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A CASE HISTORY IN RETROGRADE EVOLUTION: THE *ONCA* LINEAGE IN ANOLINE LIZARDS.

I. *ANOLIS ANNECTENS* NEW SPECIES, INTERMEDIATE BETWEEN THE GENERA *ANOLIS* AND *TROPIDODACTYLUS*.

ERNEST E. WILLIAMS

ABSTRACT. A new anole species bridges the gap between the genus *Anolis*, diagnosed by the presence of adhesive subdigital pads under phalanges ii and iii, and *Tropidodactylus*, diagnosed by the absence of such pads: *Anolis annectens* has typical anoline transverse lamellae with microscopic hairs and free distal margins only under phalanx ii; the third phalanx has only keeled infradigital scales as in the species *onca* currently referred to the monotypic genus *Tropidodactylus*. The genus *Tropidodactylus* is formally synonymized with *Anolis*. A morphological series in the reduction of the anoline adhesive pad that culminates in the condition seen in the species *A. onca* is described.

The genus *Tropidodactylus* was erected in 1885 by Boulenger in the second volume of his classic Catalogue of the Lizards in the British Museum (Natural History) to receive the single species described as *Norops onca* by O'Shaughnessy in 1875.

Neither the genus nor the species has received much attention since their description. They have, up to the present, been very poorly known. The validity of the genus has not been questioned, since the difference between *Tropidodactylus* and *Anolis* in the defining character of digital structure has seemed a sharp and important one: all *Anolis* (including all those species classically referred to *Norops*) have under phalanges ii and iii expanded adhesive digital pads, the smooth, flattened, transverse lamellae of which are provided with microscopic hairs (Ruibal and Ernst, 1965; Hiller, 1968; Maderson, 1970; Lillywhite and Maderson, 1968). The adhesive pad may be narrower or wider, may be sharply set off ("raised") from phalanx i or not so set

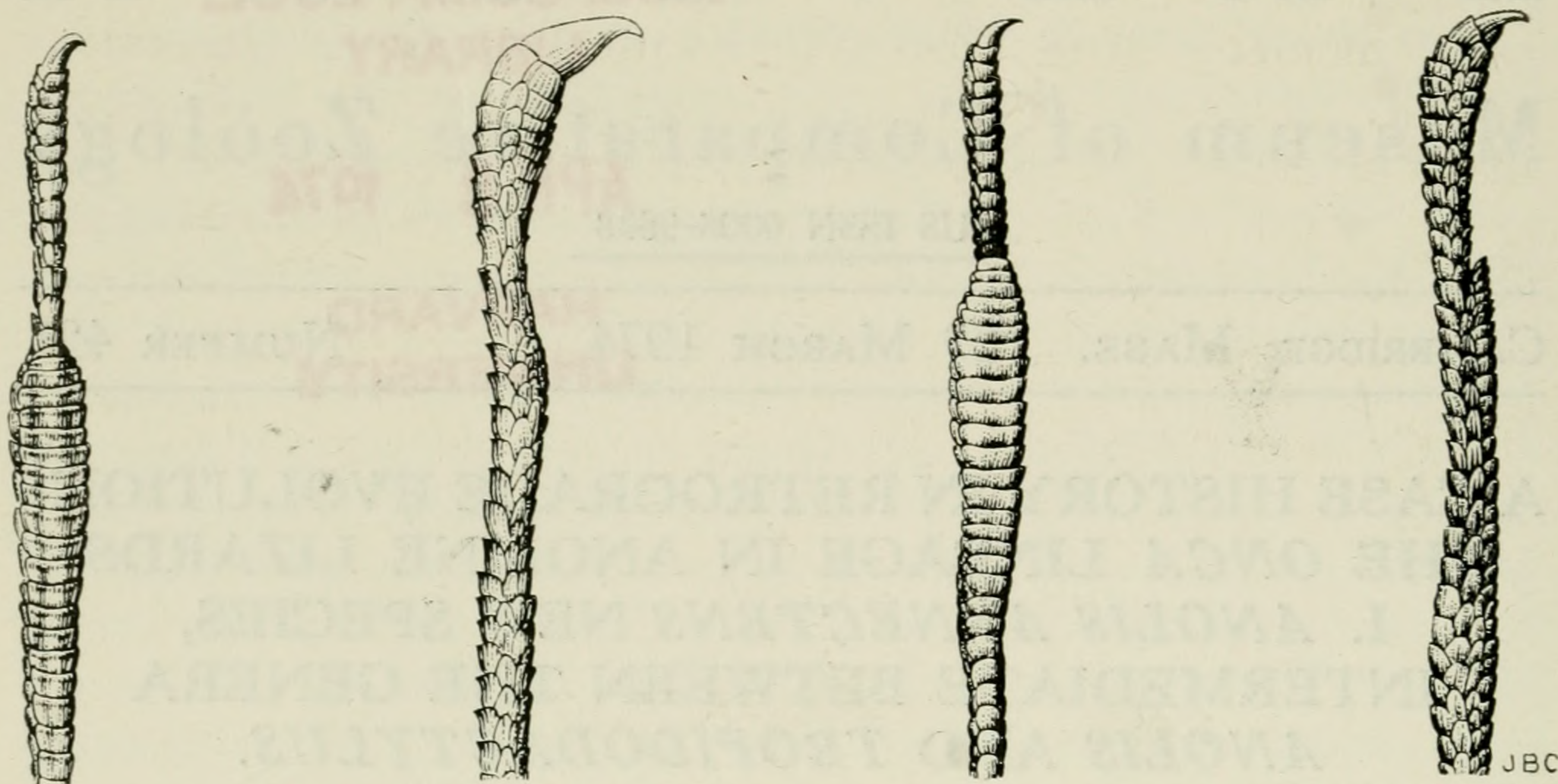


Figure 1. Left: toe of an anole showing the "*Norops*" condition; Right: toe showing the typical *Anolis* condition.

off (the *Norops* condition) (Fig. 1) and may have more or fewer lamellae, but there is always some expansion, always smooth transverse flattened lamellae under phalanges ii and iii, and always microscopic hairs. *Tropidodactylus*, as known from the single species *onca*, has been believed to differ in the complete absence of the hairs and of smooth lamellae and in the presence of multiple keels on the infradigital scales. Although in general habitus, including the presence of a large and typically anoline dewlap, the species *onca* has unmistakably the appearance of *Anolis* and is often so identified in collections; the digital difference has always been regarded as quite worthy of generic distinction. It seemed to support this position that, according to Ruthven (1922), *Tropidodactylus* seemed more terrestrial than any *Anolis*: "All of the specimens taken (17) were on the ground. It is very shy and at the slightest cause for alarm dashes into a hole."

However, Etheridge (1960) was unable to find any osteological character on which to separate *onca* generically and regarded this species as the terminal, most specialized member of his beta section of the genus *Anolis*. He was willing to retain the genus only on the basis of "the evolutionary significance of the loss of typical anole subdigital lamellae and the accompanying alteration in mode of life."

George Gorman (1969), describing the karyotype of *onca*,

found it to resemble closely two of the more primitive (or "typical") members of the beta group within *Anolis* (*A. lineatopus* and *A. opalinus*). The *onca* karyotype ($2n=30$) with seven macrobivalents and eight microbivalents is characteristic of this group within *Anolis*, and *onca* even resembles *A. opalinus* in clear heteromorphism in chromosome pair seven. The only obvious difference found by Gorman was that pair seven appeared relatively smaller in *onca* than in the two compared Jamaican anoles, "i.e. it might be considered an intermediate between macrochromosomes and microchromosomes."

New collections of *onca* have been made by James Collins on Margarita Island (reported by him in 1971), by Carlos Rivero-Blanco and Abdem R. Lancini on the mainland of Venezuela in and near Coro, by Bryan Patterson and the members of his paleontological expedition in the same region, by the author, A. S. Rand and A. R. Kiester on the neighboring Paraguana Peninsula, and by the author, Jane Peterson, K. Miyata and R. Salvato on the Paraguana isthmus and on the east side of the Goajira Peninsula.

However, very surprisingly, as a summary of our knowledge of the species *onca* was being prepared, a unique specimen in the collection of the Field Museum of Natural History demonstrated the existence of a new species that is an ideal intermediate between the genera *Tropidodactylus* and *Anolis* as currently conceived. Differing trivially from *onca* in color and in somewhat greater size of the dorsal scales, it differs sharply in having *smooth* lamellae under phalanx ii of the fourth toe, but *keeled* scales under phalanx iii. It thus becomes impossible to make a separation of two genera in the fashion that has hitherto been customary. It is necessary either to describe a new monotypic genus for the new species or to submerge *Tropidodactylus* in the synonymy of *Anolis*. I choose the latter course and describe the new species as:

Anolis annectens new species

Holotype: FMNH 5679, adult male.

Type locality: Lago de Maracaibo, collected by W. H. Os-good between late January and early March, 1911.

Head (Fig. 2): Head stout, a little longer than tibia. Head scales unicarinate, 10 scales across snout between second canthals. A shallow frontal depression. Nasal scale separated from rostral by two intervening scales.

Supraorbital semicircles separated by one row. Supraocular

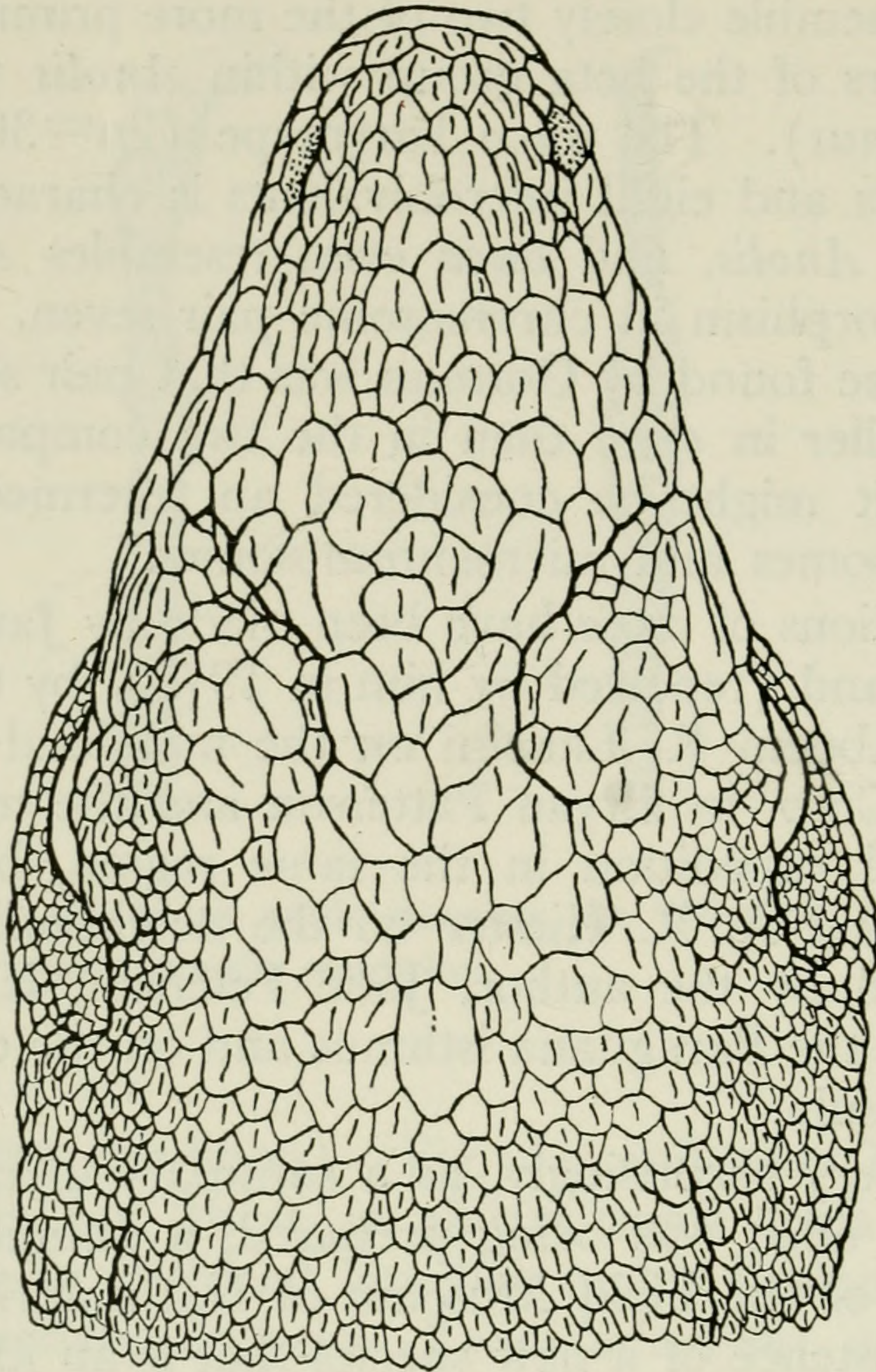


Figure 2. Head of *A. annectens* Holotype, dorsal view.

disk ill-defined, consisting of about 12 keeled scales, the largest anteromedial, the disk separated by two rows of granules from the scales of the supraciliary rows. Two parallel elongate supraciliaries continued posteriorly by a double series of moderately enlarged scales. Canthus distinct, canthal scales 5, second canthal scale largest. Loreal rows 6, the lowest row not much larger than those above it. Interparietal almost equals ear, separated from the supraorbital semicircles by 2 scales. Temporal and supraorbital scales keeled, smallest in center of temporal region, dorsally grading into larger scales surrounding interparietals. Scales behind interparietal somewhat smaller than those lateral and anterior to it.

Suboculars separated from supralabials by one row of scales, anteriorly not continued to canthal ridge, posteriorly ending abruptly with one enlarged scale. Ten supralabials to center of eye.

Mental wider than long, in contact posteriorly with 7 unicarinate scales between infralabials. No differentiated sublabials, but scales in center of throat smallest.

Trunk: Middorsal scales enlarged, hexagonal, keeled, grading laterally into much smaller but keeled flank scales. Ventrals much larger than dorsals, unicarinate, the keels in line. Post-anal scales not differentiated.

Dewlap: Large, scales smaller than ventrals, keeled, arranged in widely spaced rows except at the edge.

Limbs and digits: Hand and foot scales multicarinate. No scales on limbs as large as ventrals, unicarinate. *Eight rather narrow lamellae under phalanx ii of fourth toe, scales under phalanx iii of fourth toe multicarinate.*

Tail: Tail round, all scales keeled, only ventral scales larger than dorsals, 4 scales above, 3 below.

Size: 67 mm, snout-vent length.

Color (in alcohol): Grey-brown with vague blotching and mottling on flanks, limbs and tail more distinctly barred. A round dark spot above each shoulder and a smaller spot between these on the neck middorsally. Narrow oblique transverse bands connect the shoulder spots across the middle of the back. A transverse band directly in front of shoulder, indistinct on the right side. On posterior midline two black spots, one in front of sacrum, and one between two lateral sacral spots. Dewlap scales are white, with black pigment around the bases of some of them.

Comparison with onca. Scales: The variation in squamation seen in *onca* O'Shaughnessy completely includes that of the single specimen of *annectens* except in two regards: the greater size of the dorsal scales in *annectens* (Fig. 3) and the presence under phalanx ii of smooth lamellae (Fig. 4).

Color: The color of *annectens* may also differ from that of *onca* but the variability of *onca* is so great that the rudimentary pattern seen in the type of *A. annectens* seems easily derivable from an *onca* pattern. Nevertheless there is no exact or nearly exact match in any of the extensive series of *onca*. The shoulder spots of *onca* are roughly triangular or elongate, not round, as in *annectens*. The neck spot and the two posterior midline spots of *annectens* are not exactly matched in *onca*. The peculiar distribution of dark pigment on the dewlap skin in *annectens* is again without real parallel in *onca*.

Color in life of *annectens* is unknown. However, it may be presumed from its similarity to *onca* that at least in body pattern the preserved animal gives a very fair impression of the live ani-

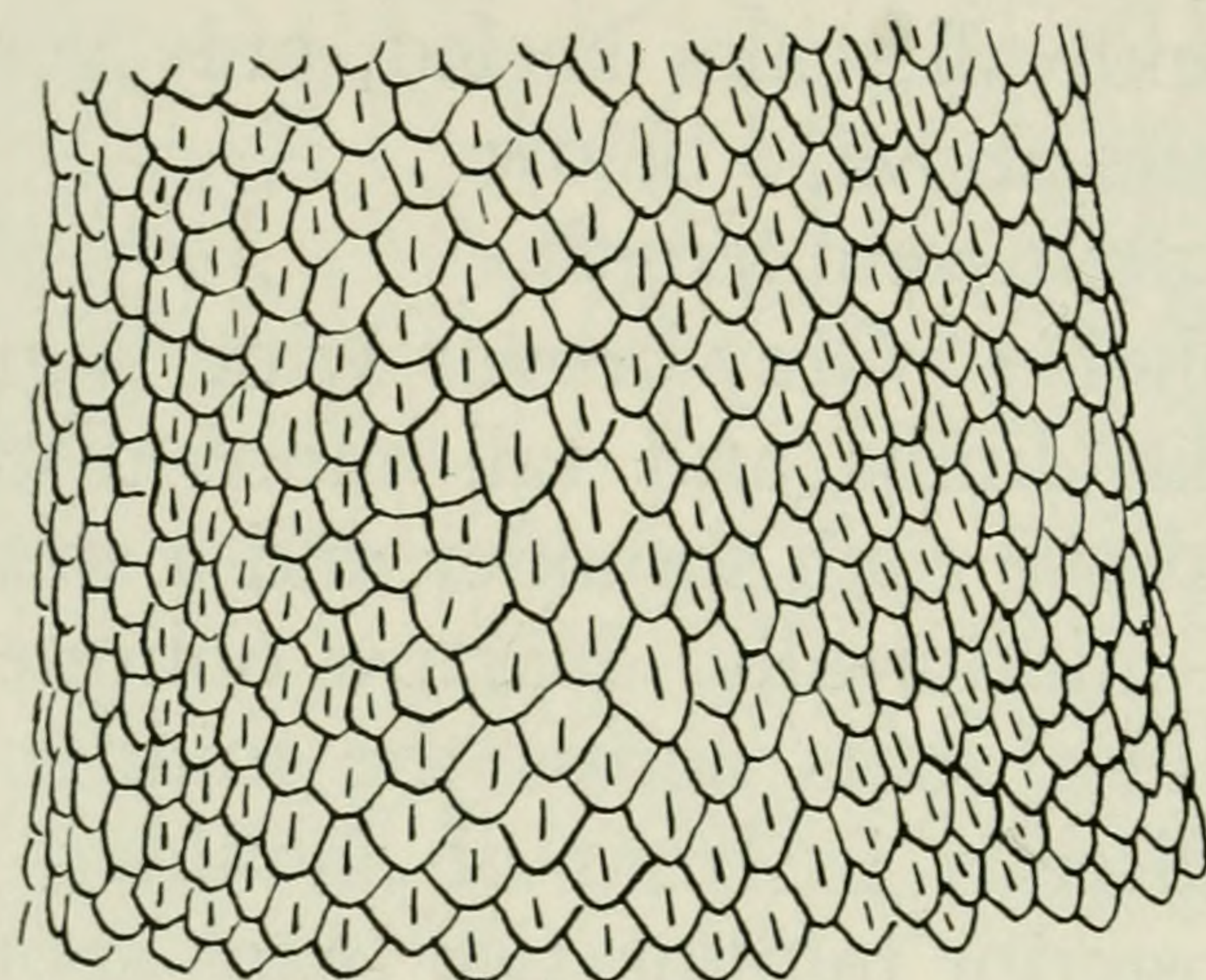
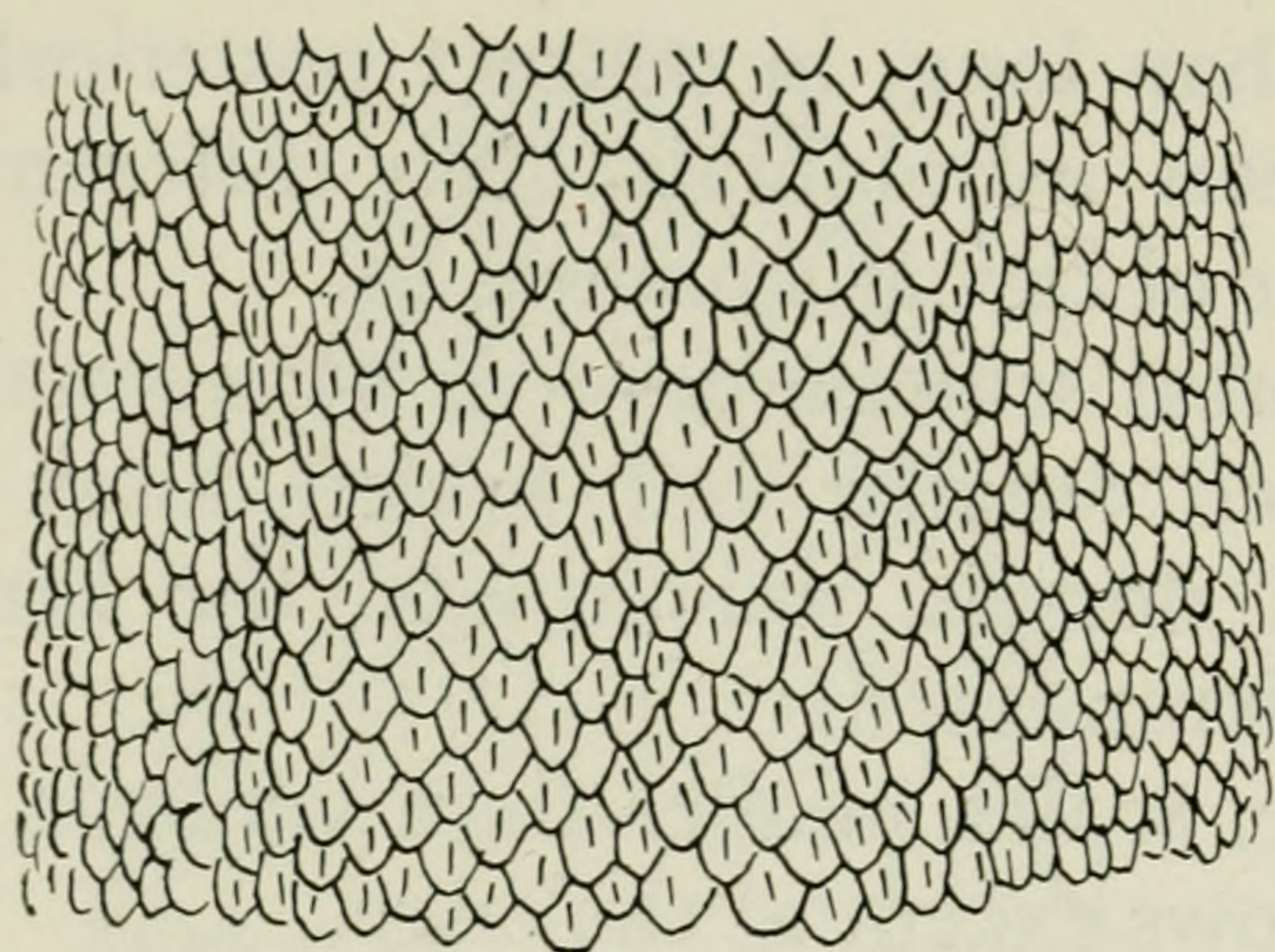


Figure 3. Dorsal scales. Above: *A. onca*. Below: *A. annectens* Holotype.

mal. Dewlap color, however, cannot safely be inferred from specimens long preserved and this might be important.

A good description of color in life by William E. Duellman of *onca* from 3 km SW of Cumana in Sucre, Venezuela, follows: "Dorsum light brown mottled with gray, gray brown and black. Venter creamy white, lightly flecked with grayish brown. Tail medium brown above, cream below. Dorsolateral mottling on WED 28685 forms more or less distinct paravertebral blotches which are gray centrally and outlined in black. Dewlap bright greenish ochre centrally, becoming orange peripherally, the whole dewlap reticulated with bright orange brown and bearing white scales. Iris bronze. Lining of throat bluish gray." [WED field notes.]

Distribution: The locality for *A. annectens* is, most unfortunately, inexact. It is not known whether Osgood collected the

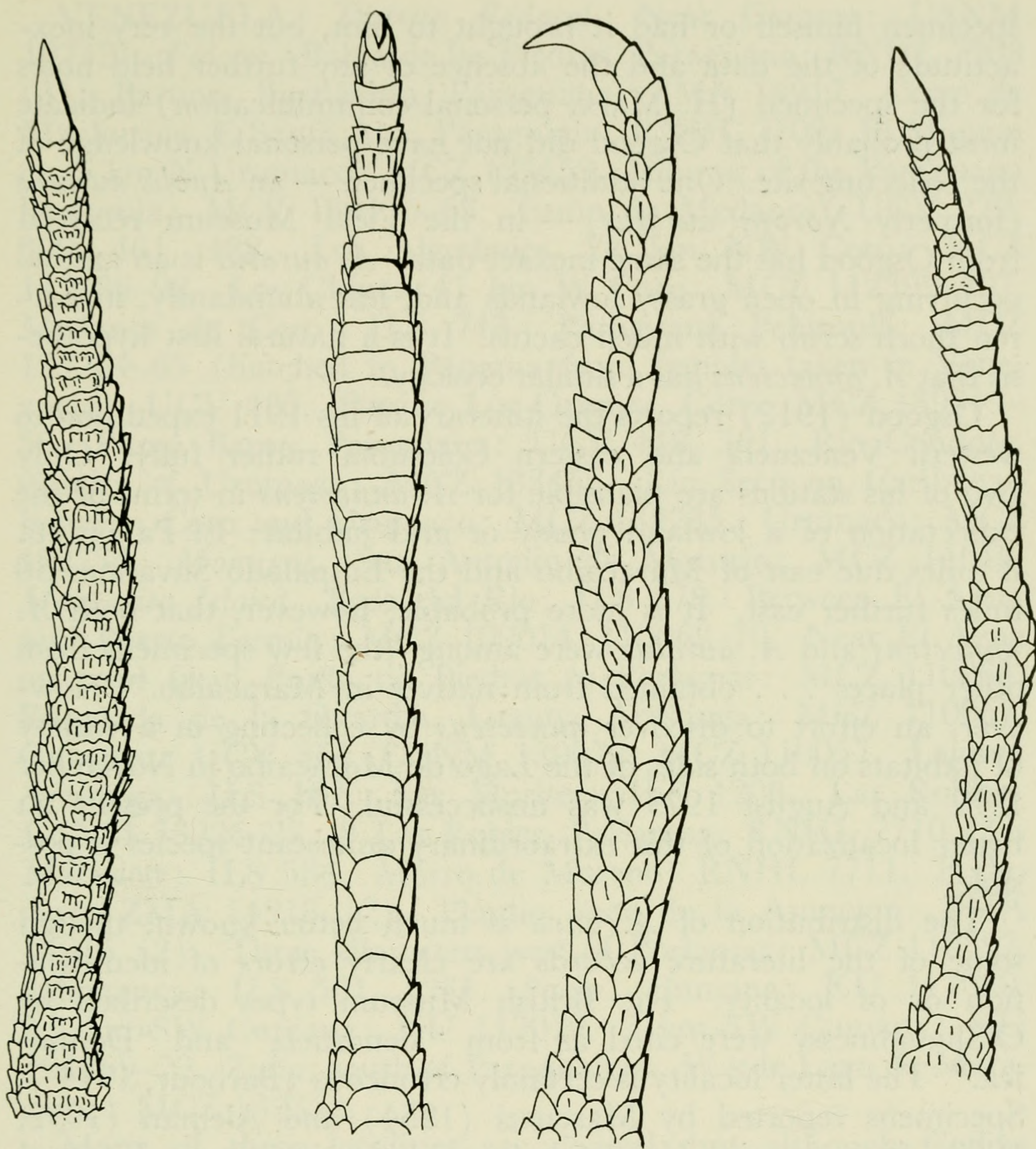


Figure 4. Fourth toe lamellae. Left: *A. onca*. Right: *A. annectens* Holo-type. In the center the 4th toe of *Anolis* ("Norops") *auratus* is shown in ventral and lateral view for comparison.

specimen himself or had it brought to him, but the very inexactitude of the data and the absence of any further field notes for the specimen (H. Marx, personal communication) indicate most probably that Osgood did not have personal knowledge of the collecting site. One additional specimen — an *Anolis auratus* (formerly *Norops auratus*) — in the Field Museum received from Osgood has the same inexact data. *A. auratus* is an animal occurring in open grassy lowlands and, less abundantly, in barren thorn scrub with much cactus. It is a natural first hypothesis that *A. annectens* has a similar ecology.

Osgood (1912) reports the itinerary of his 1911 expedition to western Venezuela and eastern Colombia rather fully. Only two of his stations are plausible for *A. annectens* in terms of the expectation of a lowland grassy or arid habitat: El Panorama 8 miles due east of Maracaibo and the Empalado Savannas 30 miles further east. It is more probable, however, that both *A. annectens* and *A. auratus* were among “the few specimens from other places . . . obtained from natives in Maracaibo.” However, an effort to discover *annectens* by collecting in a variety of habitats on both sides of the Lago de Maracaibo in November 1972 and August 1973 was unsuccessful. For the present no better localization of this extraordinary annectant species is possible.

The distribution of *A. onca* is much better known, though some of the literature records are clearly errors of identification or of locality. The British Museum types described by O'Shaughnessy were cited as from “Venezuela” and “Dominica.” The latter locality is certainly erroneous (Barbour, 1914¹). Specimens reported by Marcuzzi (1954) and Aleman (1952, 1953) from interior Venezuela are misidentifications. I record below only the localities that I have personally verified by examination of specimens (see Fig. 5):

COLOMBIA. *Guajira*. Cabo de la Vela: FMNH 165159. Two hours E El Cabo, near Cabo de la Vela: MCZ 85441. El Cardon, S Cabo de la Vela: RNHL 7707. Maicao: USNM 115067. Manaure and Pajaro areas: USNM 151517–23. Media Luna, E Cabo de la Vela toward Bahia de la Protete: MCZ 85440. Puerto Lopez, E shore Bahia Tucacas: MCZ 81554. Rancheria del Cabo de la Vela: ZMA 14916. Riohacha: UMMZ 54799, 54801–07, 54810–13; MCZ 14637.

¹On Barbour's inquiry Boulenger wrote “The *Tropidodactylus onca* was purchased of a dealer (Mr. Cutler). The locality Dominica is, therefore, open to doubt.”

VENEZUELA. *Distrito Federal*. Near Caracas: USNM 107321. *Falcon*. Bahia de las Piedras, Paraguana: RNHL 7708 (3). Barunu, Buenavista, Paraguana: ZMA 14917. Cerro de Machuruia, E Santa Ana, Paraguana: RNHL 7709. El Mainon ca. 5 km N Urumaco: MCZ 133453. Isthmus of the Paraguana Peninsula: MCZ 133456-65. Istmo de Medanos: UCV 272, 300, 461, 488. Los Algodones, 28 km NW Coro: MCZ 112386-98. Los Chipies, 41 km W Coro: MCZ 112399-407. Medanos de Coro: ILS 743. Paraguana Peninsula: MCZ 133264-65 (hatched in Panama from females taken in Venezuela), UCV 485. Parque Los Orumos, Coro: MCZ 139349-50. Punta Baroa, Paraguana: UCV 448, 561. Rio Condore, vicinity of Urumaco: MCZ 133455. Rio Seco on Caribbean between Coro and Urumaco: MCZ 132735. Urumaco: MCZ 132734. *Monagas*. San Antonio de Maturin: MCZ 14648. *Margarita Island*. Boca del Rio: ILS 578. Between El Agua and Puerto Fermin: MCZ 109014, 110068-70. Near El Agua on road from Punta de Piedras to Porlamar: MCZ 110064. Ensenada de la Guardia, Laguna Arestinga: MCZ 110067. Guacuco: UCV 364, USNM 139072, MCZ 110057. Laguna Arestinga: ILS 102. Las Morites: ILS 1208. Las Robles: USNM 79226-27. S Las Robles, Porlamar: RNHL 7710 (3). Matasiete: ILS 584. Morro de Moreno: RNHL 7711. Porlamar: ZMA 14918 (2). Plantio oeste de la Asuncion: ZMA 14915 (2). Three kilometers west of Porlamar: MCZ 110397. Salamanca: ILS 561, 1231. *Sucre*. Cumana: KU 117080. 2.5 km SW Cumana: KU 117079. 3 km SW Cumana: KU 104369-70. *Zulia*: south of Paraquaiipoa, W side Lago de Maracaibo: MCZ 139352.

Many of these localities are coastal, but although Collins believes *onca* to be a beach animal on Margarita Island, some verified continental localities are well inland (*e.g.*, Urumaco, Falcon, Venezuela). All localities, however, are extremely arid lowland, usually within the zone called in the Holdridge terms adopted by Ewel and Madriz (1968) for Venezuela "monte espinoso tropical." A few records appear to lie in an adjacent zone, "monte muy seco tropical." A few lie outside even this zone, *i.e.*, USNM 107321 "near Caracas" and MCZ 14648 "San Antonio de Martin." These, however, are very imprecise localities. Figure 5 shows the distribution of "monte espinoso tropical" and "monte muy seco tropical" for Venezuela according to Ewel and Madriz. The Colombian localities are similar.

However, the observations of the field party in the summer

of 1973 suggest that the requirements of *onca* are more specific than just the zone "monte espinoso tropical." Search for additional specimens of *A. annectens* led us into zones clearly within the mapped areas but in which *onca* was apparently absent. *Anolis auratus* was taken in these areas. (See the ecological remarks below.)

ECOLOGY

The relictual digital pad of *annectens* would seem to imply a somewhat greater arboreal adaptation than that of *onca*. But how terrestrial is *onca*?

No more recent observer supports the apparent implication of Ruthven's (1922) statement that *onca* uses burrows. On Margarita Island Collins (1971) looked particularly into this point. He remarks: "At times, a specimen being pursued would run into a large hole in the sand opening into a tunnel. It should be noted, however, that these holes are resting places made by ghost crabs (*Ocypode*) and are not dug by *Tropidodactylus*. It should also be noted that this was a rather infrequent mode of escape, used by the lizard only when almost completely exhausted." Collins points out that *onca* does climb when the vegetation permits this. Where the vegetation was only a mat of vines and branches, *onca* would clamber over or into this. However, "in the area just north of Punta Montadero where *Mallotonia*, a woody-stem plant, is dominant, the animal's behavior was very different. Here, when sighted, the lizard was always on the ground. When pursued, the majority of animals observed would merely run among the ground cover. A few specimens, however, were observed to climb the *Mallotonia*, some to a height of 30.0 cm. Their climbing was clumsy and ineffective."

Collins also took one animal sleeping on a branch of a low bush.

On the continental mainland the observations of Carlos Rivero-Blanco in July and August, 1970, are very useful. He reports nine specimens taken on trunks of planted trees in a park (Parque Los Orumos in Coro) within one meter from the ground and two more taken in the same park from low branches between one meter and a meter and a half above ground. Elsewhere, in more natural situations, he reports them from piles of dry branches and *inside* hollow dried cardon and cactus branches partly buried in sand. He reported, however, that the local

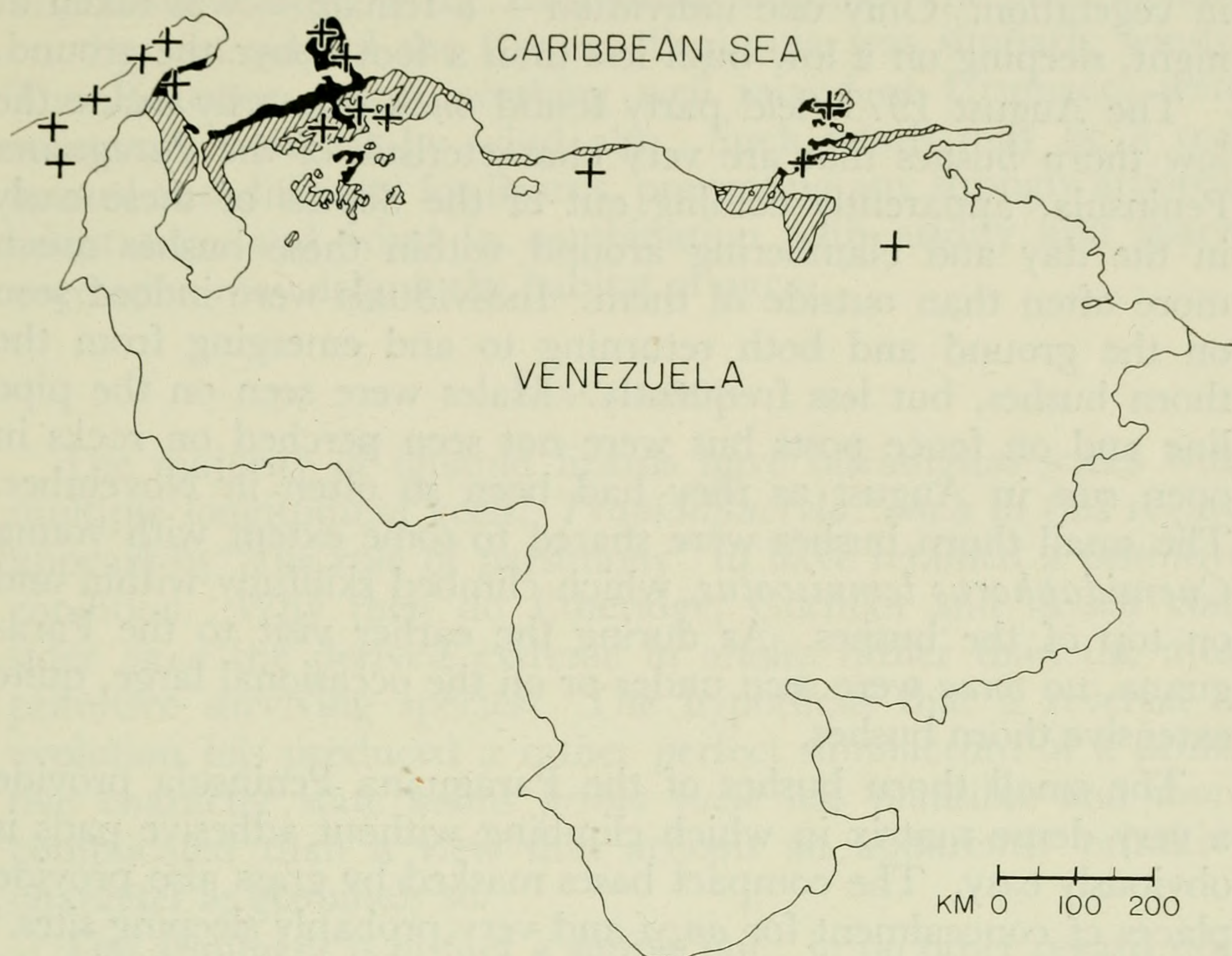


Figure 5. Map of the distribution of *A. onca*. Shading shows two vegetational zones in Venezuela (after Ewel and Madriz): black = "monte espinoso tropical;" cross-hatched = "monte muy seco tropical." + marks known localities for *onca*.

people said that *onca* could be seen on the branches of a local spineless euphorbiacean.

One of the animals obtained by the Patterson party in July to August, 1972, had been taken on the outside wall of the doctor's house in Urumaco. Again, most specimens observed were among the branches of piles of dead plants buried in sand (at Rio Seco, one to a pile). In another area one specimen was seen lying motionless on a cobble in the full sunlight. Another in still another area was seen on open ground in full sunlight, very cryptically colored and detected only by its motion.

The November 1972 party found males widely spaced out on top of the pipe line that runs much of the length of the Isthmus of the Paraguana Peninsula. Some were displaying. Others had climbed to the top of posts, including fence posts. The remainder, taken by day, including all females and the one juvenile, were on the ground in bare open spaces. None were seen

in vegetation. Only one individual — a female — was taken at night, sleeping on a low bush less than a foot above the ground.

The August 1973 field party found *onca* primarily inside the low thorn bushes that are very characteristic of the Paraguana Peninsula, apparently coming out of the depths of these early in the day and clambering around within these bushes much more often than outside of them. Individuals were indeed seen on the ground and both returning to and emerging from the thorn bushes, but less frequently. Males were seen on the pipe line and on fence posts but were not seen perched on rocks in open sun in August as they had been so often in November. The small thorn bushes were shared to some extent with young *Cnemidophorus lemniscatus*, which climbed skillfully within and on top of the bushes. As during the earlier visit to the Paraguana, no *onca* were seen under or on the occasional large, quite extensive thorn bushes.

The small thorn bushes of the Paraguana Peninsula provide a very dense matrix in which climbing without adhesive pads is obviously easy. The compact bases masked by grass also provide places of concealment for *onca* and very probably sleeping sites.¹

The August 1973 party searched for *onca* and *annectens* in many areas between Coro and Maracaibo, but only located *onca* again S of Paraguaipoa on the east side of the Goajira Peninsula (= the west side of Lago de Maracaibo). This area closely matched the Paraguana Peninsula in appearance and especially in the character of the vegetation, including the sparse cover of thorn bushes of small to moderate size.

Anolis auratus was repeatedly observed in areas in which *onca* was lacking and never where *onca* occurred. It is clear that *auratus* is less stenotopic than *onca*. It has been seen in lush grassland, abundantly on a fence row beside a cattle pasture, and sparsely in bare and harsh thorn scrub, often in situations that seem climatically more rigorous than those from which *onca* is known.

Aridity is certainly not the factor determining the presence of *onca*. A special vegetational structure does seem characteristic but there is another feature that may be even more important. The notes by Rivero-Blanco call attention to the constant high wind in the areas in which he observed *onca*. The November 1972 and August 1973 field parties also found the winds an

¹Further data on the ecology, including thermal ecology, of *onca* will be presented by Kenneth Miyata.

impressive feature of the Paraguana isthmus. The *onca* locality on the east side of the Goajira Peninsula was similarly windy. The Patterson group, working well inland at Urumaco, were constantly buffeted by wind also. Such winds may be a real hazard and difficulty for lizards, preventing any strongly arboreal adaptation, and wind in combination with aridity and sparse vegetation may delimit the habitat of *onca*.

DISCUSSION

The majority of iguanid lizards have infradigital scales with multiple longitudinal keels. *Tropidodactylus onca* in this regard appears by "the rule of parsimony" to have retained a primitive condition. Why then do Etheridge, Gorman and myself consider *onca* the derived extreme in anoles rather than the most primitive surviving species? The hypothesis that a reversal of evolution has produced a rather perfect simulacrum of a primitive character state seems *prima facie* less plausible and more complicated than a view that accepts an apparently primitive character as genuinely so.

The argument is in fact a simple one: in no other regard does *onca* seem primitive. In every character that Etheridge's skeletal analysis regards as important, *onca* stands closest to the most derived members of the beta section of *Anolis*. Etheridge (1960: 60) comments: "Except for the absence of specialized lamellae, it is in no way distinguished from other anoles. Other features of the genus, e.g. the absence of both splenial and angular, absence of pterygoid teeth, reduction of the parasternum (= inscriptional ribs, Etheridge, 1965) etc. indicate that "*Tropidodactylus*" is a specialized rather than a primitive anole. According to Ruthven (1922), the genus is strictly terrestrial, yet all other features which mark the anoles as arboreal lizards are present. Evolutionary loss of the anoles' specialized lamellae, rather than retention of the pre-anole condition, probably offers the most reasonable explanation of the [loss of] lamellae in *Tropidodactylus*."

In karyotype also *onca* departs very much from the 12 macrochromosome-24 microchromosome pattern that occurs repeatedly in primitive anoles, other diverse groups of iguanids (and in other lizard families) and is believed to be primitive for the Sauria generally (Webster, Hall, and Williams, 1972). The primitive karyotype is found in many members of Etheridge's alpha section of *Anolis* but in no betas, and, as Gorman (1969)

has noted, *onca* belongs karyotypically, as in skeletal characters, to one of the more highly derived groups of beta anoles.

Two external features are very characteristic of most *Anolis* — the throat fan or dewlap and the adhesive pad with microscopic hairs. Both are sometimes reduced within the genus (Williams, 1963). Both *onca* and *annectens*, however, have the dewlap very large and very mobile, extremely well developed. *A. onca* is known to use the dewlap very actively (observations of the field party in November 1972), flashing it repeatedly, a derived and not a primitive feature (Rand and Williams, in preparation).¹ Of the two most basic anole characters, it is only the second — the adhesive pad — that is absent in *onca* and transitional in *annectens*.

Some of the species that show the first stages of the degradation of the digital pad have been separated taxonomically as the genus *Norops*. Schmidt (1939), describing the Mexican species *A. barkeri*, called attention to the difficulty, made obvious by more than one generic assignment for several of the species, of making consistent distinctions between the genera *Anolis* and *Norops*. Schmidt himself, though he placed *barkeri* in *Anolis*, recorded the terminal phalanges of *barkeri* as "less distinctly set off from the widened portion than in the normal *Anolis*."

Moreover, it is now clear that any definition of *Norops* based on digital features includes species that cannot be closely related. *Anolis aequatorialis* and *A. mirus* of the trans-Andean regions of Ecuador and Colombia have *Norops*-type digits but are members of the alpha subdivision of the genus (Etheridge, 1960; Williams, 1963) and hence are on the other side of a basic dichotomy within anoles from Cuban *A. ophiolepis*, Mexican *A. barkeri*, *A. tropidonotus*, Colombian *A. notopholis*, central Brazilian and northern Bolivian *A. meridionalis*, and northern South American and Panamanian *A. auratus*, all anoles with *Norops*-type digits (or an approach to them but belonging to Etheridge's beta subdivision).

Even within the beta subdivision the species showing the *Norops*-type condition are not closely related to one another. Figure 6 adapts Etheridge's 1960 figure of beta anole relationships to show the independent origin of the species of "*Norops*." The numerals refer to the number of attached and free inscrip-tional ribs; both the total number and the number of attached ribs tend to decrease from primitive to advanced forms.

¹Dewlap "flashing" is very characteristic of the possibly related forest species, *Anolis chrysolepis*.

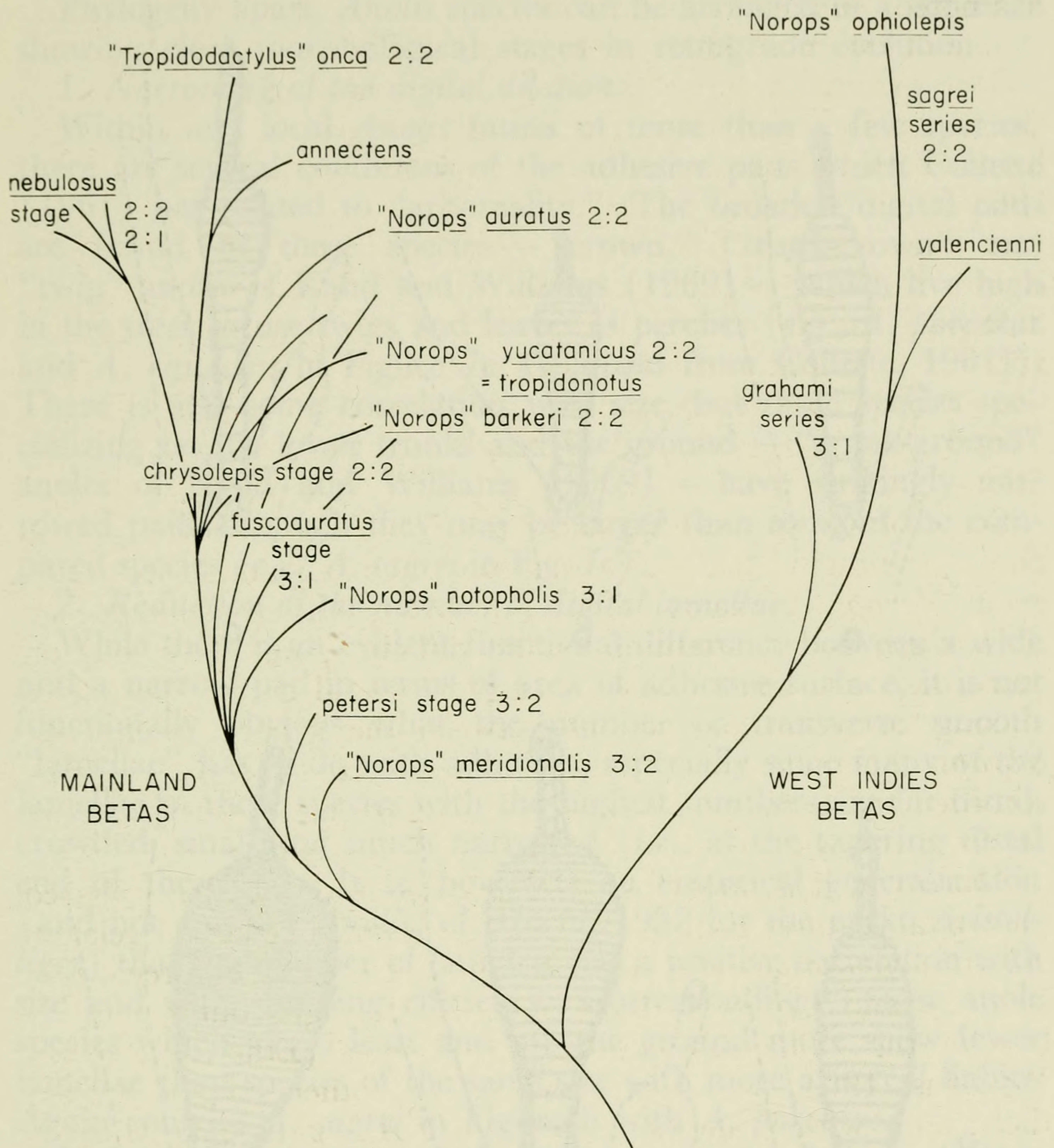


Figure 6. A dendrogram of relationship within the beta anoles. Modified from Etheridge (1960).

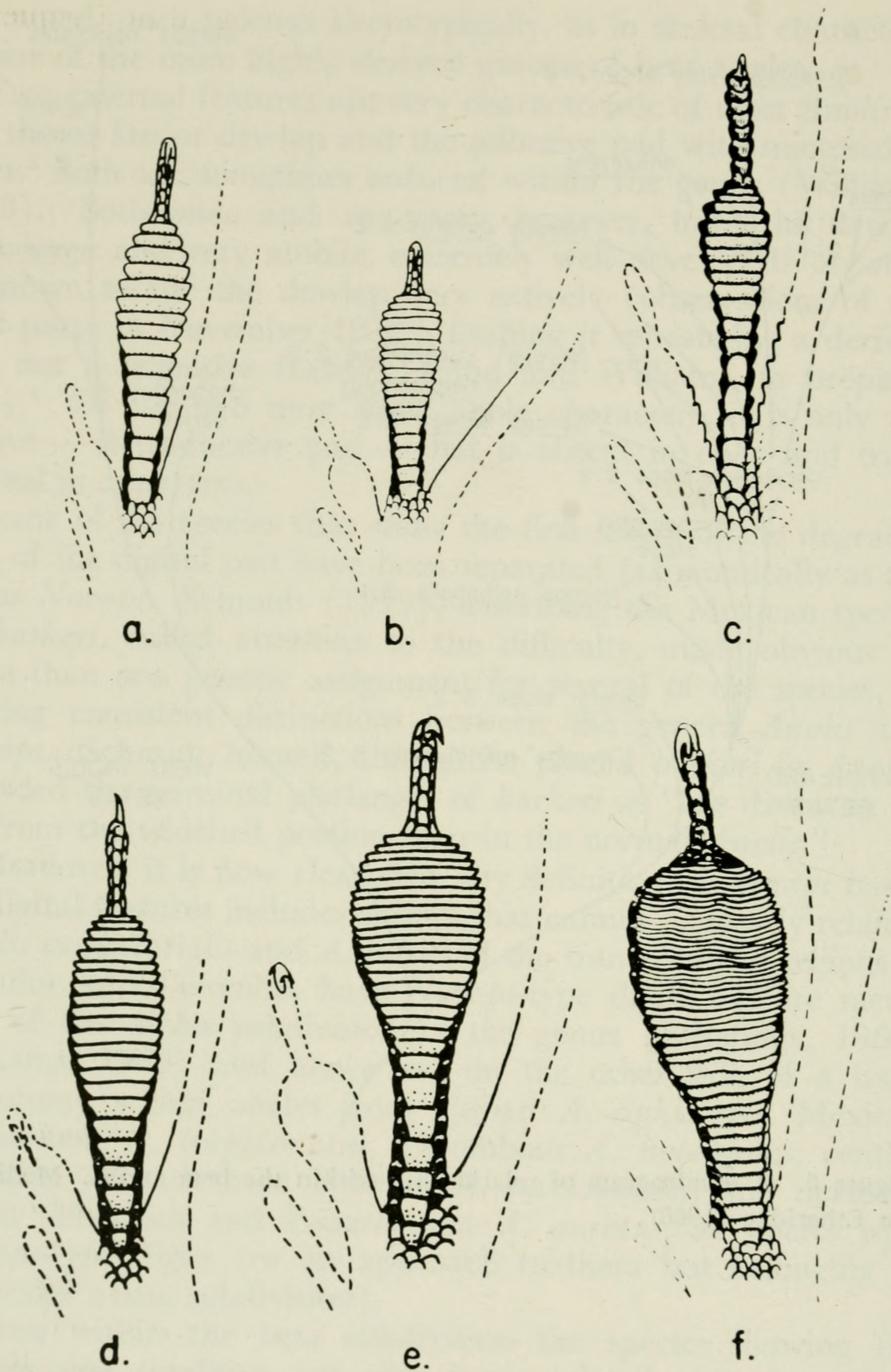


Figure 7. (from Collette, 1961). Feet of five Cuban and one mainland species of *Anolis* showing lamellae on the third toe of the left hind foot: (a) *alutaceus*, (b) *angusticeps*, (c) *sagrei*, (d) *carolinensis*, (e) *porcatus*, (f) *equestris*. Not to scale.

Phylogeny apart, *Anolis* species can be arranged in a sequence showing clear morphological stages in retrograde evolution.

1. *Narrowing of the digital dilations.*

Within any local *Anolis* fauna of more than a few species, there are several conditions of the adhesive pads which Collette (1961) has related to "arboreality." The broadest digital pads are found in those species — "crown," "trunk-crown" and "twig" anoles of Rand and Williams (1969) — which live high in the trees or use twigs and leaves as perches (*e.g.*, *A. porcatus* and *A. equestris* in Figure 7e, f [copied from Collette, 1961]). There is also some correlation with size, but those species specializing on the lower trunks and the ground — "trunk-ground" anoles of Rand and Williams (1969) — have strikingly narrowed pads although they may be larger than some of the compared species (*e.g.*, *A. sagrei* in Fig. 7c).

2. *Reduction of the number of digital lamellae.*

While there is an evident functional difference between a wide and a narrow pad in terms of area of adhesive surface, it is not functionally obvious what the number of transverse smooth "lamellae" has to do with adhesion, especially since many of the lamellae in those species with the highest numbers are far distal, crowded, small and much narrowed (*i.e.*, at the tapering distal end of the pad). It is, however, an empirical generalization (and not only for *Anolis*; cf. Hecht, 1952 for the gecko *Aristelliger*) that the number of lamellae has a positive correlation with size and with climbing efficiency. Correspondingly, those anole species which climb least and use the ground more show fewer lamellae than species of the same size with more arboreal habits. Again contrast *A. sagrei* in Figure 6 with *A. porcatus*.

3. *Loss of distinctness of the anterior margin of the pad (that part under phalanx ii) as against the scales under phalanx i.*

This is the character — the loss of "raised" character of the pad — that has classically defined *Norops* (*e.g.*, Boulenger) (see Fig. 3 center: "*Norops*" *auratus*) and is the maximal degree of dedifferentiation of the pad seen except in *annectens* and *onca*.

The functional meaning of this stage is again unclear. But it should be pointed out again that the phenomenon is not anoline only and that genera have classically been recognized in the Gekkonidae on whether the claw arises at the end of the adhesive pad or "within the pad," *i.e.*, dorsal to it, in the latter case providing the pad with a projecting lip just as in Schmidt's "normal *Anolis*."

4. The fourth and next to final stage in this retrograde series

is found in *annectens*. As an intermediate between "*Norops*" and *Tropidodactylus* it is interesting and perhaps unexpected. In *annectens* the scales under phalanx iii are no longer either wide or smooth; they are instead narrow and keeled. Under phalanx ii, however, there is a residual pad, very narrow, it is true, and the lamellae few in number, but still recognizably a remnant of the classic anoline pad. The area under phalanx ii is in any anole the region of the pad's maximum width (and presumed effectiveness). One must assume that there is still some selective value to the presence of a minimal adhesive pad in *annectens*. However, the partial reversion to keeling in *annectens* and the total reversion in *onca* may, perhaps, be more easily understood in terms of morphogenetic patterns than in terms of direct function in the environment: supradigital scales are usually keeled in *Anolis*; unkeeled scales there are exceptional. The modified scales underneath the digit — the adhesive pad — are obviously a specialized and limited morphogenetic field. The distinctness and perfection of this field must be maintained by a continuing functional need greater than the cost in ontogenetic complexity of maintaining the specialized field. A reversion to the keeled condition of the infra-digital scales, first under phalanx iii and then also under phalanx ii, may therefore be no more than the spread of the morphogenetic field of the supradigital scales around and under the digit once the utility — *i.e.*, the selective value — of and hence the need for local differentiation of very specialized adhesive lamellae has diminished.

5. The culmination of the retrograde series in *onca* is in one regard imperfect. Hatchling *onca* have what appear macroscopically to be lamellae under phalanges ii and iii, *not* keeled scales. First discovered in the collection of the Leiden Museum, the only preserved collection to have any very small specimens, it is now confirmed on hatchlings from eggs laid by captive female *onca* in Panama.

The "lamellae" of *onca* hatchlings are astonishing enough to require histological study. How closely do these lamellae match the lamellae of "normal" *Anolis*? Hatchlings and near hatchlings 27–30 mm in snout–vent length show "lamellae"; juveniles just a few millimeters larger (34 mm, 41 mm) already show keeled infradigital scales. How is this sharp ontogenetic change accomplished?

A proper study of this question would be a digression here. The problem has been referred to P.F.A. Maderson and he will be reporting on it. Some of his preliminary observations are,

however, germane at this time. The "lamellae" of hatchling *onca* are pseudo-lamellae without the "hairs" (spinules) of the true lamellae of an *Anolis* adhesive pad. They also lack the spikes characteristic of larger juveniles (almost equal 34 mm snout-vent length) and of adults of *onca*. In contrast *annectens* has under phalanx ii anoline hairs and the lamellae have the free distal edge that is characteristically anoline.

Hatchling *onca*, thus, though they seem superficially very different, are on their way to the adult *onca* infradigital condition. The lamellar field, to return to that interpretation of the embryological basis of these several conditions, is already extremely weakened at the time of hatching and soon thereafter is wholly substituted for by the field that produces spikes and keeling.

We have here emphasized a morphological series. The *onca* hatchling is in this regard an intermediate in the series but a very different intermediate from adult *annectens*. The *onca* hatchling already shows a breakdown of the lamellae and adhesive pad and in the adult the breakdown is total. *Annectens* is on another pathway. The pad under phalanx iii — always in *Anolis* the least significant portion of the total adaptation — has in *annectens* gone completely; retrograde evolution is for this area complete. But under phalanx ii the pad is only narrowed and the lamellae reduced in number; the latter are still fully pilose, presumably still fully adhesive. A habitat for *annectens* more genuinely "arboreal" than that of *onca* does seem plausible.

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