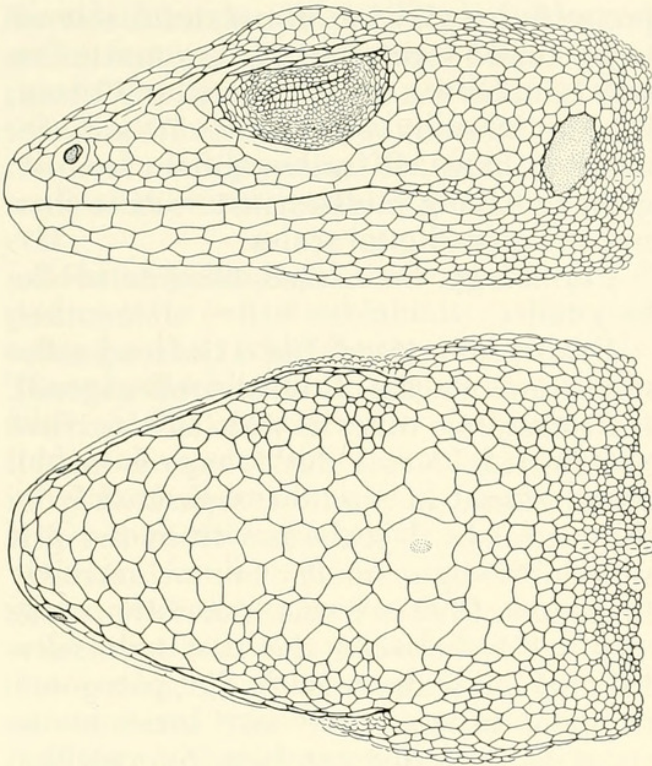


Figure 9. Head scales of *Anisolepis undulatus*, MCZ 84031 from Rio Grande do Sul, Brazil: Top, left lateral. Bottom, dorsal.

herpetofauna of Buenos Aires Province that this species climbs on the trunks of trees and bushes, but he does not say that this is his personal observation. He may have inferred the habitat and behavior of this species from that of the related species *A. grilli*, which he had seen in Brazil (see above).

Reproduction. Rand (1982) found four eggs in an individual 63 mm snout-vent length. Each egg had a volume of 0.5 ml, and the entire clutch a volume of 2.0 ml.

Miscellaneous. Zug (1971) reports the following characteristics of the arterial system: the sternohyoid and external carotids are separate but continuous; there is a short common subclavian trunk; the origins of the subclavians and dorsal aorta are clearly separated and lie beneath the heart; the celiac artery arises anterior to and well separated from the mesenterics; and the mesenterics arise as a common trunk.

Discussion. Werner (1896) listed *A. bruchi* as a synonym of *A. undulatus*, but in his discussion he compared *undulatus* only

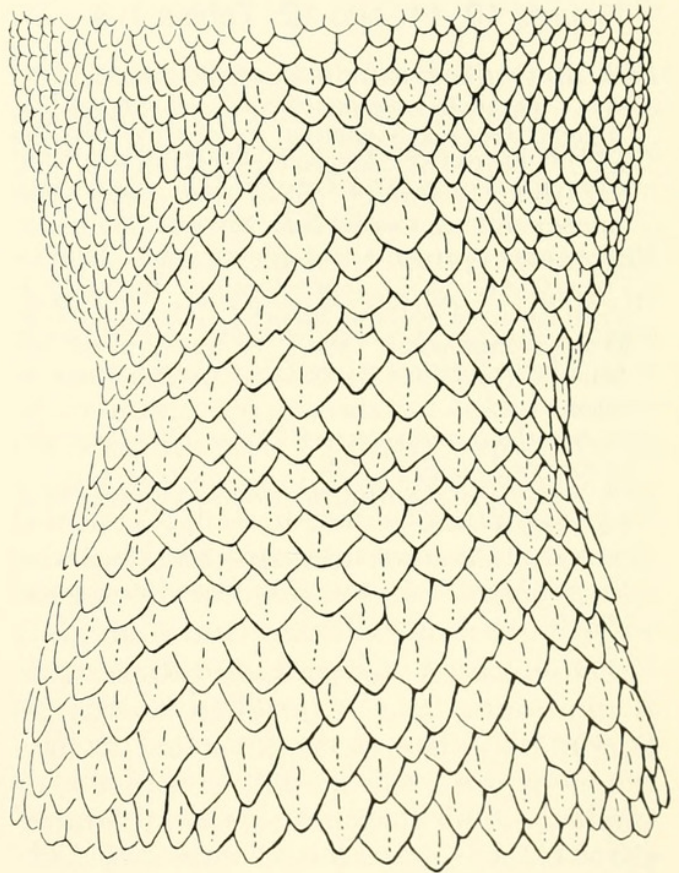
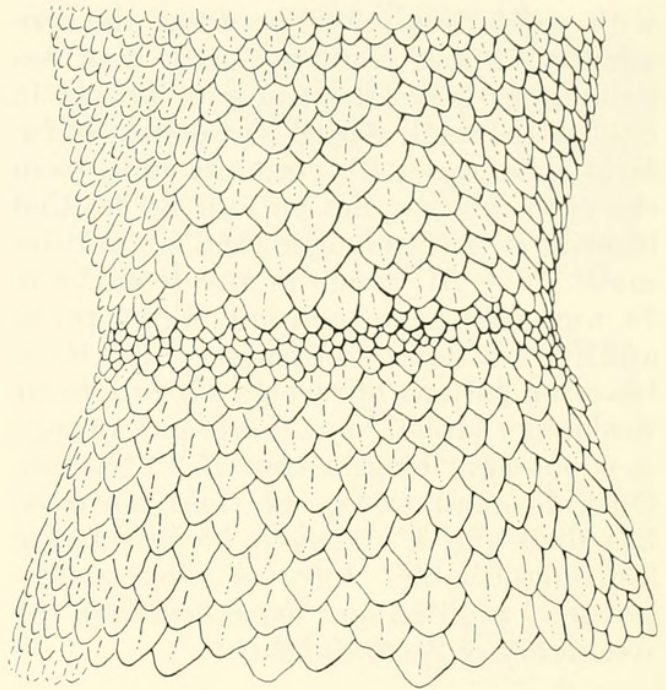


Figure 10. Ventral view of the posterior throat and anterior body region illustrating the presence of a transverse gular fold in (Top) *Anisolepis undulatus*, MCZ 84031 from Rio Grande do Sul, Brazil, and its absence in (Bottom) *Anisolepis longicauda*, MCZ 147353, syntype from mouth of the Río del Oro, Chaco, Argentina.

with *grilli*. Berg (1898) accepted the synonymy without comment. Our own examinations leave the status of *bruchi* in doubt. In Brazil, where *Anisolepis undulatus* is known with certainty only from the type locality, the pattern is like that illustrated by Boulenger (1885c), and females (N = 24) range in size from 54 to 74 mm. We have seen only three males and five females from Uruguay. All of them have the pattern illustrated for *bruchi* by Koslowsky (1895), and the females range in snout-vent length from 75 to 88 mm. On scale counts and proportions, however, Brazilian and Uruguayan specimens are indistinguishable. Here we adopt a conservative position and leave *bruchi* in the synonymy of *A. undulatus*.

Anisolepis longicauda (Boulenger, 1891)
new combination

Figures 10, 11, and 12; Tables 1–4

- 1891 *Aptycholaemus longicauda* Boulenger, Ann. Mag. Nat. Hist., London, (6)8: 85.—Type locality: "Riacho del Oro, Argentina" = mouth of the Río del Oro into the Río Paraguay. (Syntypes: Brit. Mus. Nat. Hist. No. 91.6.17.1; Zool. Mus. Køb., 2 unnumbered; Mus. Comp. Zool. No. 147353.)
- 1895 *Anisolepis argentinus* Koslowsky, Rev. Mus. La Plata, 6: 419; pl. 2.—Type locality: "Sierra de la Ventana, cerca de Bahía Blanca".—Corrected type locality (Koslowsky, 1898): "el territorio de Misiones." (Holotype: ? Museo de La Plata, not located.)
- 1897 *Anisolepis undulatus*—Günther, Ann. Mag. Nat. Hist., London, 20(6): 365.
- 1898 *Anisolepis argentinus*—Koslowsky, Rev. Mus. La Plata, 8: 167.
- 1898 *Aptycholaemus longicauda*—Berg, Ann. Mus. Buenos Aires, 6: 4 (*Anisolepis argentinus* synonymized).

Diagnosis. *A. longicauda* differs from *A. undulatus* and *A. grilli* in lacking an antehumeral-transverse gular fold, in having an external ear opening conspicuously smaller, rather than larger, than the interparietal scale, and a longer tail (mean tail/total length 0.77 in males, 0.74 in females). It further differs from *A. undulatus* in having less distinctively heterogeneous scalation: enlarged dorsal body scales grading into, rather than abruptly distinct from lateral body scales, nape without enlarged,

projecting scales, no dorsolateral row of large, keeled scales, and a larger maximum size (snout-vent length in males 79 mm, females 98 mm, versus males 70 mm, females 83 mm). It further differs from *A. grilli* in having multicarinate rather than smooth supradigital scales.

Etymology. So named because of the long tail.

Description. *Head* (Fig. 11). Head scales small, smooth, flat. Rostral subhexagonal, more than two times as wide as long. Five postrostrals. Nasal flask-shaped, nostril posterodorsal in position, separated from the rostral by 1 scale and from the first supralabial by a smaller one or narrowly in contact. Five to 6 small, smooth, polygonal scales between the nasals dorsally. Frontonasal scales smooth, flat, polygonal, irregular in size. Five to 8 scales across snout at posterior canthals. Supraorbital semicircles separated medially by 1 to 3 rows. Supraoculars little differentiated, the centromedial scales a little enlarged, 4 to 5 scales across supraocular area. A circumorbital series separating supraoculars from semicircles.

Scales of the interparietal region small, smooth, flat, irregular in size. Interparietal larger than surrounding scales, subpentagonal, separated from the semicircles by 2 scales on each side and from the nape granules by 6 to 7 scales grading in size posteriorly. Canthals 4, the anteriormost above and in contact with the nasal. Superciliaries 7 to 8, the first largest and longest, distinctly oblique, the next 3 or 4 still elongate and with slightly oblique sutures, the remaining rectangular. One to 2 preoculars, in contact with the first canthal or separated by 1 scale. One subocular. Postoculars 2 or 4, not sharply differentiated from temporals. Loreals 18 to 25, grading from large posteriorly to small anteriorly. A single row of more or less elongate lorilabials extending anteriorly below the nasal and backward to separate the subocular from the supralabials. Supralabials 9 (the eighth below the center of the eye).

Lower temporals small, smooth, flat, 11 to 14 between orbit and ear. A rather dis-

tinct double intertemporal line of enlarged scales separating upper and lower temporals. Anterior auriculars not distinct from temporals, margin weakly beaded. Posterior auriculars granular. Ear small, oblique, somewhat or much smaller than interparietal.

Mental pentagonal, in contact with 2 postmentals (=first sublabials), as long as or longer than wide, between infralabials. Three to 6 sublabials in sequence with the first sublabial of each side. Only the first sublabial on each side in contact with the infralabials. Infralabials 9, all deeper, hence larger than the supralabials.

Central gulars small, smooth, juxtaposed, grading into larger imbricate keeled scales that join the ventrals without any intervening granular zone (Fig. 10). No antehumeral-transverse gular fold.

Body. A dorsal zone of distinctly enlarged subimbricate scales (11 to 12 rows) tending to be largest middorsally, all keeled. Nape scales subimbricate, granular, irregular in size, grading above the shoulder into the keeled scales of the dorsal zone. No enlarged rows on nape. Flank scales below the dorsal zone smaller, subimbricate, still keeled but more frequently elongate, irregular in size. Near the ventrals an interrupted line of imbricate keeled scales, again irregular in size.

Ventrals much larger, strongly keeled, imbricate, mucronate, in 15 to 19 transverse rows, keels in line. Scales at the anterior margin of the vent tending to be transverse, smooth in a single row and much smaller than the ventrals. Vestiges of a lower lateral line of enlarged scales present or absent. Anterior to the vent, three rows of keeled scales much smaller than the ventrals, but much larger than the immediately preanal scales.

Limbs. Brachials: suprabrachials and prebrachials keeled, imbricate except at immediate insertion of arm. Infrabrachials keeled but smaller than suprabrachials. Postbrachials subgranular. Anterior brachials: keeled and imbricate all around, smaller at elbow. Carpals: supracarpals keeled, imbricate. Infracarpals smooth,

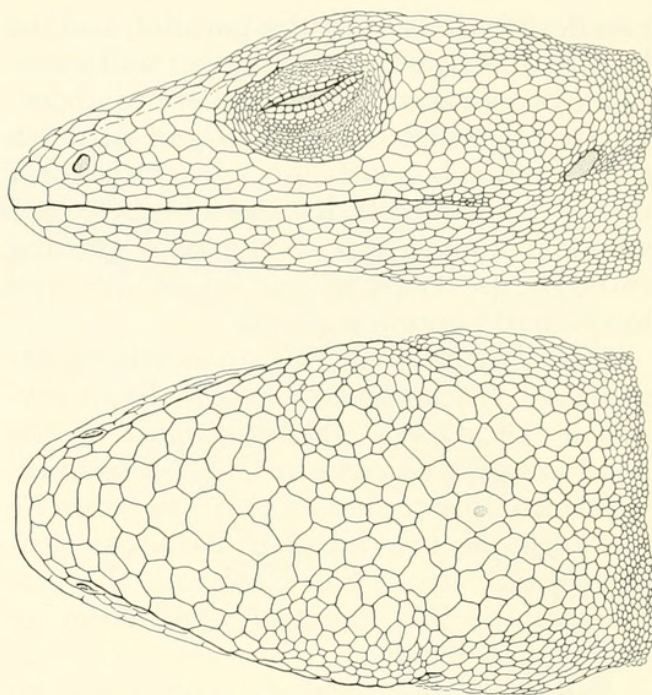


Figure 11. Head scales of *Anisolepis longicauda*, MCZ 147353, syntype from mouth of Río del Oro, Chaco, Argentina: Top, left lateral. Bottom, dorsal.

imbricate. Digitals of hand: supradigitals multicarinate, imbricate, truncate, very little wider than long. Infradigitals smooth, imbricate, a little wider than long proximally, narrower distally.

Femorals: supra-, pre-, and postfemorals imbricate, keeled, truncate, as large as middorsals. Infracapitals granular. Scales at knee smaller. Tibials: keeled, imbricate all round except granular at ankle, smaller than middorsals. Tarsals: supratarsals keeled, imbricate. Infracapitals smooth, imbricate. Digitals of foot: supradigitals multicarinate, imbricate, truncate. Infracapitals smooth, imbricate, wider than long only at digital joints. Lamellae under fourth toe 20 to 29. Groin granular. No axillary pit. No inguinal pit.

Tail. Compressed. Scales of dorsum of tail in size and keeling like middorsal zone. Scales of base of tail immediately behind vent granular. Distally all scales keeled, somewhat larger than middorsals, subequal.

Color and Pattern. (Fig. 12). The syntypes now are faded, and color freshly preserved has been described only by Boulenger (1891b) and Koslowsky (1895). The

two descriptions are quite parallel, and the briefer description of Boulenger will serve: "Pale brown above, with darker broad dorsal stripe, which may be edged on each side by a fine blackish line; a blackish streak on the canthus rostralis, and a black-edged streak from the eye to the neck passing through the tympanum; upper lips and lower parts cream-colored."

Distribution. (Map 2). In northern Argentina, *A. longicauda* known from several localities near the west bank of the Río Paraguay in eastern Chaco Province, and from unspecified localities in Santa Fé and Misiones Provinces. In Paraguay, it is known only from San Pedro on the east bank of the Río Paraguay, and from an unspecified locality.

Behavior. For ecology and behavior there are no reports at all. In *Anolis* the conjoined features of a dorsal zone of enlarged keeled scales, keeled ventrals, and a pattern of light lines on the lower flanks occur in those anoles adapted to life on bushes and grasses (e.g., *Anolis notopholis*, *A. auratus*), and in the grass-bush anoles of Hispaniola and Puerto Rico (Williams, 1983) or in semiaquatic anoles such as the *lionotus* group of Central America and northwest South America, the latter found only at the borders of streams or the rocks within them (Williams, 1984). In neither ecological situation are the patterns of scales and color quite consistent, only very usual. From the descriptions and pictures of the habitats of *Anisolepis longicauda* and *A. undulatus* that have been made available to us, it seems probable that these are typically inhabitants of bushes and tall grasses, particularly in areas (*esteros* or *bañados*) that are seasonally flooded. (See also our remarks under *A. undulatus* comparing that species with *Urosaurus*.)

Miscellaneous. The thyroid gland is reported to have two well-defined lobes connected by a narrow isthmus (Lynn, O'Brien, and Herhenreader, 1966). Underwood (1970) reported 13 scleral ossicles, numbers 1, 6, and 8 plus, and 4, 7, and 9 minus, the most common number and pattern found in pleurodont igua-

nians. Arnold (1984) states that this species has a distinctive, swollen insertion of the *m. retractor lateralis anterior*, a condition it shares with *A. grilli*.

RELATIONSHIPS (R. Etheridge)

The para-anoles were first so-called by Williams and me during the course of informal discussions of anole relationships when it appeared to us that the presence of a spinulate scale surface, with elongate spinules on the scale organs and elongate and differentiated spinules on the subdigital surface implied a close relationship between these five species and the vast radiation of anoles. Except for their loss of caudal autotomy and a middorsal scale row it seemed to us at the time that para-anoles were almost ideal ancestors of anoles. I have today all but abandoned (Williams has quite abandoned) that assessment, having learned much more about other components of what has recently been formally recognized as the iguanian family Polychridae (Frost and Etheridge, 1989). The relationship implied by the term "para-anole" may well be misleading. Here follows the history of my thoughts and the thoughts of others on the questions of para-anole relationships.

Boulenger (1885b) was first to note the similarities of para-anoles in his description of *Anisolepis*, noting that it is "allied to *Enyalius*, *Urostrophus*, and *Leiosaurus*, which have likewise smooth infradigital lamellae, no femoral pores, and, like *Polychrus* and the Gekkonidae, abdominal ribs and no fontanelle in the sternum," and in his description of *Aptycholaemus* (Boulenger, 1891b), in which he said that it is allied to *Urostrophus* and *Anisolepis*, "but differs from both in the absence of a gular fold and dorsal lepidosis." In his Catalogue, Boulenger (1885c) also transferred the Chilean lizard described as *Leiosaurus torquatus* (Philippi, in Philippi and Landbeck, 1861) to the genus *Urostrophus*. This was the first suggestion of possible close relationship between *Pristidactylus* and *Urostrophus*.

In a thesis on the osteology and rela-

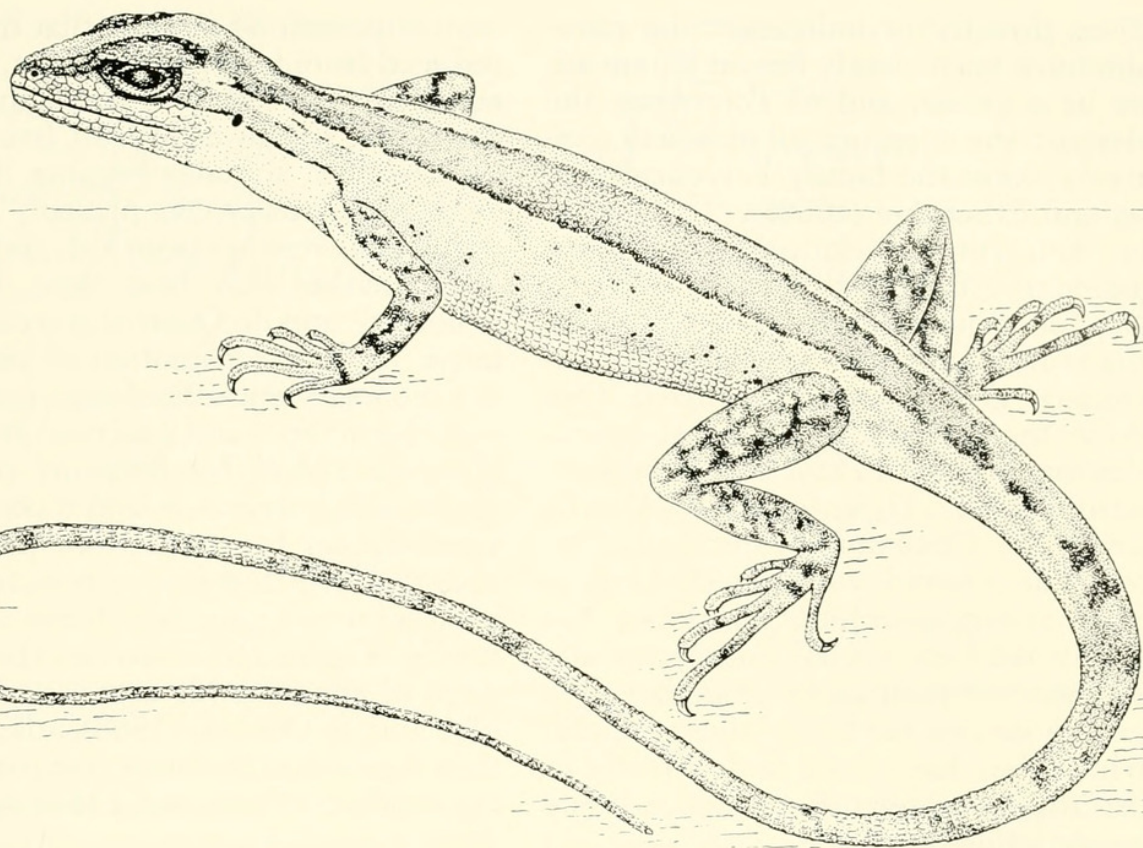


Figure 12. *Anisolepis longicauda*, Nat. Mus. Wien No. 12971, female, snout-vent length 90 mm, from Paraguay.

tionships of anoles (*Chamaeolis*, *Phenacosaurus*, *Chamaelinorops*, *Anolis*), I compared anoles with *Polychrus* and *Aptycholaemus* (Etheridge, 1960, table vii). The data on *Aptycholaemus* was based upon a misidentified specimen of *Anisolepis grilli*. The suggestion was made that “*Polychrus* shows the closest affinities with the anole group,” and although insufficient data were available to form a proper evaluation of the position of *Anisolepis* (i.e., *Aptycholaemus* of the thesis), it was said of the latter that “with respect to the anoles, correspondence in characters was very nearly as close as that between *Polychrus* and the anoles.”

In a review of the genus *Enyalius*, Etheridge (1969) concluded that “*Anisolepis* and *Aptycholaemus* are indeed very similar to each other, and of iguanids are most like *Enyalius*” and that “the differences that separate *Anisolepis* and *Aptycholaemus*, considering the two together, from *Enyalius* are few and relatively trivial,”

and also remarked that “*Enyalius bilineatus* is in some respects transitional between *Anisolepis* and *Aptycholaemus* on the one hand and the remaining species of *Enyalius* on the other.”

Recently Etheridge and Williams (1985) reviewed the confusion in allocation to *Urostrophus* of species now referred to *Pristidactylus scapulatus* and *Pristidactylus torquatus*. Following the then unpublished work of Etheridge and de Queiroz (1988), we considered the genera *Pristidactylus*, *Leiosaurus* (including *Aperopristsis*), *Diplolaemus*, and *Enyalius* to form a monophyletic group called the “leiosaurs.”

Williams (1988) accepted the monophyly of anoloids, but in a footnote he included the para-anoles within the leiosaurs without further comment. Most of his discussion is irrelevant to present issues. However, relevant to the present work is his suggestion that anoles and *Polychrus* are sister taxa.

Thus, directly or indirectly, the para-anoles have been closely linked to one another as a group, and to *Polychrus*, the anoles and the leiosaurs, all of which, collectively, form the family Polychridae of Frost and Etheridge (1989).

In their formal, cladistic analysis of "Iguanidae," Etheridge and de Queiroz (1988) found no evidence for monophyly of the family, but eight monophyletic, suprageneric groups were recognized. One of these, the anoloids, contained the para-anoles together with *Polychrus*, *Enyalius*, *Pristidactylus*, *Diplolaemus*, *Anolis*, *Chamaeolis*, *Chamaelinorops*, and *Phenacosaurus*. Anoloids were specified by numerous synapomorphies, including the uniquely derived nuchal endolymphatic sacs. Thus, the para-anoles, together with all of the genera (and only those genera) to which they have been said, directly or indirectly, to be related, formed a single monophyletic group.

Polychrus was recognized as the sister taxon to all of the remaining anoloids, called the "spinulate anoloids," the latter specified by the loss of femoral pores, elongation of the dentary, and the acquisition of a spinulate oberhautchen with the spinules of the scale organs and subdigital scales longer than the background spinules. Three groups of spinulate anoloids were recognized: leiosaurs (*Enyalius*, *Pristidactylus*, *Diploaemus*, *Leiosaurus*, incl. *Aperopristsis*), para-anoles (*Urostrophus*, *Anisolepis*, *Aptycholaemus*), and anoles (*Chamaeolis*, *Anolis*, *Chamaelinorops*, *Phenacosaurus*). Monophyly of both the leiosaurs and anoles was thought to be well supported, the former by presence of the uniquely derived divided distal subdigital scales and other derived features, the latter by the acquisition of an extensile gular fan with elongate second ceratobranchials, a distinctive digital pad, scale organs with elongate filaments, and other synapomorphies. Eight synapomorphies were provided for para-anoles: 1) lateral margins of the clavicles become angular and hooked, 2) a very small secondary coracoid fenestra

was acquired, 3) sternal ribs have been reduced from four pairs to three, 4) caudal autotomy was lost, 5) scale organ spinules attained a height of at least five microns, 6) subdigital spinules became differentiated, with seta-prongs present, 7) a mid-dorsal scale row has been lost, and 8) sexual dichromatism has been lost. However, Etheridge and de Queiroz were more tentative in their recognition of para-anoles as a monophyletic assemblage, pointing out that characters 1 and 2 (above) are possible synapomorphies for leiosaurs plus para-anoles, characters 3, 5, and 6 possible synapomorphies for anoles and para-anoles, and that the remaining transformations have occurred numerous times within the family. Figure 13a illustrates the relationships of the anoloids proposed by Etheridge and de Queiroz (1988), adapted from their figure 9 to facilitate comparison with the work of Frost and Etheridge (1989) discussed below.

No synapomorphies uniting *Urostrophus* *vautieri* with *U. gallardoi* were discovered; thus, *Urostrophus* was considered paraphyletic with respect to *Anisolepis* and *Aptycholaemus*. The latter genera were said to share a reduction in the secondary cusps of the marginal tooth crowns, loss of the posterolateral processes of the basisphenoid, and the acquisition of a ventrolateral row of enlarged scales and ventral body scales with sharp keels in parallel rows. *Aptycholaemus* was diagnosed by loss of the transverse gular fold, elongation of the tail, and reduction of the external ear, but in the absence of synapomorphies that would unite *Anisolepis undulatus* with *A. grilli*, the genus *Anisolepis* was considered paraphyletic.

The most recent work on the possible affinities of para-anoles is contained in Frost and Etheridge's (1989) phylogenetic analysis of the Iguania. The anoloids of Etheridge and de Queiroz (1988) were discovered to form a monophyletic group in all obtained trees, and the group was formally proposed as the iguanian family Polychridae Fitzinger 1843. Monophyly of

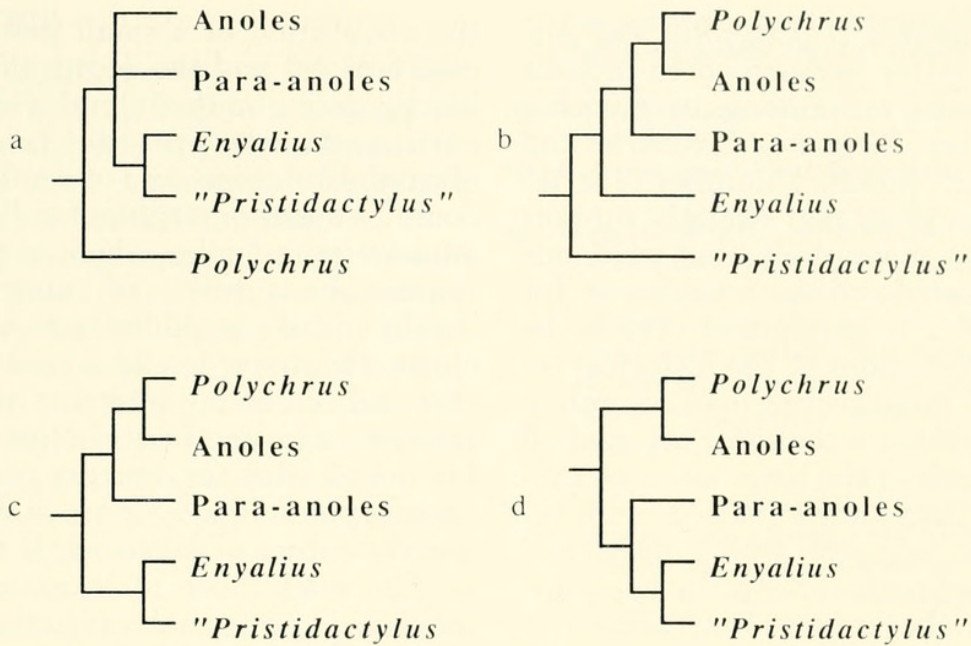


Figure 13. Four possible patterns of relationships of para-anoles to other polychrid iguanians: a) according to Etheridge and de Queiroz (1988); b), c), and d) according to Frost and Etheridge (1989).

the family was supported by endolymphatic sacs that penetrate the nuchal musculature, and strongly bicapitate, bisulcate hemipenes (unicapitate in some *Anolis*, presumably reversed). Five polychrid terminal taxa were employed: *Polychrus*, the anoles, the para-anoles (i.e., *Urostrophus* and *Anisolepis*; *Aptycholaemus* was synonymized with *Anisolepis* based on our unpublished manuscript of the present work), *Enyalius*, and "*Pristidactylus*," the latter considered to be paraphyletic with respect to *Diplolaemus* and *Leiosaurus* (including *Aperopristsis*) and thus placed in quotes. Following Etheridge and de Queiroz (1988), *Urostrophus* was considered to be a metataxon, i.e., a supraspecific taxon for which evidence for monophyly is either lacking or ambiguous. Three equally parsimonious tree topologies were discovered for the relationships of these five terminal taxa (Figs. 13b, c, and d). In all three, *Polychrus* and the anoles were sister taxa, corroborated by four unambiguously placed characters: long second ceratobranchials, anterior elongation of the sternum (incorrectly stated as anterior process of interclavicle by Frost and Etheridge, 1989, p. 22), loss of cervical ribs on

vertebra four, and loss of a gular fold. In two trees, para-anoles were the sister taxon of *Polychrus* + anoles (Figs. 13b and c), supported by the following characters: three (or fewer) sternal ribs, loss of caudal autotomy (reversed in some *Anolis*), and, ambiguously, acquisition of anole-type caudal vertebrae, difficult to evaluate in para-anoles and *Polychrus*. In one tree topology (Fig. 13d) para-anoles were the sister taxon of *Enyalius* + "*Pristidactylus*," supported by the presence of a small posterior coracoid fenestra. Thus a strict consensus tree (*sensu* Nelson, 1979) showed the para-anoles in an unresolved polytomy with *Enyalius*, "*Pristidactylus*," and the anoles + *Polychrus*. Additionally, although para-anoles were treated as a terminal taxon, they were not united by any apomorphies whose placement was independent of the network, so that their monophyly was not supported unambiguously, i.e., *Urostrophus* and *Anisolepis* may be more closely related to other polychrid genera than to each other.

In summary, the analyses of Etheridge and de Queiroz (1988) and Frost and Etheridge (1989) provide a strong consensus that Polychridae is a monophyletic family

and that the genera *Urostrophus* and *Anisolepis* (the latter understood to include *Aptycholaemus*) are among its member genera. Further, the genus *Polychrus* and the anoles each possess a number of striking synapomorphies that strongly support their separate monophyly, but evidence for the monophyly of the leiosaurs or for the para-anoles is ambiguous. Yet to be resolved are questions of the historical relationships of these groups to one another: whether *Polychrus* is the sister taxon of all other polychrids or the sister taxon of anoles, whether para-anoles share a more recent common ancestor with anoles (and perhaps *Polychrus*), or with the leiosaurs, and whether the para-anoles themselves are monophyletic.

The polarities of a number of transformations depend on whether *Polychrus* is considered the sister taxon of anoles or of all other polychrids. The choice appears to depend on which set of homoplastic transformations is considered less likely to have occurred. If *Polychrus* is the sister taxon of other Polychridae, then homoplasy (in anoles) is indicated in: 1) elongation of second ceratobranchials, 2) loss of a transverse gular fold, 3) anterior elongation of the sternum, 4) loss of ribs on the fourth vertebra, 5) division of the mental scales, and 6) adherence of the scales above the supralabials to the underlying periosteum (the latter two characters described by Williams, 1988). If *Polychrus* is the sister taxon of the anoles, then homoplasy (in *Polychrus*) is indicated in: 1) reacquisition of subdigital keels, 2) loss of subdigital spinules, 3) loss of scale organ spinules, 4) reacquisition of femoral pores, 5) reacquisition of a short dentary, and (in anoles) 6) reacquisition of caudal autotomy.

The question of choice between a sister taxon relationship of para-anoles and anoles (with or without *Polychrus* as the latter's sister taxon) or between para-anoles and leiosaurs similarly requires a choice between conflicting sets of homoplasies. If para-anoles and anoles are sister taxa, then homoplasy is indicated (in para-anoles) in

the acquisition of a small posterior coracoid fenestra and the acquisition of hook-like processes on the interclavicle. If *Polychrus* and anoles are sister taxa, then loss of caudal autotomy and of a middorsal row could be synapomorphies for *Polychrus* + anoles + para-anoles, which, in turn, would require reacquisition of autotomy within *Anolis* and of a middorsal row within *Polychrus*. However, loss of a middorsal scale row and of caudal autotomy is also characteristic of some (e.g., *Leiosaurus belli*), but not all leiosaurs, and are potential synapomorphies linking para-anoles with a specific subset of leiosaurs. If para-anoles are the sister taxon of leiosaurs, then homoplasy in para-anoles is indicated in the elongation of the subdigital spinules and in the loss of one pair of sternal ribs.

The suggestion of Etheridge and de Queiroz (1988) that *Urostrophus* may be paraphyletic rested upon the assumption that the scalation pattern common to *U. vautieri* and *U. gallardoi* is primitive, but no evidence was provided that this is the case. The *Urostrophus* pattern closely resembles that found in some *Enyalius* (e.g., *E. iheringi*) and *Pristidactylus*, while that found in *Anisolepis* closely resembles that found in other *Enyalius* (e.g., *E. bilineatus*). If, instead, the *Anisolepis* pattern is primitive (and para-anoles are, indeed, a monophyletic group), then *Urostrophus* may be considered monophyletic on the basis of a derived scale pattern.

The linking of *A. undulatus*, *A. grilli*, and *A. longicauda* to form a monophyletic group on the basis of shared derived conditions of the marginal teeth and basisphenoid (Etheridge and de Queiroz, 1988) appears to be justified. However, no derived feature has been found to be shared by *A. undulatus* and *A. grilli*, but not *A. longicauda*. Thus *Anisolepis* is a paraphyletic genus if *A. longicauda* is excluded. This conclusion is independent of the problem of polarity of scale patterns and led us to recommend in the preceding section that *Aptycholaemus* be considered a synonym of *Anisolepis*.

CONCLUSIONS

1. There is strong support for the hypothesis that: a) Polychridae is monophyletic, and b) the five species referred to *Urostrophus* and *Anisolepis* (the para-anoles) are members of that family.

2. There is strong support for the monophyletic status of *Polychrus*, the leiosaurs and the anoles, but evidence that the para-anoles form a monophyletic subset within Polychridae is not strong, and weaker still if para-anoles are nested within (rather than being a sister group of) the leiosaurs.

3. Evidence can be cited for a possible sister taxon relationship between *Polychrus* and the anoles, as well as for a sister taxon relationship between *Polychrus* and the spinulate polychrids.

4. If the para-anoles are monophyletic, and if the scalation pattern of *Urostrophus* is primitive, relative to that of *Anisolepis*, then *Urostrophus* is paraphyletic. However, monophyly of *Anisolepis* is based on other characters and is independent of whether its scalation pattern is primitive.

5. No synapomorphies united *A. undulatus* with *A. grilli* to the exclusion of *A. longicauda*. Recognition of the latter as representative of a monotypic genus by Boulenger may reflect a consideration that the absence of a transverse gular fold was a generic character. *Aptycholaemus* Boulenger 1891 is placed in the synonymy of *Anisolepis* Boulenger 1885.

6. It is clear that resolution of the relationships of the five para-anole species must await a more detailed examination of the interrelationships of Polychridae as a whole. Especially critical are questions of monophyly of the para-anoles and appropriate outgroups for polarity assessments.

or scarcely larger than interparietal scale; all scale counts lower (Tables 2 & 3)

..... *U. vautieri*

3a. An antehumeral-transverse gular fold present (4)

3b. No antehumeral-transverse gular fold
..... *A. longicauda*

4a. Dorsal body with paravertebral rows of large, keeled scales separated medially by one to three rows of smaller scales and laterally abruptly larger than adjacent flank scales; flank scales distinctly heterogeneous, with a dorsolateral series of patches of large, keeled scales and a ventrolateral row of enlarged, keeled scales, evident also on the neck *A. undulatus*

4b. Dorsal body scales slightly convex and keeled, grading into smaller flank scales that are smooth or weakly keeled and nowhere markedly smaller than dorsal scales; dorsolateral patches and ventrolateral rows of enlarged scales inconspicuous on the body and absent on the neck *A. grilli*

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A KEY TO THE SPECIES OF *UROSTROPHUS*
AND *ANISOLEPIS*

- 1a. Ventral body scales smooth *Urostrophus* (2)
- 1b. Ventral body scales distinctly uncarinate
..... *Anisolepis* (3)
- 2a. External ear opening large, up to three times diameter of interparietal scale; all scale counts higher (Tables 2 & 3) *U. gallardoi*
- 2b. External ear opening smaller than, equal to,

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LOCALITIES AND SPECIMENS EXAMINED

Museum numbers represent specimens seen by us; those represented by a skeleton or accompanied by radiographs ("x rays") are so indicated. Museum abbreviations are provided in the Acknowledgments. Specific localities are followed by degrees and minutes south latitude and west longitude.

Urostromphus gallardoi

ARGENTINA: **Córdoba:** *Dpto. Cruz del Eje:* Cruz del Eje, 300 m (30 44–64 48) BMNH 1902.5.22.4; *Dpto. Río Seco:* Sebastián Elcano (30 09–63 35), Bee de Speroni and Cabrera, 1984; *Dpto. Sobremonste:* 7 km N Puesto Nuevo (29 31–65

34) AC 070; *Dpto. Tulumba:* Isla de San Antonio (30 02–64 26) AC 159. **La Rioja:** *Dpto. Arauco:* Aimogasta (28 33–66 49) (possibly in error fide R. Laurent, in litt.) MZUSP 45908. **Misiones:** Eldorado (26 24–54 38) AC 079. **Salta:** Estancia Gutierrez (1,650 m), southern Salta, Laurent, 1985; *Dpto. Anta:* El Quebrachal (25 17–64 09) ABarrio 746; *Dpto. Orán:* Urundel (23 43–64 47) MACN 11043 (holotype of *Urostromphus gallardoi*); *Dpto. La Poma:* Quebrada Río Las Conchas (24 55–66 09) FML 01266; *Dpto. La Viña:* Río Chuña Pampa (=Chuñapampa), 10 km WNW La Viña (25 27–65 35, La Viña) FML 01296 + x ray; *Dpto. Metán:* Puesto San Borja, Sierra de Metán, 15 km W Metán (25 30–64 58) FML 00847 + x ray; *Dpto. Rosario de la Frontera:* Rosario de la Frontera (25 48–64 58) MCZ 162922, MACN 4311–24; Joachim V. Gonzalez (25 10–64 00) FML 2417–20; *Dpto. San Carlos:* 35 km N Cafayate (25 06–65 57) MCZ 162920: skeleton, MACN 12016. **Santa Fé:** No additional data: Gallardo, 1964, MACN 19740. **Santiago del Estero:** No additional data: MACN 8019–21 + x ray; *Dpto. Matará:* Campo del Cielo (27 52–61 50) Gallardo, 1964; *Dpto. Capital:* Suburbios [? de Santiago del Estero (27 47–64 16)] ABarrio 121; *Dpto. Belgrano:* Bandera (28 54–62 16) ABarrio 345. **Tucumán:** No additional data: MACN 4318–25; *Dpto. Burruyacu:* probably from 7 de Abril (26 17–64 29) or Garmendia fide R. Laurent, in litt. FML 00483.

BOLIVIA: **Santa Cruz:** Santa Cruz de la Sierra (30 44–64 48) MACN 2786–8.

Urostromphus vautieri

BRAZIL: No additional data: BMNH xxiii.3a, 57.10.28.66, 94.9.15.3: skeleton, 1913.9.30.2, ZMB 4326, 9060. **Minas Gerais:** No additional data: MCZ 5566 + x ray; Antonio Carlos (21 19–43 45) MZUSP 7068; Engenheiro Trompowski (21 18–46 17) MZUSP 4472; Lagoa Santa (19 38–43 52) Reinhardt and Lütken, 1861; Machado (21 41–45 56) MZUSP 4480, 4482, 4552–4; Poços de Caldas, 1,200 m (21 48–46 34)

MZUSP 13982; Santa Rita da Extrema (22 52–46 19) MZUSP 4477. **Paraná:** Campo do Tenente (25 59–49 41) MZUSP 36666; Curitiba (25 25–49 16) MZUSP 43010; Rio Itararé (23 10–49 42, mouth of Rio) FMNH 28863. **Rio de Janeiro:** Itatiaia (22 23–44 39) FMNH 83576, MZUSP 2273, 44681–86; Nova Friburgo (22 18–42 31) ZMB 7446(3), ZMH 02769–71 + x ray; Petrópolis (22 32–43 11) MCZ 7319, MZUSP 563, 36342; Rio [? de Janeiro], Reinhardt and Lütken, 1861; Rio de Janeiro (22 48–43 32) MNHNP 6779–80 (syntypes of *Urostrophus vautieri*); Serra de Macaé (22 10–41 50) MZUSP 418; Teresópolis (22 26–42 59) BMNH 88.9.21.1. **Rio Grande do Sul:** No additional data: BMNH 82.10.4.50–51; Passo Fundo (28 15–52 24) MZUSP 4469; Porto Alegre (30 00–51 10) ZMB 6823. **São Paulo:** Alto da Serra (=Paranapiacaba) (23 48–46 03) MZUSP 4479; Barueri (23 33–46 54) MZUSP 4473, 4481; Boraceia (23 38–45 50) MZUSP 42914–5, 45642, 49209; Botucatu (22 54–48 27) MZUSP 4467; Bragança Paulista (22 57–46 33) MZUSP 4470; Cabreúva (23 18–47 08) MZUSP 470; Caçapava (23 06–45 42) MZUSP 42699; Campo Limpo (23 12–46 48) MZUSP 11867; Campos do Jordão (22 45–45 34) MZUSP 4475, UMMZ 108632(2) + x ray; Casa Grande (23 38–45 54) MZUSP 36103; Cotia (23 37–46 56) MZUSP 8259; Faveiro (21 40–47 18) MZUSP 4483; Fazenda Barreiro Rico, Anhembi (22 48–48 08) MZUSP 7063; Fazenda Pedra Branca, Botucatu (22 52–48 26) MZUSP 29615; Garça (22 13–49 44) SDSU unnumbered; Mato Dentro, São Roque (23 42–47 08) MZUSP 10377; Mogi das Cruzes (23 31–46 11) MZUSP 999; Osasco (23 32–46 46) MZUSP 13417; Perus (23 24–46 46) MZUSP 543; Piquete (22 36–45 10) MZUSP 565, 576; Piracicaba (22 42–47 38) MZUSP 153–6, 2831–3, MCZ 133154–6; Salesópolis (23 32–45 51) MZUSP 32270, AMNH 120474; Santa Rita (21 40–47 30) Von Ihering (1899); São Paulo (22 33–46 38) FML 00830, MZUSP 2549, 3190, 4460; São Paulo: Interlagos, UMMZ 108633 + x ray; São Paulo: Represa de Santo Amaro (23 40–46 43) AMNH 120473,

MZUSP 3366, 8404; São Paulo: Villa Jaguara, MZUSP 36114; Serra da Bocaina, Bananal (=Fazenda do Bonito) (22 44–44 33) MZUSP 10297; Serra Negra (22 37–46 42) MCZ 84036–7: skeleton, 84037, MZUSP 4468; São José do Barreiro, near Fazenda do Veado (22 49–44 39), Serra da Bocaina USNM 208136; São Bernardo do Campo (23 42–46 33) AMNH 120467–8; Tupi (22 45–47 32) MZUSP 4478.

PARAGUAY: No additional data: USNM 12329. PARAGUAY or ARGENTINA: ZMH 02772 + x ray.

No data: REE 2507: skeleton.

Anisolepis grilli

ARGENTINA: **La Rioja:** *Dpto. Independencia:* Patquia (30 03–66 53), Estancia Breyer (locality probably in error) USNM 73504. **Misiones:** *Dpto. Caingúas:* Dos de Mayo (27 02–54 39) MLP S.957–62; *Dpto. Guaraní:* Río Victoria (26 52–54 39, mouth of Río Victoria) MLP S.963.

BRAZIL: No additional data: ZMB 495 (type of *Laemactus fitzingeri*), 496 (type of *Laemactus obtusirostris*), ZMH 02764 + x ray. **Minas Gerais:** Delfinópolis (20 20–46 51) MZUSP 42688. **Paraná:** No additional data, NMW 12970 + x ray; Araucaria (25 36–49 25) MZUSP 4532–5; Curitiba, Boettger, 1905 (as *Laemactus* tibia and Serra between Rio Negro and dCuritiba, Boettger, 1905 (as *Laemactus undulatus*); Dorizon (25 55–50 58) MCZ 133190, MZUSP 4496–8, 6866–9, 10132–3; Morretes (25 28–48 49) MZUSP 6693; Palmeira (25 26–50 00) BMNH RR 1946.8.5.58, RR 1946.8.12.35: skeleton (syntypes of *Anisolepis grilli*); Paranaguá (25 31–48 36) REE 1952: skeleton, ZMH 02757–60 + x ray; Piraí Mirim (now Piraí do Sul) (24 31–49 57) MZUSP 6699; Porto União da Vitoria (26 15–51 05) MZUSP 4546–9: skulls; Rio Azul (25 43–50 47) MZUSP 29611; Umbará (25 53–49 19) MZUSP 8419. **Rio Grande do Sul:** Alfredo Chaves (28 57–51 33) MZUSP 4520; Carlos Barbosa (29 18–51 30) MZUSP 3726; Canela (29 22–50 50) MZUSP 4530; Farroupilha (29 14–51 21), 18 km S, FMNH

80115; Garibaldi (29 15–51 32) MZUSP 4523; Porto Alegre (30 00–51 10) ZMB 6246. **Rio de Janeiro:** Rio de Janeiro (22 48–43 32, locality possibly in error fide P. Vanzolini, in litt.) MZUSP 463. **Santa Catarina:** No additional data: UMMZ 123813–5; Blumenau (26 55–49 04) NMW 18904 + x ray (type of *Anisolepis lionotus*); Caçador (26 47–51 00) MZUSP 4524; Ipomeia (26 57–51 06) MZUSP 4527–8; Joinville (26 18–48 50) UMMZ 122439, NMW 12969(3) + x rays; Lagoa (27 35–48 28) MCZ 133189, MZUSP 4488–92, 4499, 4501–8; Nova Teutonia (27 16–52 20) MZUSP 10344, CMNH 68364–70, UMMZ 122147, 123122–6, 123248, 123812–3; São Bento do Sul (26 15–49 22) MZUSP 4539; Valões (now Ireneópolis) (26 12–50 48) MZUSP 4545. **São Paulo:** No additional data: UMMZ 138813–4, ZMH 02761, Boettger, 1882 (as *Laemanctus undulatus*); Alto da Serra (now Paranapiacaba) (23 48–46 03) MZUSP 545, Gallardo, 1977; Alto Pimenta (now Bento de Abreu) (21 17–50 48) MZUSP 4537; Américo Brasiliense (21 43–48 07) MZUSP 4544; Barueri (23 33–46 54) MZUSP 4511, Belém (now Francisco Morato) (23 16–46 45) MZUSP 4513; Caieiras (23 21–46 45) MZUSP 4500; Campinas (22 53–47 04) MZUSP 4525; Campo Largo (23 11–46 42) MZUSP 4536; Campo Limpo (23 12–46 48) MZUSP 4509–10, 42738, 54752; Cotia (23 37–46 53) MZUSP 4514; Estrada de Poá (23 32–46 22) MZUSP 44692; Ferraz de Vasconcelos (23 33–46 22) MZUSP 44690; Ibaté (21 57–48 00) MZUSP 36111; Ibiúna (23 34–47 13) MZUSP 42700; Itaquaciara (23 47–46 51) MZUSP 4529; Itatuba (22 28–47 38) MZUSP 42747; Jandira (23 31–46 54) MZUSP 4540, 4542; Osasco (23 32–46 46) MZUSP 2679, 7064; Pirituba (23 30–46 44) MZUSP 8392; Santa Rita (21 40–47 30) Von Ihering (1899); São Bernardo do Campo (23 42–46 33) AMNH 120467–8, MCZ 96031, 133199: skeleton, MZUSP 773, 10139–54, 11872–3, 13908, BMNH 1977.2274–6, UMMZ 138813–4; São Paulo (23 33–46 38) MZUSP 167–9, 263, 286, 540, 542, 555, 560, 561, 569, 809, 842,

2307–8, 2798–9, 3269, 3473, 4494–5, 4512, 4519, 4551, 8276, 8278, 8438, 11461, 29719, 45782: skull; São Paulo: Butantan, MZUSP 4515–8, CMNH 65044; São Paulo: Cantareira, MZUSP 591, 4521; São Paulo: Caxinguí, MZUSP 36116–7; São Paulo: Indianopolis, MZUSP 4550; São Paulo: Ipiranga, MZUSP 574, 2796; São Paulo: Santo Amaro, MZUSP 54399; São Paulo: Vila Galvão, MZUSP 4493; Santana do Parnaíba (23 26–46 55) MZUSP 42697; Santo André (23 41–46 26) MZUSP 4538, 4552, 8261–2.

URUGUAY: **Montevideo:** Montevideo (34 50–56 10) ZMB 7989(2)—possibly in error.

No data: (“Chile,” in error) ZMH 02761–2 + x ray.

Anisolepis undulatus

ARGENTINA: **Buenos Aires:** *Dpto. La Plata:* Punta Lara, near La Plata (34 49–57 59) Koslowsky, 1895 (as *Anisolepis bruchi*).

BRAZIL: No additional data: ZMB 497 (type of *Laemanctus undulatus*), ZSM 504/0(2), ZMH 02765 + x ray. **Rio Grande do Sul:** No additional data: MCZ 84031–2, 84033: skeleton, 59273, MZUSP 541, 682, 2692–5, 2784–7, 2789, 2790, BMNH 86.10.4.4–5, 87.5.18.9 (syntypes of *Anisolepis iheringi*), ZMH 02755–6 + x rays; São Lourenço (now São Lourenço do Sul), southern border of Laguna dos Patos (31 22–51 58) BMNH 1946.8.5.90–1, MZUSP 548, 683, 2783, 2791–4, ZMB 3507(2).

URUGUAY: **Canelones:** Bañados near Carrasco (34 47–56 01) DZVU 280. **Paysandú:** Paysandú [?Department or city] (city: 32 19–58 04) USNM 65545–7. **San José:** Arazati (34 35–56 55) MHNH 2201; Pascual Beach, 4 km west of bus stop, Estero del Tigre (34 45–56 30) MHNH 3021.

Anisolepis longicauda

ARGENTINA: **Chaco:** *Dpto. Bermejo:* Mouth of the Río del Oro into the Río Paraguay (27 02–58 33) BMNH 91.6.17.1 [RR 1946.8.9.2] (syntypes of *Aptycholaemus longicauda*), MCZ 147353 + x ray

TABLE 1. MEASUREMENTS AND PROPORTIONS OF THE BODY, HEAD, AND TAIL OF *UROSTROPHUS* AND *ANISOLEPIS*. PROPORTIONS ARE BASED ON SPECIMENS THAT HAD ATTAINED AT LEAST 83% OF THE MAXIMUM KNOWN SNOUT-VENT LENGTH, BEYOND WHICH THERE APPEARS TO BE LITTLE ALLOMETRIC GROWTH. MEAN FIGURES ARE IN PARENTHESES. N = NUMBER OF SPECIMENS MEASURED. METHODS FOR TAKING MEASUREMENTS ARE GIVEN IN THE APPENDIX.

Species	Sex	N	Maximum S-V in mm	N	Specimens ≥ 85% maximum S-V	
					Tail as % of total length	Head as % of S-V length
<i>U. vautieri</i>	M	30	83	11	58(60)62	23(24.0)25
	F	47	108	8	56(58)59	21(22.5)24
<i>U. gallardoi</i>	M	8	75	6	64(66)76	23(24.7)26
	F	11	78	5	62(64)66	23(23.4)25
<i>A. grilli</i>	M	31	79	3	73(73)74	22(22.0)22
	F	36	97	13	69(71)72	20(21.3)23
<i>A. undulatus</i>	M	11	70	3	72(73)75	21(21.2)22
	F	28	88	6	69(71)73	19(19.8)21
<i>A. longicauda</i>	M	5	79	4	76(77)78	20(20.3)21
	F	8	98	7	73(74)75	19(20.1)22

TABLE 2. BODY SCALE COUNTS, BY SEXES, OF *UROSTROPHUS* AND *ANISOLEPIS*. MEAN FIGURES ARE IN PARENTHESES. N = NUMBER OF SPECIMENS EXAMINED. METHODS FOR COUNTING ARE GIVEN IN THE APPENDIX.

Species	Sex	N	Paravertebral scales	Midbody scales	Ventral scale rows
<i>U. vautieri</i>	M	24	99(117)14	78(87)106	—
	F	43	106(122)138	73(85)110	—
<i>U. gallardoi</i>	M	8	153(161)199	104(117)134	—
	F	11	136(157)178	104(115)123	—
<i>A. grilli</i>	M	21	103(122)139	70(85)106	17(19.4)23
	F	30	111(129)149	71(86)99	17(20.1)25
<i>A. undulatus</i>	M	11	99(104)110	78(79)80	13(15.5)17
	F	21	110(114)122	60(72)85	14(16.0)19
<i>A. longicauda</i>	M	5	107(131)153	78(87)100	15(15.5)16
	F	8	114(126)134	78(88)96	15(17.0)19

TABLES 3A AND 3B. HEAD SCALE AND FOURTH TOE LAMELLAE COUNTS OF *UROSTROPHUS* AND *ANISOLEPIS*. COUNTING METHODS ARE GIVEN IN THE APPENDIX. MEAN FIGURES ARE IN PARENTHESES. N = NUMBER OF SPECIMENS EXAMINED.

Species	N	Postrostrals	Between nasals	Between canthals	Supraorbital semicircles	Between semicircles
<i>U. vautieri</i>	76	3(5.1)6	5(6.0)6	4(6.3)8	7(9.1)11	0(1.0)2
<i>U. gallardoi</i>	21	5(5.7)6	5(6.4)8	7(8.0)11	8(9.9)13	1(2.0)3
<i>A. grilli</i>	55	4(5.5)7	5(6.4)8	6(8.8)11	9(11.0)14	1(1.3)3
<i>A. undulatus</i>	38	3(4.9)6	5(5.9)7	6(7.8)11	7(9.9)13	0(1.0)2
<i>A. longicauda</i>	13	4(5.0)5	6(6.0)7	7(8.1)10	9(10.2)13	1(1.9)3

Species	N	Between suboculars & supralabials	Supralabials	Infralabials	Temporals	Fourth toe lamellae
<i>U. vautieri</i>	76	0(0.7)1	6(7.3)9	6(7.8)10	7(8.9)11	21(24.2)30
<i>U. gallardoi</i>	21	0(0.9)1	7(8.7)10	8(10.6)13	11(12.4)14	22(26.2)29
<i>A. grilli</i>	55	0(1.0)2	6(8.1)10	6(8.4)11	8(10.4)14	22(22.5)30
<i>A. undulatus</i>	38	0(0.8)1	6(7.7)10	7(8.2)10	8(9.3)12	21(24.1)27
<i>A. longicauda</i>	14	1	7(8.0)9	8(8.8)10	10(12.0)14	20(23.3)26

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APPENDIX: SCALE DEFINITIONS, MEASUREMENTS, AND COUNTS

We follow the useful scale definitions of Smith (1946) except in the instances below:

Pileus. All the dorsal head scales from the rostral to the occipital region when these are differentiated and large. Used in the sense of Friederich (1978).

Lorilabials. Scales below the loreals and suboculars and between these and the supralabials. Usually smaller than the loreals, but the loreals may vary much in size. The definition employed here is more restrictive than that of Smith (1946). As understood in this paper these scales are *not* adherent to the underlying periosteum, as are the loreals, but are, instead, lifted with the supralabials by forceps or dissecting needle, as the loreals cannot be.

Upper and lower temporals. Two levels of temporal scales distinguished by the planes—vertical or horizontal—in which they occur. The *lower temporals* lie in a vertical plane between orbit and ear. The *upper temporals* lie in a horizontal plane above the lower temporals, and may or may not be larger than the lower temporals, i.e., if supratemporals are, as defined by Smith (1946), necessarily larger than the lower temporals, these are *not* supratemporals. Usually the two sets of temporal scales are separated by a more or less enlarged double row of intertemporal scales that lie superficial to the postorbital-squamosal arch that is the inferior border of the upper temporal fossa of the skull.

Posterior auriculars. The scales posterior to the ear opening. In most taxa these are granular, but in some iguanians they are large and imbricate.

Sublabials. As used here these are equivalent to the “chin shields” of Smith (1946) and *not* synonymous with “sublabials” as defined by him. They are enlarged scales (=“plates below the infralabials” in Van Denburgh, 1922, p. 46) medial to the infralabials on each side, the anteriormost usually in contact with the first infralabial. More posterior sublabials may or may not be in contact with the infralabials. Sub-

labials in the sense used here may be separated from the infralabials by one to several rows of smaller scales (=the “sublabials” of Smith = the “lateral gulars” of this paper).

Lateral gulars. Small scales—when present—between the plate-like sublabials and the comparably plate-like infralabials. These are distinguished from “central gulars”—the smaller scales medial to the sublabial series. When sublabials are not differentiated or at the point at which the sublabials become unrecognizable posteriorly, the distinction between lateral and central gulars ceases to be valid and these scales become simply “gulars.”

Antehumeral-transverse gular fold. A transverse skin fold enclosing markedly reduced scales, crossing the posterior gular region and on each side continuing up and over the forelimb insertion as an antehumeral fold.

Pregular fold. A transverse skin fold across the middle or anterior gular region, not enclosing markedly reduced scales.

Counts of the scales of the head, body, and digital lamellae were taken as follows:

Postrostrals. All scales in direct contact with rostral between anterior supralabials.

Between nasals. All scales crossed by a line drawn horizontally between the midpoints of the nasal scales.

Between canthals. All scales crossed by a line drawn horizontally between the anterior extremities of the posterior canthals.

Supraorbital semicircles. Enlarged scales in the supraorbital arc beginning with the first in contact with the posterior canthal.

Between supraorbital semicircles. Minimum number of scales between semicircles at their closest approach.

Between subocular(s) and supralabials. Minimum number of scales between subocular(s) and supralabials at their closest approach.

Supralabials. Counted back from the rostral to, and including, the most posterior scales that take part, however slightly, in the margin of the mouth.

Infralabials. Counted back from the mental to, and including, the most poste-

rior scale that takes part, however slightly, in the margin of the mouth.

Temporals. Number of scales crossed by a line drawn horizontally across the temporal region, between the postorbital(s) and the anterior border of the external ear.

Paravertebrals. Number of scales crossed by a line drawn just to the left of the midline between the posterior parietal scales and a line drawn horizontally across the back even with the anterior margins of the hindlimb insertions.

Midbody scales. Number of scales around the body midway between the forelimb and hindlimb insertions.

Ventral scale row. Number of large, keeled ventral scales crossed by a line drawn horizontally across the belly halfway between the forelimb and hindlimb insertions (*Anisolepis* only).

Fourth toe lamellae. Number of scales on the ventral surface of the fourth toe, beginning with the first scale below the free proximal part of the digit and counting to, but not including, the scale just posterior to the claw.

Snout-vent length. Measured from the anterior margin of the rostral scale to the anterior border of the vent.

Measurements were taken as follows:

Tail length. Measured from the anterior margin of the vent to the distal extremity of the tail.

Head length. Measured from the anterior margin of the rostral scale to the middle of the inferior border of the tympanum (the latter marking the center of the articular fossa of the articular bone).

Serial homologues of the axial skeleton were counted as follows:

Presacral vertebrae. Counted as all vertebrae anterior to the first sacral, including the atlas. Asymmetrical counts such as 23/24 or 24/25 are due to an asymmetrical sacrum.

First cervical rib. Counting the atlas as the first vertebra, the number of the most anterior vertebra to bear a pair of ribs, the third or fourth in this group.

Lumbar vertebrae. The number of vertebrae immediately anterior to the first sacral vertebra from which ribs are entirely lacking; asymmetrical counts such as 0/1 indicate the absence of a rib on one side.

Total caudal vertebrae. The total number of vertebrae between the posterior sacral vertebra and the distal extremity of the tail.

Caudal transverse processes. The number of anterior caudal vertebrae that bear at least some trace of transverse processes; since the processes may become smaller gradually, determination of the exact vertebra of disappearance may be subjective.

Sternal ribs. The number of inscriptional ribs that join bony dorsal ribs to the lateral margin of the sternum.

Xiphisternal ribs. The number of inscriptional ribs that join bony dorsal ribs to the xiphisternal rods; "lf" indicates the presence of free posterior extensions of the xiphisternal rods beyond the xiphisternal rib.

Attached chevrons. The number of continuous inscriptional chevrons that join the bony dorsal ribs, posterior to the xiphisternum.

Unattached chevrons. The number of inscriptional chevrons that are continuous midventrally but do not reach the distal extremities of their corresponding bony dorsal ribs.

Isolated splints. Calcified cartilages within the inscriptions of the myomeres, not connected midventrally, nor to the bony dorsal ribs above.

Total inscriptional ribs. The total number of inscriptional ribs beginning with the most anterior sternal rib and counting back to include the xiphisternal ribs, chevrons, and splints. The number actually represents the number of postcervical inscriptional ribs, as short inscriptional ribs are also present on the bony ribs anterior to the first attached to the sternum.



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