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Central American Lizards Related to *Anolis pentaprion*: Two New Species from the Cordillera de Talamanca

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ABSTRACT

New species of lizards are described from the Talamanca Mountains of Costa Rica and western Panama. *Anolis fungosus*, from lower montane rain forest of the Atlantic slopes, is a tiny, fungus-patterned anole with a pair of bony parietal knobs on the rear of its head. *Anolis vociferans*, which lives on the drier Pacific slopes and squeaks when handled, undergoes an ontogenetic transformation of the ventral granules—from obliquely conical and juxtaposed to keeled and imbricate. Both species appear related to the lowland *Anolis pentaprion* Cope, and a *pentaprion* species group is defined. Evolution within the group has included selection for lichenose and fungous camouflage; on the basis of osteology, color pattern, and scale features, *A. vociferans* is suggested as the most primitive member and *A. fungosus* as the most divergent.

Notes are presented on the distribution, variation, behavior, and synonymy of *Anolis pentaprion* Cope, 1862; a lectotype is designated for the nominal *Anolis panamensis* Boulenger, 1890. A Colombian species, *Anolis sulcifrons* Cope, 1899, is resurrected from the synonymy of *pentaprion*. The importance of describing dewlap color in anoles is widely recognized, but collectors are also urged to record the coloration (or absence thereof) of the iris, the tongue, and the throat lining.

INTRODUCTION

The Talamanca Mountains rise in central Costa Rica and stretch

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southeastward into extreme western Panama, where they abut against the Serranía del Tabasará, a lower range that carries the continental divide toward the central part of the isthmus. These mountains stand as a barrier to the northeast trade winds, and the Atlantic drainage consequently receives a greater abundance of precipitation than do most areas on the Pacific side, where rainfall is more seasonal.

The heart of the Atlantic highlands has yet to be penetrated by roads, and the biota is likely to remain little known for some years to come, especially in the rain-swept forests of the higher slopes, where access is difficult. Some progress toward an understanding of the amphibian and reptile faunas of this region was made by William E. Duellman, Linda Trueb, and me in the course of a month spent camping on the Atlantic slopes of Cerro Pando, the summit of which is the three-way junction between the borders of Costa Rica and the Panamanian provinces of Chiriquí and Bocas del Toro. Included in our collections is a miniature anole that represents an undescribed species seemingly related to *Anolis pentaprion*, a wide-ranging lizard of the Middle American lowlands. The new species has several peculiarities, but it will be named after the most obvious characteristic, the odd fungus-like markings that presumably serve as a protective camouflage.

A second new species, more definitely related to *Anolis pentaprion*, has been taken by several collectors, as it occurs on the drier Pacific watershed—on the slopes of Cerro de la Muerte and the Volcán de Chiriquí, which faunistically are the best known parts of the Cordillera de Talamanca. Individuals of this species protest capture by squeaking, and it will be named in recognition of its vocal abilities.

The genus *Anolis* is large, burdensomely so, in fact, and these new species are named with my apologies, as it should be common knowledge that it is “a wicked and sinful affection to describe more Anoles” (Thomas Barbour, 1932).

ABBREVIATIONS

AMNH, the American Museum of Natural History
ANSP, Academy of Natural Sciences of Philadelphia
BMNH, British Museum (Natural History)
CWM, field series of Charles W. Myers
FMNH, Field Museum of Natural History, Chicago
KU, University of Kansas Museum of Natural History, Lawrence
MCZ, Museum of Comparative Zoology, Harvard University
UCR, Universidad de Costa Rica, Museo de Zoología, Ciudad Universitaria
USNM, United States National Museum, Smithsonian Institution

***Anolis fungosus*, new species**

Figures 1, 2, 9, 11A

HOLOTYPE: KU 113451 (Field No. CWM 6730), an adult male found on Friday, May 13, 1966 by Charles W. Myers, at "Campo Mojica," a clearing on a trail at 1450 meters elevation, on the north slopes of Cerro Pando, upper watershed of Río Changena, in the Cordillera de Talamanca, Bocas del Toro Province, Republic of Panama (figs. 3, 4).

ETYMOLOGY: The specific epithet is an adjective formed from the noun *fungus* plus the suffix *-osus* (abounding in), in reference to the distinctive color pattern.

DEFINITION AND DIAGNOSIS: A tiny (47 mm. snout to vent in only known specimen, an adult male), short-legged anole of the beta group, having transverse processes on some autotomous caudal vertebrae and a pair of scale-covered, bony parietal protuberances atop rear of head. White fungus-like markings on brown dorsum, red dewlap, brown iris, yellow tongue, and black mouth and throat lining; no color repertory. All scales smooth except some on tail; middorsal caudal scales not raised in serrated crest. Upper trunk with flat granules disposed in oblique rows except for about a dozen longitudinal rows on middorsum; belly with slightly larger, conical granules. Plates atop head relatively large, frontal ridges weak, canthal ridges absent; elongated supraciliary scales lacking; no enlarged postanal scales.

The small size, white-on-brown fungous pattern (fig. 1), and a pair of small but distinct parietal knobs (figs. 2A, 9) immediately distinguish *Anolis fungosus* from its congeners. The absence of strongly carinate scales on top of the tail (fig. 11) is also useful in separating the species from its geographically close relatives, *Anolis pentaprion* and *A. vociferans*. See also the sections on comparisons.

DESCRIPTION OF HOLOTYPE: Snout to vent length 47 mm., total length 103 mm.; limbs short, longest toe of appressed hind limb falling short of axilla, longest finger of extended forelimb not approaching nostril; humerus 6.0 mm., ulna 4.3 mm., femur 8.1 mm., and tibia 5.8 mm. (bones measured from radiograph); lower leg between outer limits of knee and heel 7.8 mm., fourth toe 6.8 mm.; head length 12.0 mm. from snout to front edge of ear; head width between corners of mouth 6.4 mm., head height 6.1 mm. Specimen an adult male, as indicated by sperm in testes and by well-developed hemipenes and dewlap.

Color of dorsal surfaces striking in life (brightness of colors faded in preservative but no change in pattern): specimen medium brown above with irregular blotching of white (fig. 1), as though sporting little patches

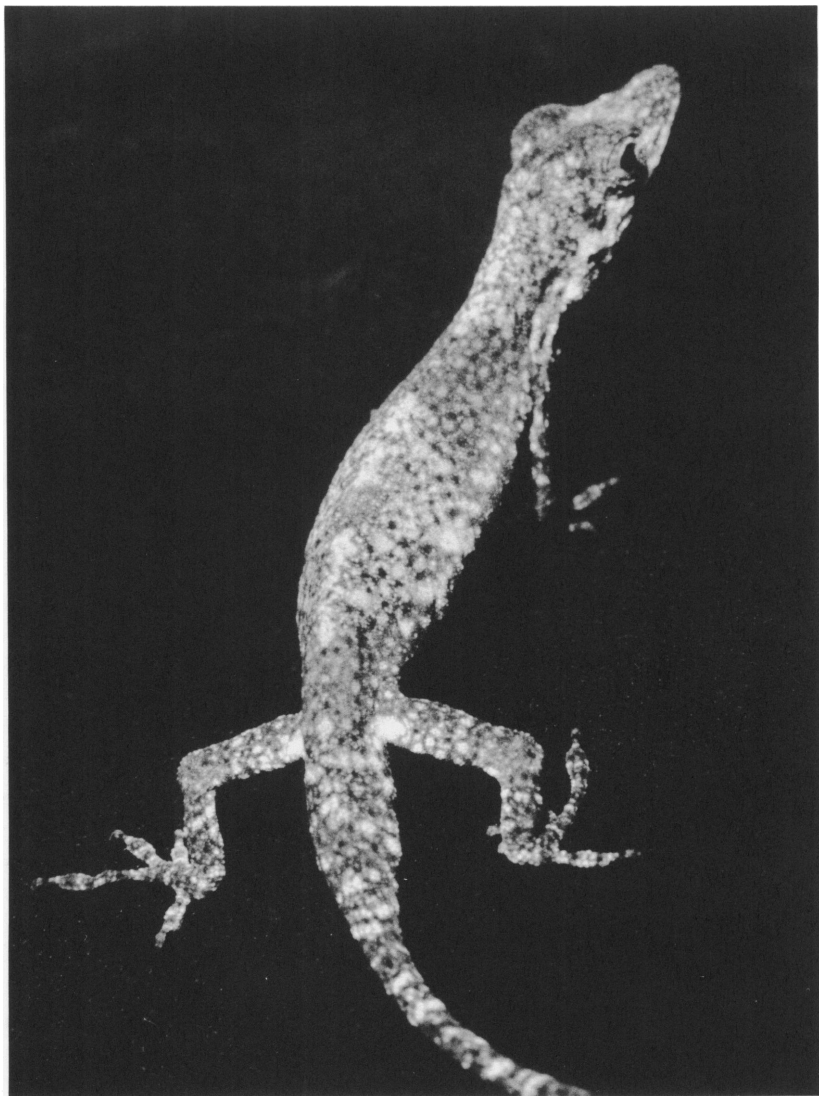


FIG. 1. *Anolis fungosus*, new species, the holotype photographed in life. Approximately $\times 2.5$.

of fungus or sprinkled with white flour; no particular pattern on body and top of head, but a slight tendency for narrow white rings on limbs and about 10 pairs of indefinite white rings on tail; intervening brown

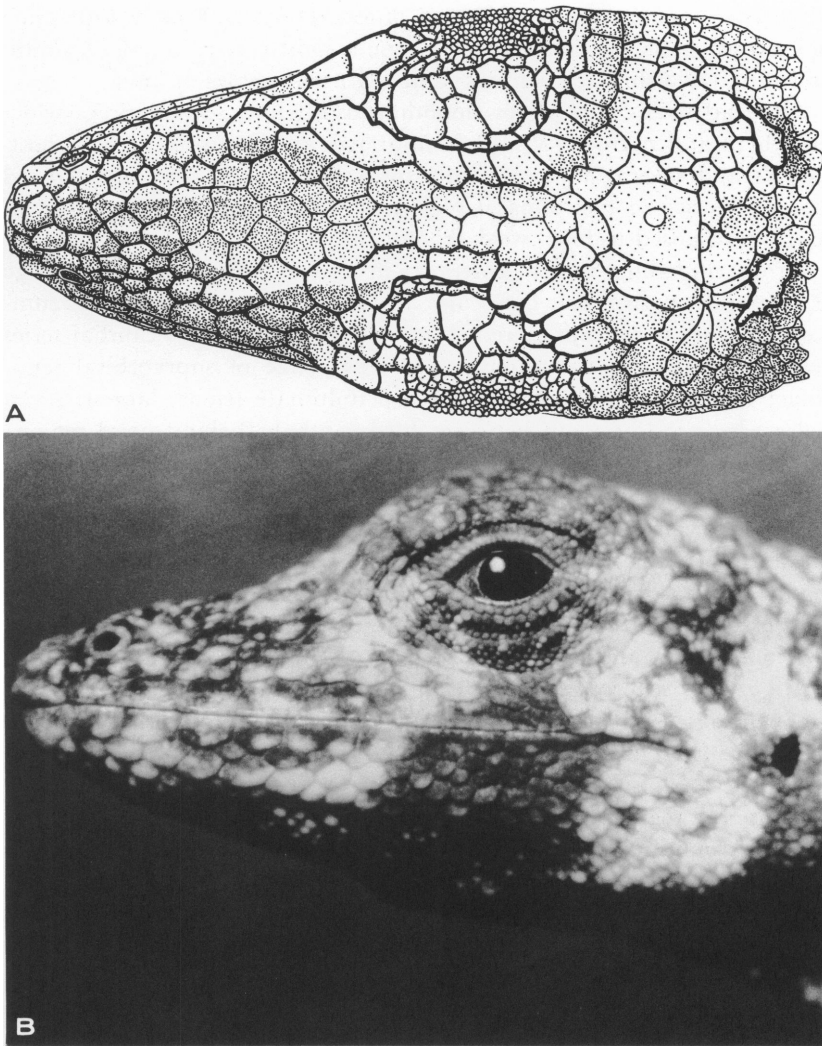


FIG. 2. *Anolis fungosus*, new species, head of holotype. A. Dorsal aspect, in which outlines of scales covering posterior bony protuberances are purposely exaggerated. B. Lateral view from life. All $\times 8$.

rings very narrow underneath tail but dorsally about equal in area to white. White chin crossed by brown line; two wider brown stripes commencing on lips and below ear (fig. 2B) interrupted by dewlap. Dewlap red with a few rows of white granules. Undersides of limbs and belly

white with encroachment of brown onto sides of belly and with some tiny brown spots. Iris of eye brown; tongue light yellow; lining of mouth and throat bluish black, turning bluish gray at angles of jaws.

All head scales and plates smooth. Rostral low, several times wider than high and narrowly visible from above; five postrostral scales; postrostrals and several adjacent scales markedly protuberant; dorsal head scales posterior to rostral-nasal region relatively large and platelike except where raised to form weak frontal ridges. Nasal scale (circumnasal) a narrow ring about nostril, anteriorly in contact with posterodorsal edge of lowermost postrostral; five scales across top of snout between circumnasals. Canthus rostralis rounded; a series of six scales in canthal series between bottom of circumnasal and front edge of supraorbital semicircle; ultimate canthal (left side) or penultimate (right) largest; seven scales across top of snout between third canthals (behind nasal region) and seven larger scales between posterior canthals. Frontal depression shallow. Supraorbital semicircles separated by two rows of enlarged scales; a few irregularly shaped small scales separate semicircles from supraorbital disks; approximately 10 large scales in each disk; approximately a half-dozen lines of granules between disk and supraciliary margin, which is comprised of undifferentiated granules except for a few small scales anteriorly; no enlarged or elongated supraciliary scale.

About 16 loreal scales, disposed in maximum of three horizontal rows; subocular scales in single row and anterior ones indistinguishable in size and shape from loreals; eight (left) or seven (right) supralabials to center of eye.

Temporal region with small, flat scales grading above to larger flat scales surrounding interparietal plate; interparietal about twice size of ear, separated by one or two scales from semicircles. Ear opening not much higher than wide and less than half length of eye opening. Pair of small but prominent bony protuberances rising (apparently from rear of parietal bone) atop rear of head; seemingly one major scale covering each protuberance, but scale surface rubbed off revealing black basal layer. No external bulges from muscle masses of temporal fossae.

Mental distinctly wider than deep and partly divided in middle. Eight (left) or nine (right) infralabials to a point beneath center of eye; sublabials moderate in size, there anteriorly being five on each side in contact with infralabials; chin between sublabials with large granules that turn smaller on throat. Greatest depth of extended dewlap about 7 mm., length 16 mm., extending from under center of head to short distance past axillae. Rather close-set granules along margin of dewlap, but only five or six rows of widely spaced granules within.

Dorsum of trunk with subequal, smooth, flat granules, arranged in oblique rows on flanks and in about a dozen longitudinal rows on mid-dorsum. Ventral granules larger, smooth, slightly conical with posterior slant, arranged in oblique, poorly defined rows. About 40 midventral granules and about 52 dorsolateral granules in one head length.

No pocket in axilla. Limbs covered by smooth granules similar to those of dorsal and ventral surfaces of trunk; dorsal digital scales also smooth; digital pads dilated; distal phalanx narrower than, and raised from, the dilated pad; 17 lamellae under second and third phalanges of fourth toe.

No enlarged postanal scales. That part of tail base containing the hemipenes swollen and covered by granules like those on trunk, but greatest length of tail moderately compressed and bearing the only keeled scales on specimen. Top and sides of tail with irregular mixture of smooth and keeled scales, but those on dorsal midline not raised to form crest (fig. 11A). Ventrolateral rows and two large ventral rows strongly carinate, with scale apices protruding to give serrated appearance; ventral scales larger than any others on tail; verticils weakly defined, containing about 4–7 lateral scales in length.

Everted hemipenis small and bilobate, the two lobes being quite bulbous relative to stalk. Sulcus spermaticus forked; forks extend onto lobes and appear tremendously expanded, an illusion caused by close spacing of lips over basal, unforked part of sulcus. Stalk with transverse flounces that merge to small calyces on lobes; flounces inconspicuous on sulcate side of stalk.

DISTRIBUTION, HABITAT, AND BEHAVIOR

Anolis fungosus is possibly confined to the wet Atlantic slopes of the Cordillera de Talamanca, and almost certainly occurs in Costa Rica as well as in Panama. The only known locality is in extreme western Panama, on the upper watershed of the Río Changena, a high tributary of the Río Changuinola, but maps of the region are inadequate and it is impossible to be precise. The general location of the type locality is shown in figure 3; the locality is indicated as station number three in a published sketch (Trueb, 1968, fig. 1) that is based partly on a drawing made in the field by Ratibor Hartmann, who made his sketch from the vantage of a helicopter after having been over the ground on foot.

The type locality, at 1450 meters elevation, is in a region of lower montane rain forest that is subject to torrential rains (Myers, 1969, pp. 33–36). The forest is moderately tall and there is a well-developed stratum of herbaceous vegetation; palms are relatively scarce in the understory,

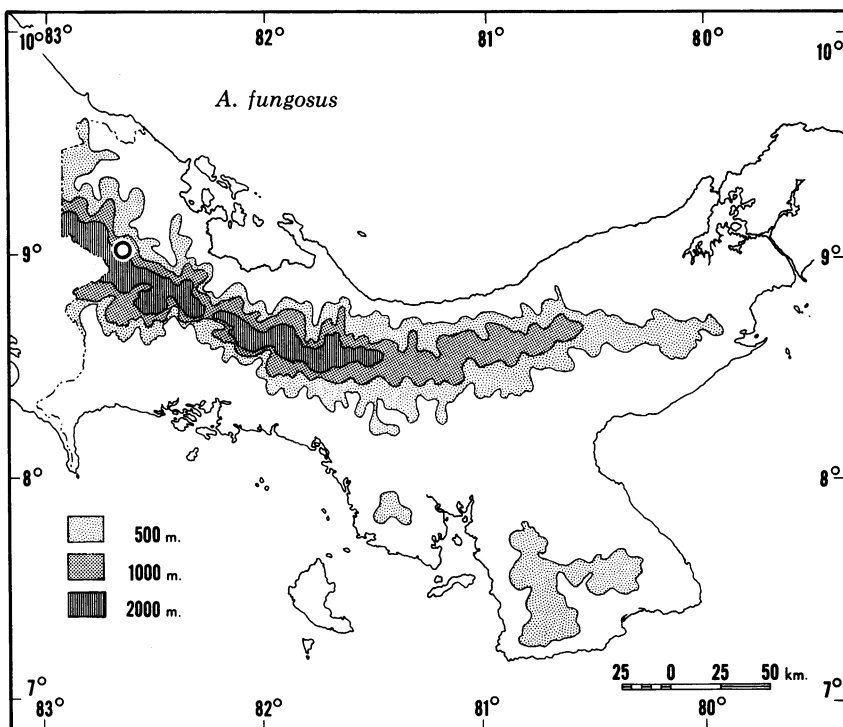


FIG. 3. Western Panama, showing the type locality (circle) of *Anolis fungosus*, new species.

in contrast to the situations above 1800 meters elevation (Myers, *op. cit.*, p. 36) and also lower down on the coastal plain. No human being resides permanently on these wet slopes, although pre-Columbian Indians once buried their dead here, often with *huacos* of clay, stone, and gold. The region is accessible by occasional foot trails made by small bands of men, who pillage the ancient graves, and by a few energetic farmers, who cross the divide from Chiriquí Province and make small clearings in order to plant crops far from market. The type locality of *Anolis fungosus* is at such a clearing, known to the *chiricanos* as "Campo Mojica," after the man who made it. The holotype was found a few feet above ground on a little bush on a sunny morning, in a small plot that had been planted to coffee (fig. 4 top). The rarity of ecologically disturbed situations on the Atlantic slopes, where even natural clearings made by falling trees are scarce, suggests that *Anolis fungosus* is normally an inhabitant of the deep forest (fig. 4 bottom), where it should be well con-



FIG. 4. Habitats at the type locality of *Anolis fungosus*, new species. Top. Small clearing (*cafetal*) in which the holotype was found. Bottom. Physiognomy of the surrounding lower montane rain forest. Both scenes at approximately 1450 meters above sea level; May 17, 1966.

cealed on some tree trunk infested with thallophytes.

The specimen was a good climber but did not run when placed on a flat surface where, if hurried, it moved by short little hops. It made no attempt to bite and evidently was not capable of undergoing any changes in color.

***Anolis vociferans*, new species**

Figures 5, 6, 10, 11B

Anolis pentaprin (not of Cope): WALTERS, 1953, p. 126 (specimen referred to is now AMNH 69621, the holotype of *A. vociferans*).

HOLOTYPE: AMNH 69621, an adult male taken on December 13, 1948 by Vladimir Walters, on road about 4 kilometers¹ west of Cerro Punta, about 6000 feet [1829 meters] elevation, Chiriquí Province, Republic of Panama.

PARATYPES: Seven specimens, as follows: Costa Rica, San José Province: KU 104015, 18.5 kilometers north of San Isidro El General, 1700 meters elevation, William E. Duellman collector. Panama, Chiriquí Province: ANSP 26287 and FMNH 68151, Palo Santo [=Finca Palosanto], 4600 feet [=1402 meters, but probably closer to 1300 meters], *ca.* 7 kilometers northwest of El Volcán, Harold Trapido collector; FMNH 130694, Cerro Punta, \pm 5300 feet elevation, Conrad E. Yunker collector; FMNH 130707, Bambito, \pm 5000 feet elevation, Conrad E. Yunker collector; KU 75961, Finca Bambito, 1475 meters elevation, *ca.* 6 kilometers north-northeast of Hato del Volcán, caught by Frank Todd in company of W. E. Duellman and C. W. Myers; MCZ 38686, at or near Mr. Lewis's place [*ca.* 2.5 kilometers west of Cerro Punta, \pm 1830 meters], Volcan Panama [Volcán de Chiriquí], Río Chiriquí Viejo and branches, S. F. Hildebrand collector.

ETYMOLOGY: The specific epithet is the present participle of the Latin *vociferor* (to cry aloud), in allusion to the squeaking noises made by specimens when they are first captured.

DEFINITION AND DIAGNOSIS: Medium-size (snout to vent length 57 mm. in largest specimen), short-legged anole of the beta group, having trans-

¹ This distance, as published by Walters (1953, p. 126), is considered correct, even though the field tag reads "abt. 4 mi. W" [6.4 km.]. If the longer distance had been intended, the locality would be situated southwestward of Cerro Punta, near the community of Bambito (a name familiar to Walters, *op. cit.*) and at a lower elevation. The American Museum catalogue entries read in kilometers for other specimens collected by Walters on this trip.

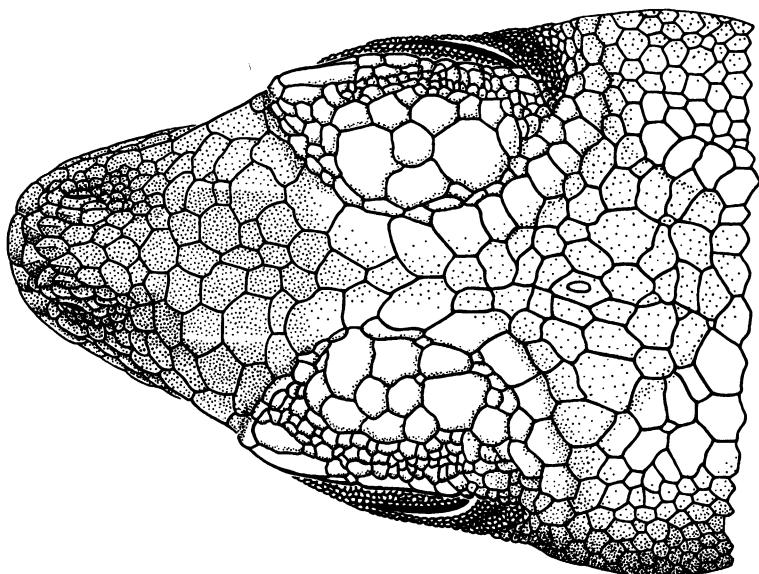
Cerro Punta is a town on the northwestern slopes of the Volcán de Chiriquí. Walters's (1953, p. 126) parenthetical "western slope" refers to the volcano.

verse processes on some autotomous caudal vertebrae. Brown or gray-brown above with variable, in some cases partly reticulate, dark pattern usually including interorbital bar, short postocular stripe, V-shaped marking between forelimbs, and butterfly-shaped mark on base of tail between hind limbs; red dewlap, bright blue sliver of color at corners of mouth, and black throat lining. Trunk granulation variable: granules small and convex on sides, sometimes larger and flattened on middorsum, either without definite arrangement or weakly disposed in horizontal rows dorsally and in oblique rows laterally; some dorsal granules keeled; ventral granules ontogenetically changing from conical and juxtaposed to keeled and imbricate. Middorsal caudal scales carinate but not projected in dorsal crest. Plates atop head relatively large, frontal ridges virtually absent, canthal ridges distinct, elongated supraciliary scale(s) present. Male with pair of moderately enlarged postanal scales.

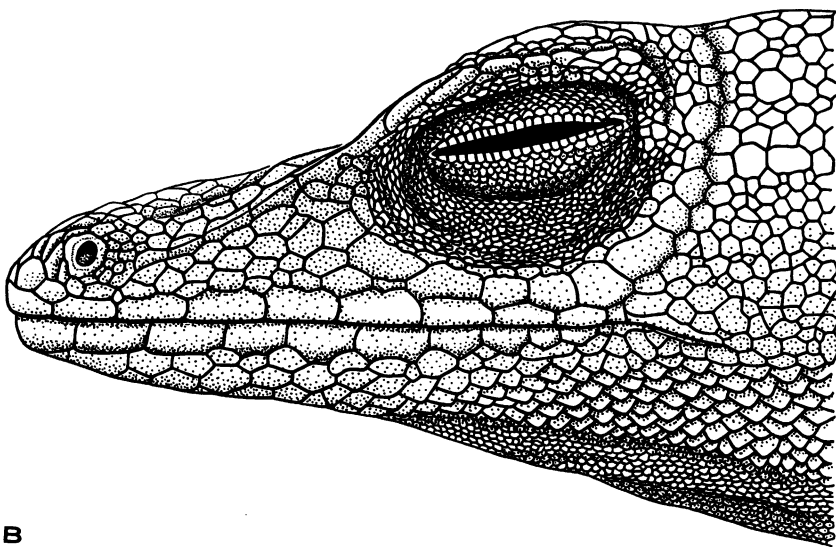
Anolis vociferans is most likely to be confused with the related *A. pentaprion*, but *vociferans* can be distinguished by the presence of a dark interorbital bar, enlarged postanal scales in males, keeling on scattered middorsal granules (and keeled ventrals in older specimens), and fewer supralabials to center of eye (*vociferans*, 6–8, usually 7 at least on one side; *pentaprion*, 7–10, usually 9 at least on one side). The species also differs from southern populations of *pentaprion* in that the middorsal caudal scales, although carinate, are not projected in a low, serrated crest (fig. 11). The absence of bony parietal projections, presence of enlarged postanal scales in males, different caudal scutellation (fig. 11), and a very different color pattern, among other characters, easily distinguishes *Anolis vociferans* from its smaller highland relative, *A. fungosus*.

DESCRIPTION OF HOLOTYPE: Snout to vent length 52 mm., total length 121 mm.; limbs fairly short, longest toe of appressed hind limb extending past axilla to shoulder, longest finger of extended forelimb reaching midway between eye and nostril; humerus 8.4 mm., ulna 7.4 mm., femur 10.3 mm., tibia 6.0 mm. (bones measured from radiograph); lower leg between outer limits of knee and heel 10.2 mm., fourth toe 10.0 mm.; head 14.5 mm. from snout to front edge of ear; head width between corners of mouth 9.7 mm., head height 7.9 mm. Specimen an adult male, as indicated by the presence of sperm in testes.

Color in alcohol pale brown above, with medium brown markings (fig. 6A): a dark-edged, slightly wavy interorbital bar; a vague, posteriorly pointed V-shaped line across body between forelimbs; a hint of a reticulate pattern on sides of body; a few nearly indistinguishable cross-bands on limbs; about nine indefinite bands on tail; a short, oblique postocular stripe extending toward, but not reaching, ear; a vague blotch



A



B

FIG. 5. *Anolis vociferans*, new species, head of holotype, $\times 7.5$. (Both views are drawn from an ocular grid of a dissecting microscope, without adjustment for parallax, which accounts for the illusory shortening of the snout in dorsal aspect.)

on each side of dorsal midline of snout, not extending below canthus rostralis; several dark markings on upper and lower lips, including a vertical line on supralabials below center of eye and an oblique line pointing toward anterior corner of eye opening; small spot close to ear, behind angle of jaws, and a slightly larger spot below ear. Ventral surfaces dirty white, inconspicuously but uniformly marked with small, pale brown spots, and turning pale brown under chin and beyond base of tail. Skin of dewlap faded, but with reddish tinge; scales on dewlap white, except for several anterior gray ones. In life, the "angles of the jaws were turquoise and the dewlap was red" (Walters, 1953, p. 126).

Head scales and plates mostly smooth except for a few keeled ones within supraorbital disks and canthal-loreal region and, especially, near tip of snout in supranasal region. Rostral low, several times wider than high; six slightly protuberant postrostral scales; scales behind postrostrals (supranasal region) distinctly raised and keeled; dorsal head scales posterior to rostral-nasal region relatively large and platelike; only a hint of weak frontal ridges. Nasal scale (circumnasal) a ring of moderate width around nostril, anteriorly separated from postrostrals by a single row of scales; seven scales across snout between circumnasals. Canthus rostralis distinctly keeled; a series of five or six canthal scales, posteriorly increasing in size, between infranasal region and front edge of supraorbital semicircle; about 12 scales across head behind nasal region, between third canthals, and seven scales between posterior canthals. Frontal depression shallow. Supraorbital semicircles in contact at one point, otherwise separated by one or two scales; semicircles largely separated from supraorbital disks by single row of granules; approximately seven or eight large scales in each disk; three or four rows of granules intervening between disk and supraciliary margin; about seven supraciliary scales, larger than adjacent granules, the anterior two being elongated and overlapping one another.

About 25 loreal scales, disposed in maximum of four horizontal rows; subocular scales larger than loreals and in single row; seven supralabials on each side to center of eye.

Temporal region with small, flat scales grading above to larger flat scales surrounding interparietal plate; interparietal tiny, smaller than ear and smaller than some neighboring scales, separated from semicircles by two or three scales. Ear opening twice as high as wide and little more than half the length of eye opening. External bulges from muscle masses of temporal fossae present.

Mental large, wider than deep and divided in middle. Seven infralabials on each side to a point beneath center of eye; sublabials moderate in

size, there anteriorly being three on each side in contact with infra-labials; chin between sublabials with small granules of about same size as those on throat. Greatest depth of extended dewlap about 8 mm., length about 12 mm., extending from rear of jaws to level of axillae. Rather close-set granules along margin of dewlap, but only about a half-dozen rows of contiguous granules within.

Dorsum of trunk with small convex granules, those on middorsum almost indistinguishably arranged in about nine longitudinal rows and those on flanks somewhat smaller and vaguely disposed in oblique rows; some middorsal granules weakly keeled. Ventral granules larger than those on sides but smaller than dorsals, smooth, conical with posterior slant, and arranged in oblique, poorly defined rows. About 42 dorsal granules, 57 laterals, and 52 ventrals in one head length.

No pocket in axilla. Ventral surfaces of limbs with granules as on body; dorsal surfaces of limbs covered with larger scales, some being imbricate and others juxtaposed, and with some on lower parts of limbs weakly keeled. Dorsal digital scales smooth; digital pads dilated, distal phalanx narrower than, and raised from, the dilated pad; 18 lamellae under second and third phalanges of fourth toe.

A pair of enlarged postanal scales. Swollen part of tail base with granules proximally, and small, imbricate, weakly keeled scales more distally; greater part of tail moderately compressed and covered completely with imbricate, keeled scales, of which the dorsal and ventral rows are largest; enlarged dorsal row strongly carinate and with scale apices protruding to give serrated appearance in lateral aspect, but not forming a dorsal crest (fig. 11B); the two large ventral rows, and the slightly smaller ventrolateral rows, also strongly carinate and serrated; verticils poorly defined, containing about 5–10 lateral scales in length.

Hemipenes not everted.

VARIATION IN THE TYPE SERIES

The largest specimen is a female 57 mm. snout to vent, 132 mm. total length; the two largest males are each 56 mm. snout to vent and 125 mm. total. The males have a well-developed dewlap and a pair of moderately enlarged postanal scales, whereas the females have vestigial dewlaps and lack differentiated postanal scales. Females seem to have proportionally somewhat larger heads (compare head measurements of FMNH 130707, in table 1, with the two larger males). The longest toe of the appressed leg extends to the neck in one specimen, to the axilla or shoulder in the others.

Variation in head scutellation is not extensive, and the illustrations of

TABLE 1
DATA FOR THE TYPE SERIES OF *Anolis vociferans*
(MEASUREMENTS ARE IN MILLIMETERS)

Museum number	Sex	Snout to vent	Snout to ear	Head width ^a	Head height ^a	Enlarged postnasal scales	Ventrals distinctly keeled	Ventral granules ^b	Fourth toe lamellae, phalanges ii and iii	Scales between circumnasals	Scales between posterior canthals	Scales between supraorbital semicircles	Scales between and interparietal	Maximum number of loreal rows	Supralabials to center of eye
FMNH 130694	♀	57	16.4	10.3	8.8	No	Yes	a	18	8	5	0	1	4/5	6/6
ANSP 26287	♂	56	15.7	9.5	8.2	Yes	Yes	b	20	8	7	1	2	3/4	7/7
FMNH 68151	♂	56	15.5	9.6	7.8	Yes	Yes	a	18	8	6	1-2	3	4/5	7/8
FMNH 130707	♀	55	15.7	10.2	8.7	No	Yes	a	18	6	6	1	2	4/4	7/8
AMNH 69621 ^c	♂	52	14.5	9.7	7.9	Yes	No	b	18	7	7	0-1	3	4/4	7/7
MCZ 38686	♂	52	14.7	8.8	7.1	Yes	No	b	17	7	7	0-1	2	4/4	7/7
KU 75961	♂	41	10.6	7.7	6.5	Yes	No	c	18	7	6	1	2	4/4	,
KU 104015	♀	35	10.3	7.0	5.5	No	No	c	17	7	4	1-2	2	5/5	7/7

^a At rear corners of mouth.

^b Code: a. Granules or tiny scales that are imbricate and almost flat. b. Obliquely conical granules that are very slightly imbricate. c. Like "b" except that granules are juxtaposed rather than overlapping.

^c Holotype.

the holotype (fig. 5) are fairly representative, except that the plates in the frontal depression tend to be larger in the paratypic series. All specimens have two scales between the rostral and circumnasal scale. The number of enlarged scales in the supraorbital disks varies from about 5 to 9. In the seven Panamanian specimens, the disks are medially separated (at least partly) from the semicircles by a row of granules or small scales, and the disks are laterally separated from the supraciliary margin by three or four lines of granules. But in the single Costa Rican specimen, a juvenile, the disks are medially in full contact with the semicircles and are separated from the supraciliary margin by only two lines of granules. There is either one or two elongated, anterior supraciliary scales, in some cases with definite overlapping when there are two. The interparietal varies in size, from distinctly smaller to slightly larger than the ear, but it is to be described as "small" in any case. Variation in certain standard head counts is shown in table 1.

There is considerable variation in the extent of keeling on the scales. All the specimens have some keeling near the tip of the snout (especially on the supranasal bulges), in the canthal-loreal region, on the limbs, and on scattered dorsal granules, and the caudal scutellation is conspicuously carinate; the enlarged scales in the supraorbital disks can, or cannot, be keeled. However, the keeling is developed most strongly in the largest specimen, which even shows well-developed, multiple keeling on the supradigital scales and, most notably, on the normally smooth plates in the frontal depression. That such keeling might be partly an ontogenetic development is suggested more strongly by variation in the ventral granules of the trunk. The ventrals are definitely keeled in the four largest specimens (all adults) but are smooth, or virtually so, in the four smallest specimens (two adults and two juveniles); see table 1. Seemingly correlated with the acquisition of keels is an apparent change from juxtaposed, raised granules to slightly imbricate, flattened granules or tiny scales (table 1). The raised granules, in the smaller specimens, are nearly "conical" except for a strong posterior slant, which accounts in some specimens for a slightly imbricate aspect to the ventral granulation; a slight flattening and concurrent keeling produces a more imbricated and "scaly" condition in the larger specimens, but the variation seems to be gradual rather than abrupt.

There also is variation in shape, size, and arrangement of the dorsal granules. The flanks appear finely pebbled owing to the convexity of the granules, which usually are rather uniformly small, although enlargement of scattered granules provides some individuals (e.g., FMNH 130707) with a more heterogeneous aspect. The pebbled appearance may extend

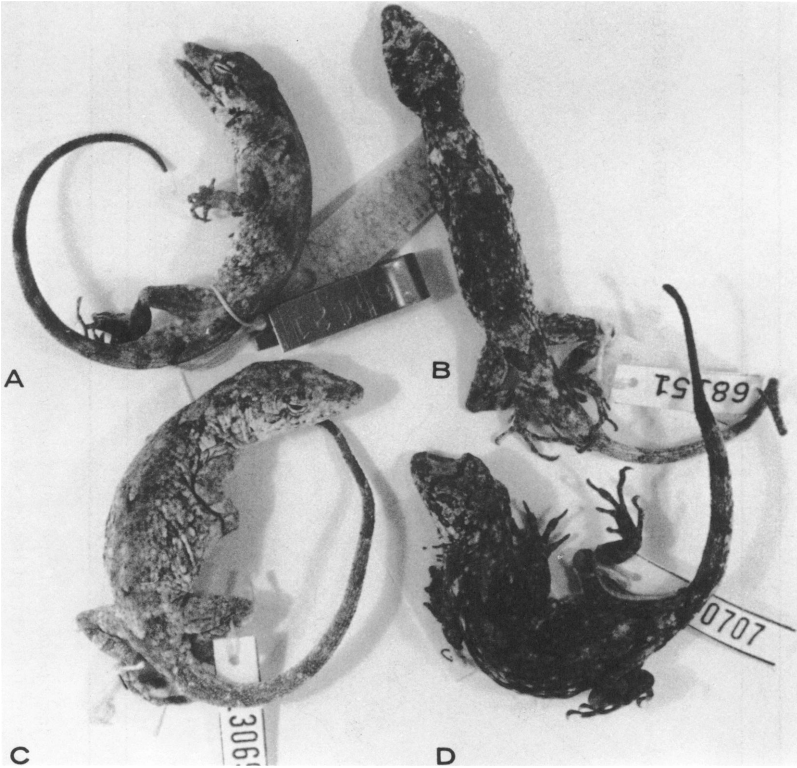


Fig. 6. Color variation in *Anolis vociferans*, new species, showing a light and a dark male (top row) and a light and a dark female (bottom row). A. AMNH 69621 (holotype). B. FMNH 68151. C. FMNH 130694. D. FMNH 130707.

onto the middorsum, where the granules tend to be somewhat larger and where some are keeled, but in some individuals (especially FMNH 130707) there is a decided tendency for the middorsal granules to be flat rather than convex. The granules in the middorsal region may lack definite arrangement or may occur in about a dozen vague, horizontal rows, whereas the lateral granules are disposed more obliquely. But, in any case, differentiation between lateral and dorsal granulation tends to be gradual and slight rather than abrupt and clear-cut.

All specimens have a dark-edged, brown interorbital bar, although it is only faintly indicated in the small Costa Rican individual, and all have a short horizontal or oblique postocular stripe that usually does not extend as far as the ear. The upper surfaces of the body (fig. 6) vary

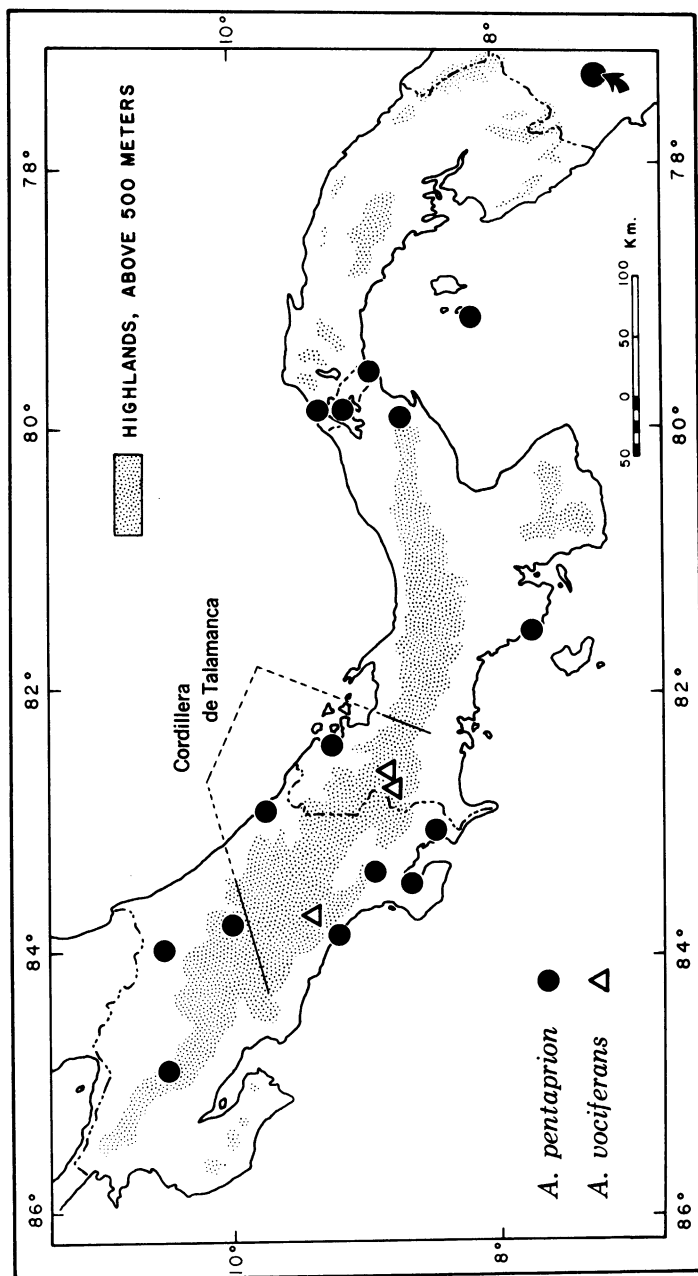


FIG. 7. Map showing collection sites for *Anolis pentaptrion* Cope and *Anolis vociferans*, new species, in lower Central America. All localities plotted represent specimens examined, except the type locality (arrow) of *A. pentaptrion*, whose holotype is lost (Río Truandó region, Colombia). The diagonal lines indicate the approximate limits of the Talamanca range.

from light brown with ill-defined darker markings, to medium brown or gray-brown with definite, albeit irregular, darker reticulation (especially on the sides). All individuals have a posteriorly pointed V-shaped dark line or band between the forelimbs; and all have at least a tendency for a dark butterfly-shaped marking (nearly absent in holotype) across the tail base, either between or slightly behind the limb insertions. Except on the holotype, there is a tendency for one to three additional dark chevrons on the dorsum of the trunk. The upper limb and tail surfaces have dark crossbands that vary from faint to distinct. The venter is white and bears few to many small spots that range from an inconspicuous pale brown to a contrasting dark brown; no sexual or size correlation is evident, as bold spotting occurs in males and females but is nearly absent in both the largest and smallest specimens in the series. The dewlap in males and females retains a pale reddish tinge in alcohol. The dewlap scales vary from white to gray, with the individual scales within rows being contiguous in some individuals and slightly separated in others. In life, a paratype agreed with a description of the holotype in having a red dewlap and a patch of turquoise at the corners of the mouth (Walters, 1953, p. 126, and personal observation of KU 75961). In a few specimens checked, the throat lining is dark gray and was probably black in life.

DISTRIBUTION, HABITAT, AND BEHAVIOR

Anolis vociferans occurs on the Pacific side of the Cordillera de Talamanca (fig. 7), from Cerro de la Muerte (= Cerro Buenavista), in Costa Rica, to the Volcán de Chiriquí in extreme western Panama. The known elevational range is narrow, about 1300–1800 meters. It is not known whether the distribution is continuous or disjunct, as there has been scant collecting at these elevations in the mountains of eastern Costa Rica. Seven of the eight specimens are from the western slopes of the Volcán de Chiriquí, but the species seemingly has not been collected in the Boquete region, on the eastern slopes of the same mountain.

At least the eastern part of the range is in a belt of temperate wet and dry (*Cw*) climate that supports an evergreen seasonal forest (Myers, 1969, pp. 5–7, fig. 2). This forest is much disturbed, however, except on the steepest slopes, and large tracts have been completely cleared for pasture and agriculture, or partially cleared for shade-grown coffee. A paratype was found on a fence post in a *cafetal*; the holotype was found on a road, according to the field tag. Both specimens make squeaking sounds when held (Walters, 1953, p. 126, and personal observation of KU 75961). This habit of vocal protest, plus the small area of bright blue color at each corner of the mouth, immediately distinguishes live

specimens from sympatric congeners. Vocalization, although unusual, is nonetheless widespread in the genus *Anolis* (see Other Comparisons).

The extensive, seemingly ontogenetic variation in ventral granulation (table 1) might suggest the possibility of sibling species, inasmuch as presence or absence of ventral keeling, as well as differences in granule shape, is often indicative of species differences. But because of similarities in color pattern and other characters, I doubt that there are actually two species living on the same slope of the Volcán de Chiriquí. Nevertheless, it will be of interest to determine if the larger specimens, characterized by keeled ventrals, also squeak and have the turquoise color at the angles of the jaws.

OSTEOLOGY AND RELATIONSHIPS

Radiographs were made of the holotype of *Anolis fungosus*, the holotype and a paratype of *A. vociferans*, and of a specimen of *A. pentaprion* from Panama. I extracted the skull from another specimen of *pentaprion* for comparison with the X-ray photographs. The information thus gleaned leaves something to be desired but is nonetheless important in analyzing relationships; I unfortunately could not properly distinguish all attachments of the abdominal skeleton, although such data are of potential use in anoline systematics (*vide* Etheridge, 1965).

SKULL: The skull of *Anolis pentaprion* is rather broad and has a somewhat rough, or coarsely granulate, surface, as is apparent even in the radiograph (but intentionally omitted from the drawing) in figure 8. The parietal foramen lies adjacent to the frontoparietal suture. The skull of *A. vociferans* is similar to that of *pentaprion*, including the feature of surface granulation (fig. 10A), thus strengthening the idea of close relationship that is suggested by external similarities between these two species.

The skull of *Anolis fungosus* (fig. 9) differs in several important respects. It is relatively narrow and seems to lack the conspicuously granulated surface of *pentaprion* and *vociferans*. The parietal foramen is situated well posterior to the frontoparietal suture. The parietal foramen is not evident in the radiograph, but its position (fig. 9A) was determined by plotting the location of the pineal eye onto a life-size X-ray (use of a fine probe indicated that the pineal eye lies immediately above the foramen in all three species). Two scale-covered, bony protuberances are externally evident on the rear of the head (fig. 2A), and are visible in side profile by radiograph (fig. 9B); their position in dorsal aspect (fig. 9A) was plotted in the same manner as the parietal foramen. The protuberances apparently arise from the rear of the parietals, but whether they are

extensions of the parietal-crest system cannot be conclusively determined from the radiographs. A transverse crest, which forms the upper rear margin of the skull, can be felt through the skin of the specimen and is conspicuous in the lateral-view radiograph (fig. 9B); it is not clear to me whether this crest is formed from the rear margin of the parietals or from elaboration of the supraoccipital, but I am inclined toward the former interpretation. Direct study of a prepared skull will be the best way to resolve these uncertainties and to determine just how basic are the differences between *Anolis fungosus* and its presumed relatives. However, even the present incomplete data on cranial morphology indicate that *A. pentaprion* and *A. vociferans* are more closely related to each other than either is to *A. fungosus*.

CAUDAL VERTEBRAE: A specimen (KU 75959) of *Anolis pentaprion* has eight basal, non-autotomic, postsacral vertebrae, which bear transverse processes that change from a posterolateral orientation in the first seven vertebrae to a lateral direction in the eighth. Postsacral vertebrae 9–13 (remainder of tail is regenerated) have small transverse processes that are pointed almost laterally, but with a slight anterior direction, and which are situated immediately posterior to the fracture planes. A paratype (KU 75961) of *Anolis vociferans* has seven, non-autotomic, postsacral vertebrae, on which the transverse processes change from a posterolateral direction in the first five to a lateral orientation in numbers 6 and 7. Postsacral vertebrae 8–19 are autotomic and have, behind the fracture planes, very small transverse processes that are distinctly directed anterolaterally; there are about 20 additional vertebrae, to the tip of the tail, that lack transverse processes but which appear to be autotomic. The holotype of *Anolis fungosus* has seven, non-autotomic, postsacral vertebrae, on which the transverse processes change from a posterolateral direction (1–5) to a lateral orientation (6–7). Postsacral vertebrae 8–15 have small transverse processes behind the fracture planes, and these are followed by 29 additional vertebrae that are seemingly autotomic but which lack transverse processes (except for a tiny, unpaired process on vertebra number 17). There is considerable variation in the orientation of the transverse processes of the autotomic vertebrae in the specimen of *fungosus*: The processes are lateral in postsacral vertebrae numbers 8, 10, and 11; slightly anterolateral in number 9; one side posterolateral and the other anterolateral in number 12; and slightly posterolateral in numbers 13–15.

Specimens of the three species compared thus agree in having seven or eight, non-autotomic, postsacral vertebrae, with transverse processes posteriorly undergoing a change in direction from posterolateral to lateral, followed by 5+ to 12 autotomic vertebrae with small transverse processes

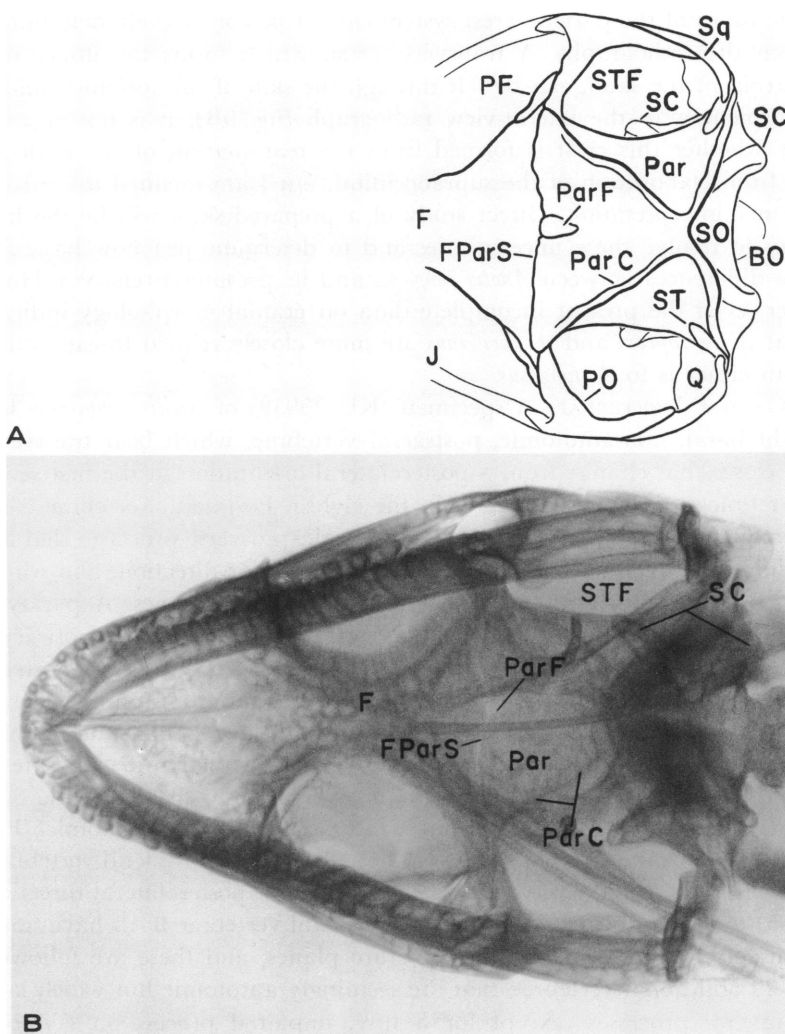


FIG. 8. *Anolis pentaprin* Cope, skulls in dorsal aspect. A. Posterior cranial morphology of AMNH 75987. B. Radiograph of KU 75959.

Abbreviations: BO, basioccipital; F, frontal; FParS, frontoparietal suture; J, jugal; Par, parietal; ParC, parietal crest; ParF, parietal foramen; PF, post-frontal; PO, postorbital; Q, quadrate; SC, semicircular canal ridge; SO, supra-occipital; Sq, squamosal; ST, supratemporal; STF, supratemporal fossa.

situated behind the fracture planes. These species therefore agree most closely with Etheridge's (1967, pp. 705, 717) "beta" section of the genus

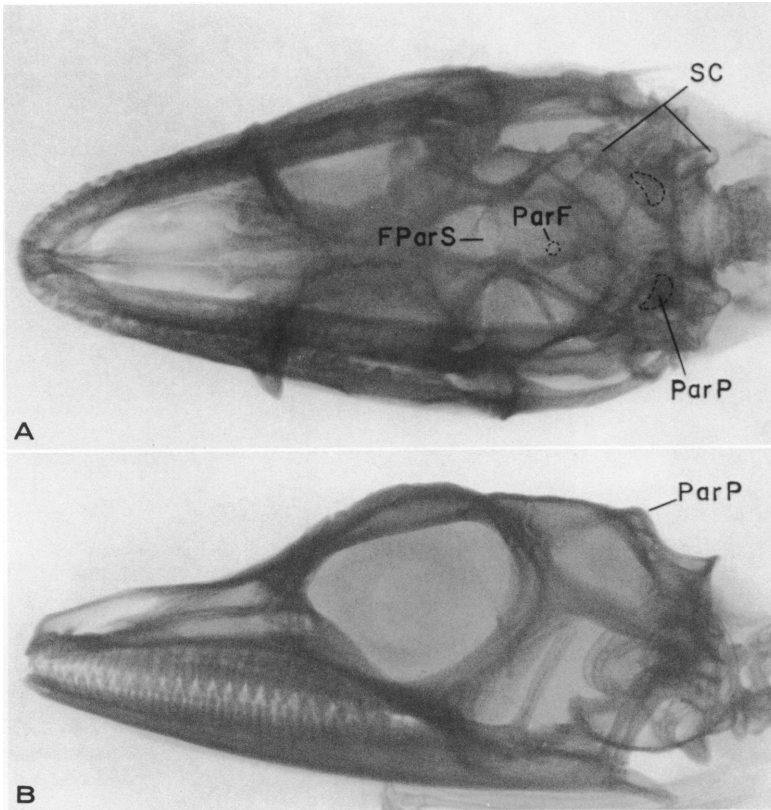


FIG. 9. *Anolis fungosus*, new species (holotype), skull as seen by radiography. A. Dorsal aspect, with approximate locations of parietal foramen and parietal protuberances drawn in ink. B. Lateral aspect.

Abbreviations: FParS, frontoparietal suture; ParF, parietal foramen; ParP, parietal protuberance; SC, semicircular canal ridge.

Anolis. They differ from Etheridge's definition (*loc. cit.*) in that the transverse processes are lost well before the end of the tail and in that the processes on the autotomic vertebrae are not necessarily oriented in an "acutely anterolateral" direction.

OTHER COMPARISONS

Following is a comparative summary of the major non-osteological characteristics of *Anolis fungosus*, *A. pentaprion*, and *A. vociferans*. Attention is called to the comments on iris and tongue color, throat pigmentation,

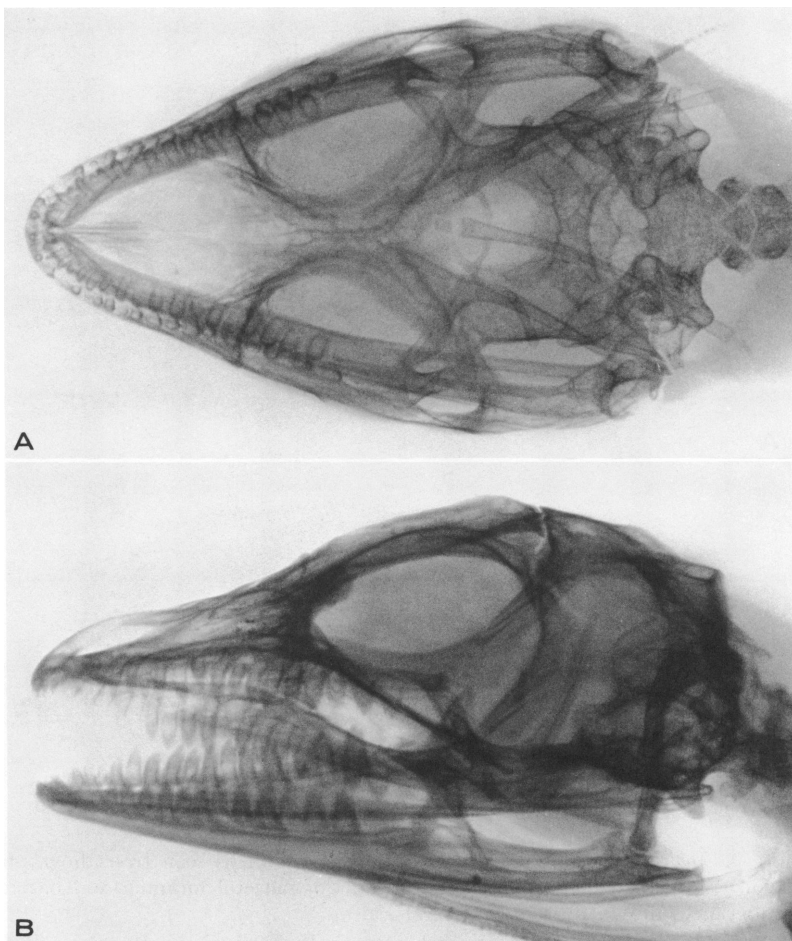


FIG. 10. *Anolis vociferans*, new species, skull as seen by radiography. A. Dorsal aspect of KU 75961. B. Lateral aspect of holotype.

and voice; these neglected features are useful in defining species of anoles, in rapid field-sorting of males and females of similar, sympatric species, and possibly also in demonstrating relationships within groups of species.

SIZE AND PROPORTIONS

Anolis fungosus is the smallest form (46 mm. snout to vent), *A. vociferans* is larger (to 57 mm.), and *A. pentaprion* is largest (to 77 mm.). The last-named species undergoes geographic variation in size, as will be discussed

later. *Anolis fungosus* is a slender lizard, and is less stocky than the other two species. *Anolis pentaprion* characteristically has a long, moderately straight slope to the snout (in lateral profile), but some individuals, especially juveniles, have a more abruptly sloping snout that approaches the condition in *vociferans*. The legs are relatively short in all three species, with the appressed hind limb usually reaching between the axilla and neck in *pentaprion* and *vociferans* but failing to even reach the axilla in *fungosus*.

Anolis vociferans has the dewlap in males relatively smaller than in males of *A. pentaprion* and *A. fungosus*. The dewlap is vestigial in female *vociferans*; female *pentaprion* have a well-formed dewlap, although smaller than in males of the same species.

COLORATION AND BEHAVIOR

DORSAL COLOR PATTERN: *Anolis fungosus* and *A. pentaprion* both have a fungous pattern that lacks definite symmetry or regularity (compare figs. 1 and 12). The pattern is more lichenose in *pentaprion*, which usually sports a dark reticulum within which are patches of pale color. The holotype of *fungosus* lacks such a reticulum and the specimen has the aspect of being irregularly dusted with a white powder. The pattern in *Anolis vociferans* (fig. 6) resembles that of many *pentaprion* in being vaguely reticulate, but the lichenous appearance is reduced or absent. *Anolis vociferans* differs from the other two species in having a definite tendency to regular dark markings, especially an interorbital bar and short post-ocular stripe, a V-shaped mark between the forelimbs, and a butterfly-shaped mark between the hind limbs. The only known specimen of *fungosus* has dark crossbands under the head, one of which reaches up to the eye (fig. 2B), but such markings are lacking in the other species. *Anolis fungosus* and *A. vociferans* seemingly lack the ability to change color (except probably for a few close shades of lighter or darker), but *A. pentaprion* can undergo rather extensive change, as observed in a specimen from central Panama: Most of the time, this specimen had a complex, mottled pattern of gray, brown, and pale greenish brown, as indicated in figure 12. Occasionally, it turned pale ashy gray—almost white—except for a faint greenish reticulation on the sides, a very pale greenish cast on the middorsum, and brown tail bands, which remained dark even when the interspaces were virtually white. It had the over-all appearance of a white lizard from just a short distance away; the stimulus for these changes, observed in a terrarium, was not obvious.

DEWLAP: The dewlap is red, with white scales, in *Anolis fungosus* and *A. vociferans*, and may also be red in *A. pentaprion* [e.g., "cherry-red, while

most of the individual scales on its sides are orange" (Taylor, 1956, p.75)]. But there evidently is variation in dewlap coloration in *pentaprion*: I noted that the dewlap of AMNH 103231, from central Panama, was purple in life, with white scales. Cochran (1946, p. 3) stated that, in 12 specimens from the Pearl Islands, the "gular fan scales are pinkish-vinaceous to salmon, with the skin between dragon's-blood red to madder-brown," but she did not indicate whether this description was copied from the collector's journal or recorded from preserved specimens. Taylor (*loc. cit.*) correctly noted that indication of the reddish gular color is retained in preservative for an unusually long time, and this is also true for *A. fungosus* and *A. vociferans*.

IRIS: The iris is brownish in all three species. Eye coloration is rarely recorded for reptiles, although it is often distinctive (e.g., the blue iris of *Anolis woodi* Dunn).

MOUTH AND THROAT: Presence or absence of pigmentation inside the mouth and throat of anoles is recorded even less than iris color although of potentially greater importance. Color similarities of these areas seem to support the idea of relationship of the three species: The tongue was light yellow in *Anolis fungosus* and a specimen of *A. pentaprion* (unrecorded for *vociferans*). All three species have a sliver of bluish tissue at the corner of the mouth; this is bluish gray in life and not conspicuous in *fungosus* and *pentaprion*, but it is bright blue in *vociferans*. All three species have a black throat lining, and in *fungosus* this is extended to include the entire buccal cavity.

Presence or absence of a black throat lining seems widespread in *Anolis* and probably is of taxonomic significance only at the level of species groups; I have not investigated the possibility that a black throat lining means also a black parietal peritoneum, although this certainly is the case in the *pentaprion-vociferans-fungosus* group. The presence or absence of dark pigmentation in the throat can be ascertained from preserved material, although it is easier to record this before the animal is preserved (as must be done anyway for the tongue and iris colors). My field notes record the presence of black throat linings in the following species of Panamanian and Colombian anoles, in addition to *A. vociferans* which is included on the basis of preserved material; an asterisk means that the species also has vocal ability (see following paragraph):

Alpha series

**A. chocorum*
A. fraseri

Beta series

**A. biporcatus*
A. fungosus
A. pentaprion
**A. vociferans*

VOCALIZATION AND THREAT DISPLAY: Vocalization is rare among non-gekkonid lizards but does occur at least in the Iguanidae (*Anolis* spp.) and possibly also in the Lacertidae (*Lacerta vivipara*, *fide* Falck, 1953). The trait occurs in both the alpha and beta sections of *Anolis*, as shown by the species starred in the list above. These are the only ones that I personally have heard to emit sound—in each case a series of a few to several easily heard squeaks when the animal was being held; the correlation in lower Central American anoles of vocal ability with a black throat lining seems odd, although perhaps fortuitous. Considering the size of the genus, it is likely that quite a few other species will prove to be vocal. I have not attempted to survey the literature for possible records, but I did notice that Thomas (1965, p. 11) described squeaking behavior in a Puerto Rican species, *Anolis occultus*. Mrs. Carol Leavens informed me of having heard squeaking by specimens of *Anolis roquet* that she collected in Barbados, and called my attention to a specimen of *Anolis grahami*, brought from Jamaica by Dr. Herndon G. Dowling, that protested handling with loud squeaks. Underwood and Williams (1959, p. 21) also recorded squeaking in *grahami* and in its close relative *A. opalinus*. These few observations make me wonder if the trait is not more common among West Indian species than on the mainland.

One possible function of having pigmented areas within the mouth is suggested by the threat display performed by an individual *Anolis pentaprion* (AMNH 103231), which, when held in the hand, would sometimes gape its mouth, showing to good advantage the pale yellow tongue against the black throat. Neither this specimen, nor the holotype of *Anolis fungosus*, made any attempt to bite. *Anolis pentaprion* is rather gecko-like in its behavior of clinging close to a tree trunk or branch and in sidling away from the observer as inconspicuously as possible; comparable observations are not available for the other two species.

SQUAMATION

Some comparative aspects of scutellation are set down in table 2. The extent of keeling on certain scales warrants additional comment: The single specimen of *Anolis fungosus* bears keeled scales only on its tail, and the keeling there is less extensive than in the other two species; this specimen even lacks a canthal keel. *Anolis pentaprion* has more extensive keeling on the tail and has a weak to strong canthal keel. In addition, there are frequently some keeled scales on the dorsal surfaces of the lower limbs (including the hands and feet but not the supradigital scales), and rarely there may be a few keels elsewhere, as on some of the middorsal trunk granules; the large scales on the dorsum of the head may be either

TABLE 2
ASPECTS OF SCUTELLATION IN PENTAPRIONID ANOLES OF LOWER CENTRAL AMERICA
(Nicaragua through Panama)

	<i>fungosus</i> N = 1	<i>vociferans</i> N = 8	<i>pentaprion</i> N = 49
Scales across snout between circumnasals	5	6-8	6-9
Scales between third canthals ^a	7	9-13	7-14
Scales between posterior canthals	7	4-7	6-11
Scales between semicircles	2	0-2	0-2
Scales between semicircle and interparietal	1-2	1-3	1-3
Maximum number of loreal rows	3	3-5	2-5
Supralabials to center of eye	7-8	6-8	7-10
Fourth toe lamellae (phalanges ii and iii)	17	17-20	19-24
Keels on some middorsal granules	No	Yes	No ^b
Keels on ventral granules (adults only)	No	Yes	No
Pair of enlarged postanal scales (males)	No	Yes	No
Tail crest	No	No	Yes ^c

^aBehind the nasal region. The first two canthals lie under the circumnasal scale and in some specimens are scarcely distinguishable from adjacent scales, except for being in the canthal line.

^bRarely present on a few scattered granules.

^cAbsent in juveniles; absent in only one adult examined (USNM 120583).

smooth or rugose in *pentaprion*, but are not keeled. Keeling is more extensive in *Anolis vociferans* in that scattered dorsal granules bear keels and so do scales at the tip of the snout and in the canthal-loreal region, as well as on the lower limbs and on the tail, and the ventral granules acquire keels as the animals approach maximum size; some specimens of *vociferans* even have keeling on the supradigital scales and in the supra-orbital disks and frontal depression.

DEFINITION AND EVOLUTION OF THE SPECIES GROUP

Anolis pentaprion is usually considered a very distinct species with few close relatives (Stuart, 1955, p. 20; Smith, 1968a, p. 195). Dunn (1930, p. 20) stated that *Anolis polylepis* Peters was "close to *pentaprion* and perhaps to *limifrons*." *Anolis polylepis* has a low caudal crest, as occurs in *pentaprion* (and various other species), and similarly shaped albeit larger ventral granules, but *polylepis* differs significantly in a number of features—including longer limbs, deeper loreal region, unpigmented throat lining,

extensive keeling on head scales and dorsal trunk granules, orange dewlap, pale line above shoulder, and a sex-influenced vertebral stripe. I do not see a close relationship between these species. Taylor (1956, pp. 75, 90) also denied such a relationship, and suggested instead that *pentaprion* was close to *Anolis microtus* Cope. This last idea, however, was negated with data extracted by Smith (1968a, p. 195) from Richard Etheridge's unpublished doctoral dissertation. Smith (1968b, p. 143) suggested his *Anolis macrinii* as a relative of *pentaprion*, but this was done only in the abstract to his paper, possibly in error for *A. gadoviae*, which was mentioned in the text. I know of no additional species having been considered in the recent literature as possible relatives of *pentaprion*, unless one accepts Smith's (1968a, pp. 195, 199) contention that a "subspecies" (*cristifer*) being described by him, on the basis of a single specimen that is "unique zoogeographically," really represents a distinct species because it "presumably is 100 per cent separable from its relatives, and therefore on 'biological' grounds qualifies as a species."

It is suggested in the present paper that *Anolis vociferans*, *Anolis pentaprion*, and *A. fungosus* form a natural series. Although intrageneric relationships of Middle American anoles are poorly understood, and other relatives may exist, it seems desirable to attempt at least a preliminary definition of a *pentaprion* species group. The following combination of characteristics delimits the group as I visualize it: Beta anoles of small to moderately large size; relatively short legs (appressed hind limbs usually failing to reach ear, never reaching eye); digital pads dilated, with distal phalanx raised from the dilated pad; low loreal region (maximum of 2-5 horizontal scale rows); black throat lining and parietal peritoneum; a bluish gray or blue-colored sliver of tissue at corner of mouth; few rows of scales on dewlap of relatively persistent (i.e., fade resistant in preservative) red or purple coloration; tendency for lichenose or fungous color pattern (in two of three species); no vertebral stripe;¹ tendency for smooth scales over most of head and body; relatively small dorsal and ventral trunk granules; ventral granules tending to be obliquely conical (ontogenetic change to flat and imbricate in one species).

I have no ideas concerning the ancestry of the *pentaprion* group, except that it presumably originated in Central America, very possibly in the Talamancan region where all three species presently occur (figs. 3, 7). Certain evolutionary events within the group, however, can be inferred from characteristics of the living species. It is suggested that *Anolis*

¹ A sex-determined character seen in some females (rarely males) of many species of the genus.

vociferans is the least divergent species and is primitive in its relatively extensive keeling, including the retention in late ontogeny of keeling and imbrication of the ventral granules; the enlarged postanal scales of male *vociferans* may also be a primitive feature. *Anolis vociferans* also lacks specialized lichenose camouflage and has discrete dark markings (e.g., interorbital bar and dorsal chevrons) typical of many other kinds of anoles and probably primitive in the *pentaprion* group. In *A. fungosus* and *A. pentaprion* there obviously has been strong selection for an asymmetrical

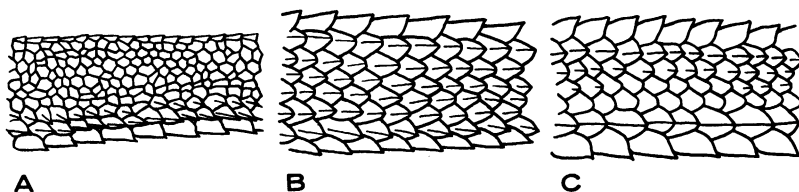


FIG. 11. Tails of pentaprionid anoles: lateral views of 5-millimeter sections of specimens from Panama. A. *Anolis fungosus*, new species (holotype). B. *Anolis vociferans*, new species (holotype). C. *Anolis pentaprion* Cope (MCZ 31582). All $\times 6$.

Section A is from near the distal end of the basal one-third of the tail, whereas sections B and C are from closer toward the middle of the tail. The dorsal crest of *Anolis pentaprion* (C) is usually even more pronounced on the basal part of the tail (but the crest is lacking in *pentaprion* from Yucatan to Honduras).

lichenose or fungous pattern, clearly a specialized kind of coloration and, considering the condition in *vociferans*, doubtlessly not primitive in the group. All three species have shorter limbs than the majority of their congeners, but the limbs are longest in *pentaprion* and *vociferans* and shortest in *fungosus*, which also is unusually small for an anole and is specialized in that regard too. *Anolis vociferans* and *A. pentaprion* show the greatest osteological similarity, whereas *A. fungosus* is clearly divergent, particularly in its acquisition of bony parietal protuberances and corresponding reduction in size of the muscle bulges of the supratemporal fossae. I do not think that data are sufficient for construction of a phylogeny, but the three species can be ranked on the basis of their character states as follows, from most primitive and generalized to derived and relatively specialized: *vociferans*—*pentaprion*—*fungosus*.

A dorsal caudal crest (fig. 11C) characterizes some populations of *Anolis pentaprion* and could easily have been derived from enlarged, carinated scales such as found in *A. vociferans* (fig. 11B), just as loss of

keeling could have resulted in the condition obtaining in *A. fungosus* (fig. 11A). In a discussion of geographic variation of *A. pentaprion*, elsewhere in this paper, I suggest that the caudal crest has been secondarily lost in some populations of the species; but this point deserves further investigation.

ADDITIONAL NOTES ON *ANOLIS PENTAPRION*

In the course of preparing the new species descriptions, I examined 57 specimens of *Anolis pentaprion* for comparison. Some observations concerning this widespread species are summarized below. The synonymy contains most of the important references to *pentaprion* but is not intended to be complete. All names applicable to the species are listed in the synonymy, although some workers will claim the right to utilize a few of the epithets for subspecies; interpopulational variation seems too slight to warrant recognition of subspecies in *pentaprion*, but this is a personal view and one that I shall not try to force on anyone. *Anolis sulcifrons*, which appears in most synonymies of *pentaprion*, is here considered a distinct species.

Anolis pentaprion Cope

Figures 8, 11C, 12

Anolis (Coccoëssus) pentaprion COPE, 1862, p. 178 (see below for type locality and holotype).

Anolis pentaprion Cope: COPE, 1874, p. 68. BOULENGER, 1885, p. 64 (part). DUNN, 1930, p. 20. BARBOUR, 1934, p. 145 (part). COCHRAN, 1946, p. 3. SMITH AND TAYLOR, 1950b, p. 61. STUART, 1955, p. 20. TAYLOR, 1956, p. 71, fig. 17. WILLIAMS AND SMITH, "1966" [1968], p. 164, fig. 1. PETERS AND DONOSO-BARROS, 1970, p. 62 (part).

Anolis beckeri BOULENGER, 1881, p. 921 (type locality, Yucatan; two syntypes, in the Royal Belgian Museum [see Stuart, 1963, p. 65, for details]).

Anolis panamensis BOULENGER, 1890, p. 81, pl. 8, figs. 3, 3a (type locality, Panama [see Dunn and Stuart, 1951, p. 56, for comment]; two syntypes, of which BMNH 1946.8.13.8 is lectotype by present designation [see below]).

Anolis pentaprion [*pentaprion*] Cope: STUART, 1958, p. 21.

Anolis pentaprion beckeri Boulenger: STUART, 1958, p. 21; 1963, p. 65. SMITH, 1968a, p. 195. PETERS AND DONOSO-BARROS, 1970, p. 63.

Anolis pentaprion pentaprion Cope: SMITH, 1968a, p. 195. PETERS AND DONOSO-BARROS, 1970, p. 62 (part).

Anolis pentaprion cristifer SMITH, 1968a, p. 195 (type locality, a small lake near Acacoyagua, Chiapas, Mexico; holotype, Univ. Illinois Mus. Nat. Hist. 37066).

TYPES: *Anolis pentaprion* was described from a single specimen obtained in "New Granada, near the river Truando . . . by Arthur Schott, Esq.,

who accompanied the U.S. Expedition under Lieut. Michler" (Cope, 1862, p. 178). The Río Truandó, a tributary of the lower Río Atrato, is in the Atlantic drainage although it rises not far from the Pacific coast, in the Chocó of extreme northwestern Colombia; the general region is indicated in figure 7. The holotype, supposedly at one time in the United States National Museum, is lost (*vide* Barbour, 1934, p. 145; Smith and Taylor, 1950b, p. 61).

The name *Anolis panamensis* Boulenger, a subjective synonym of *pentaprion*, is based on two syntypes now bearing the numbers BMNH 1946.8.13.7 and 1946.8.13.8, formerly registered as 89.7.2.31 and 89.7.2.32 (*vide* A. F. Stimson, *in litt.*). Dunn's (1930, p. 20) statement that the type is BMNH 89.7.2.31 is not to be construed as a lectotype designation; Dunn did not indicate any intention of selecting between syntypes, or even an awareness that more than one type specimen was involved; in any case, it would not be possible to tell which specimen Dunn had in mind, as the old catalogue numbers were not individually attached (*vide* A. F. Stimson, *in litt.*). I have examined BMNH 1946.8.13.8 and here designate it as lectotype because it obviously is the specimen described and figured by Boulenger. I obtained a snout to vent measurement of 49 mm. from the lectotype, which has a complete tail; Boulenger gave a measurement of 50 mm., if his figures for head length and body length are added together. According to A. F. Stimson (*in litt.*), the other syntype seems to have lost part of its tail, which has a blunt end, and measures only 44 mm. snout to vent and 36 mm. in tail length. The lectotype has a low caudal crest, three loreal rows, 8/8 supralabials to the center of the eye, and an indefinite brown reticulation on a pale ground color; it lacks the characteristic dark markings and caudal scutellation of *Anolis vociferans*.

DEFINITION AND DIAGNOSIS: *Anolis pentaprion* stands out from its congeners by the following combination of characters (to quickly distinguish from some related or very similar species, see also the diagnoses in this paper for *A. fungosus*, *A. vociferans*, and *A. sulcifrons*): A beta anole (*sensu* Etheridge, 1967, p. 717) of moderate to large size (geographically variable); relatively short legs (appressed hind limb between axilla and neck); digital pads dilated, with distal phalanx narrower than, and raised from, the dilated pad; variable lichenose pattern and a color repertory from brown to white; a red to purple dewlap in both sexes; a black throat lining; a low loreal region (usually three or four scale rows, rarely two or five); smooth dorsal trunk granules (a few middorsals rarely keeled); ventral granules smooth, obliquely conical; smooth supradigital scales; a weak to strong keel on canthal series, with other head scales smooth,

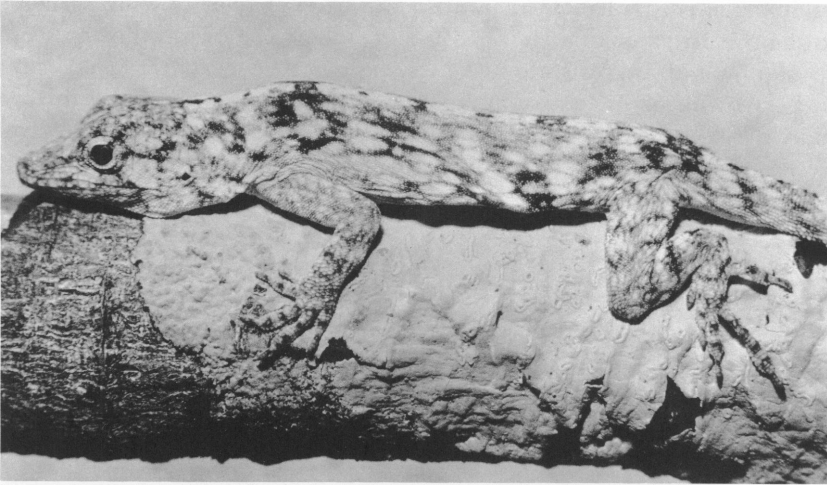


FIG. 12. *Anolis pentaprion* Cope, a specimen from Panama (AMNH 103231) photographed in life.

or sometimes rugose, but not keeled; 0–2 scales separating supraorbital semicircles; 7–10 supralabials to center of eye (usually 9); about 19–24 lamellae under phalanges ii and iii of fourth toe; no enlarged postanal scales; low caudal crest present in some populations.

DISTRIBUTION, HABITATS, AND ACTIVITY: From the Isthmus of Tehuantepec (both Atlantic and Pacific sides in Tabasco and Chiapas, *fide* Smith, 1968a) southward in the Caribbean drainage to northern Costa Rica, and then again on both watersheds from southern Costa Rica to extreme northwestern Colombia; also on the Pearl Islands in the Gulf of Panama. The species is found principally in the lowlands, mostly below 500 meters elevation, but it has invaded the northern *cordilleras* of Costa Rica (fig. 7) to elevations of nearly 1200 meters.

The range encompasses habitats as diverse as rain forest and semi-evergreen seasonal forest. In Chiapas it has been taken in a region of cattle-grazed savannas with scattered trees (Smith, 1968a). Douglas C. Robinson obtained a Costa Rican specimen (UCR, uncatalogued) in mangroves. William E. Duellman and I found one among the ruins of Panama Viejo, near Panama City. Kourany et al. (1970) characterize it as, “an arboreal lizard inhabitant of lowland, secondary forest in central Panama.” It may well be essentially a species of the forest’s edge, an invader of ecologically disturbed situations; its lichenose camouflage would make it difficult to see even on relatively exposed tree trunks. Its

camouflage is supplemented by its gecko-like behavior of clinging close to the tree trunk or branch (fig. 12) and sidling away from the observer. Its climbing ability was attested by a captive specimen that could scale the glass wall of its terrarium; it seemed to make no difference to this individual whether it was positioned head up or head down, either when asleep or awake.

Barbour (1934, p. 145) thought that it was, "not uncommon in the Canal Zone during the rainy season, excessively rare during the dry months," whereas Smith (1968a, p. 199) observed in northern Chiapas that, "adults of the species are rarely evident in the rainy season, although we secured (under bark of standing trees) and hatched large numbers of eggs." According to the field label, a Panamanian hatchling (ANSP 24542) emerged on June 29, a few months into the rainy season; the empty egg shell is 14 mm. in length, and the hatchling is 23 mm. snout to vent, 51 mm. total length.

GEOGRAPHIC VARIATION: I made no attempt to critically evaluate inter-populational variation in *Anolis pentaprion*, and only the obvious features of size and presence or absence of the caudal crest are commented on here.

In most parts of its range, *pentaprion* is a moderate-sized lizard, with adults usually measuring between 50 and 65 mm. snout to vent; males grow to larger sizes than females. However, individuals attain relatively gigantic size in the Golfo Dulce region of southern (Pacific side) Costa Rica. Eight adults (all males) examined from this region have a mean snout-vent length of 71.4 mm., range 63–77 mm.; only two of these specimens are less than 70 mm. I am aware of only one other specimen larger than 70 mm., namely the holotype of *Anolis pentaprion cristifer* from the Pacific side of Chiapas, which is reported to measure 72 mm. snout to vent (Smith, 1968a). Thirteen adult males from Panama, and Costa Rica outside of the Golfo Dulce region, have a mean snout-vent length of 63.4 mm., range 54–69 mm.; of a total of 11 specimens measured from north of Costa Rica (Nicaragua through Guatemala), the largest is a male 60 mm. snout to vent. The Pacific lowlands of southern Costa Rica, therefore, and probably the Pacific drainage of Chiapas, are inhabited by populations of giant *pentaprion*.

The other major geographically variable feature in *pentaprion* is the development of a dorsal caudal crest. A low crest on the tail (fig. 11C) is characteristic of populations south of Honduras, and, presumably, also of Pacific-side Chiapas in southern Mexico (Smith, 1968a). The crest tends, perhaps, to be a little stronger in males than in females. It is important to realize that the presence or absence of a crest is an onto-

genetic variable as well as a geographic one; a crest is lacking in a few Panamanian juveniles that I have examined (23–36 mm. snout to vent; ANSP 24542, USNM 120580–120582). Only one southern specimen of adult size, a female 58 mm. snout to vent (USNM 120583), lacks a crest, although other adults from the same population have the structure normally developed.

A caudal crest is lacking in specimens from Yucatan through Honduras, and, as pointed out by Stuart (1955, 1958), the name *beckeri* is available if one wishes to give subspecific recognition to these populations. Specimens with this type of caudal scutellation possibly average somewhat smaller in size than representatives of southern populations, but I have not noted any other major differences. Other workers have followed Stuart (1958, 1963) in recognizing *beckeri* as a valid subspecies, but have ignored his stated reason for doing so, namely that in *beckeri* the dorsal caudal scales are “reduced in size and but weakly keeled.” Thus, the diagnostic characters used in Peters and Donoso-Barros (1970, p. 62) do not reflect significant populational differences, being apparently based on differences between a few specimens and without mention of the tail. Smith (1968a, pp. 195, 199) rather incomprehensibly speaks of the “caudal crest” and “crest scales” in *beckeri*, the very features that *beckeri*, by definition, is supposed to lack. This confusion may result from Smith’s specimen of “*beckeri*” having evidently come from north of the geographic range known to Stuart, which would indicate that, at the extreme northern end of the range of the species, a caudal crest is found in populations in both the Atlantic and Pacific drainages. I leave this possibility for others to investigate, inasmuch as it is outside of the scope of this paper to bicker over the limits of weakly differentiated populations for the purpose of applying subspecific names. However, Smith’s (*loc. cit.*) claim that the “actual populational relationship of [*Anolis pentapryon*] *cristifer* [subsp. nov.] to its relatives is no doubt specific,” requires comment.

I have not seen the unique specimen of *cristifer*, but, in scutellation and proportions it seems to fall within the variational limits of southern populations of *pentapryon*. Indeed, even the low nuchal and dorsal body crest of *cristifer* can be matched in large specimens of *pentapryon* from the Golfo Dulce population, as for example KU 102418, which agrees in many respects with the description and illustrations of *cristifer*. Smith provides no objective basis for recognizing *cristifer* as a full species and, in my estimation, even his pragmatic reasons for calling it a subspecies are of dubious validity. Doubtlessly, adequate samples and close comparison would reveal at least minor differences, but as Smith (1968a,

p. 199) recognized, "*cristifer* resembles *p. pentaprion*, which is geographically remote, much more closely than it does *p. beckeri*." This phenomenon invites explanation whether or not one wishes to apply names to the different populations. As a tentative hypothesis, I suggest that the northern and southern populations of *pentaprion* are most primitive, at least in the retention of a tail crest, and that intermediate populations (*beckeri*) are derived. I have advanced precisely the same suggestion to explain evolutionary events in a species of snake that has a similarly wide distribution, with terminal populations in Mexico and lower Central America being extraordinarily similar in most characteristics (Myers, ms).

REMARKS: An apparently distinct Colombian species of *Anolis* has been buried in the synonymy of *A. pentaprion* since 1934. It can be diagnosed as follows:

Anolis sulcifrons Cope

Anolis sulcifrons COPE, 1899, p. 6, pl. 2, fig. 1a-e (Colombia, probably from "the neighborhood of Bogota"; holotype is now AMNH 38750). BURT AND BURT, 1931, p. 262 (notes on holotype). SMITH AND TAYLOR, 1950a, p. 363 (restriction of type locality). DUNN AND STUART, 1951, p. 56 (rejection of type locality restriction).

Anolis pentaprion (not of Cope): BARBOUR, 1934, p. 145 (part). DUNN, 1944, p. 79 (*sulcifrons* synonymized with *pentaprion* by implication). SMITH AND TAYLOR, 1950b, p. 61 (part).

Anolis pentaprion pentaprion (not of Cope): PETERS AND DONOSO-BARROS, 1970, p. 62 (part).

DIAGNOSIS: Similar to *Anolis pentaprion* in squamation, color pattern, and habitus (including a low caudal crest), but differing in having an unpigmented throat lining (black in *pentaprion*), more loreal rows (*sulcifrons*, 5-6; *pentaprion*, 3-4, rarely 5), fewer supralabials to center of eye (*sulcifrons*, 6-7; *pentaprion*, 7-10, usually 9), and by the presence of small black spots on the red(?) dewlap (spots absent in *pentaprion*). Only two of 53 specimens of *A. pentaprion* had as few as seven supralabials, and then only on one side of the head (8/7 and 7/9), and only five individuals had as many as five rows of loreals (4/5 in three, 5/5 in two specimens).

REMARKS: Cope (1899, p. 3) thought that the holotype of *Anolis sulcifrons* probably came from "the neighborhood of Bogota." Smith and Taylor (1950a, p. 363) restricted the type locality to "Barranquilla" without comment, an action challenged by Dunn and Stuart (1951, p. 56), who suggested that Cope's "neighborhood" of Bogota could reasonably be interpreted as a circle of 50 miles radius around Bogota.

Dunn (1944, p. 79), who stated that he could not distinguish the species from *Anolis pentaprion*, gave several locality records, at least one

of which (Andagoya, Chocó) is not likely to be based on *sulcifrons*. But his "‘eastern base of the Andes’ (? Villavicencio)" is probably based on ANSP 24285 and 24286, which I have compared with the holotype of *Anolis sulcifrons* and find to be the same species; the data slip accompanying the specimens reads, "east base of Cordillera of Bogota & extreme limit of llanos e. of Bogota, Colombia." These two specimens (collected by Nicéforo María) and the holotype are the only representatives of *sulcifrons* that I have examined. Two other localities mentioned by Dunn are Mariquita [535 meters] in Tolima, and Mocoa, 560 meters, in Putumayo. If actually based on *Anolis sulcifrons*, these records would indicate a distribution that extended north around the base of the Cordillera Oriental, from the rather dry inter-Andean valley of the Río Magdalena, and then south along the base of the Andes into the Amazonian rain forest. Such a distribution might seem unlikely, but it should be remembered that the range of *Anolis pentaprion* also includes habitats as diverse as semi-evergreen seasonal forest and rain forest.

Although for a single anoline species to have a range extending from Mexico to the Amazonian basin would be quite unexpected, *Anolis sulcifrons* might nonetheless be considered a southern subspecies of *A. pentaprion*. But the several differences indicate to me that *sulcifrons* is a distinct species and should be so considered until its relationships can be investigated in more detail. Burt and Burt (1931, p. 262) suggested that it is closely allied to the Guianan *Anolis aeneus*.

MATERIAL EXAMINED

Anolis fungosus, new species. One specimen; data given in text.

Anolis pentaprion Cope. Fifty-seven specimens. *Costa Rica*: Cartago; 8 kilometers west, 13 kilometers north of Turrialba, 1190 meters, KU 67070. Heredia: Sarapaquí, AMNH 16354. Guanacaste: Tronadora, UCR 2903. Limón: Pandora, MCZ 78389, 80855–80857. Puntarenas: Boca de Río Dominical, UCR 2438. Puntarenas (in Golfo Dulce region): Coto, UMMZ 71993, 71994; Palmar, KU 34254, 34255; Peninsula de Osa, Rincón de Osa, UCR 2542; 2 kilometers south Rincón de Osa, UCR (one uncatalogued); 4.5 kilometers west of Rincón de Osa, 45 meters, KU 102418; southwest of Rincón, near airstrip, UMMZ 126724. *Guatemala*: El Peten: Ceiba, near source of Río de la Pasión, UMMZ 79081; Tikal, UMMZ 117822. *Honduras*: Guaimas, UMMZ 58392–58395. *Nicaragua*: Zelaya: Bonanza, 260 meters, KU 85677; Río Siquia, 7 miles above Rama, UMMZ 79825; Río Siquia, UMMZ 79826; Sioux Plantation, AMNH 17124. Department unknown: Machuca, ANSP 7911. *Panama*: Bocas del Toro: Almirante, KU 80194. Canal Zone: Balboa, AMNH 42926, MCZ 25116, 25117; Barro Colorado Island, AMNH 75987, ANSP 24540–24542, KU 75960, MCZ 31582; Corozal, MCZ 22327; France Field, MCZ 29772; Las Cascadas Cocoa Plantation, MCZ 19519. Panamá: near Aguacate, Cerro Trinidad, AMNH 103231; Panama City, Punta Paitilla, MCZ 32526; Panama Viejo, KU 75959.

Pearl Islands: Isla de San José, USNM 120572–120583. Veraguas: Bahía Honda, AMNH 62773. No specific data, BMNH 1946.8.13.8 (lectotype of *Anolis panamensis* Boulenger).

Anolis sulcifrons Cope. Three specimens, including the holotype; data in text.

Anolis vociferans, new species. Eight specimens, the holotype and seven paratypes; data in text.

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