

species. There is an adult "female" in the Royal Ontario Museum (No. 76,360) found dead at Pt. Credit, Ontario on December 7, 1957, which has been thought to be a hybrid between *immer* and *adamsii* (Godfrey, 1966: 11). In the recurved lower outline of the proximal segment of the mandibular rami (character 6 of Binford and Remsen, 1974: 115) this specimen resembles *adamsii*. The size of the remaining white squares on the back are within the range of those of *adamsii* and of males of *immer*, but not of females of *immer*. In size of wing, tarsus, and bill, the bird is well within the range of males of *immer*. In the other bill characters described by Binford and Remsen, the specimen is within the range of *immer*. While the possibility that this bird is an *immer* — *adamsii* hybrid cannot be completely discounted, I think it is more probably a male *immer* which was mis-sexed by the collector, who recorded nothing concerning the size or condition of the gonads.

THE STATUS OF *pacifica*. — The three forms of the Arctic or Black-throated Loon (*arctica*) complex (*arctica*, *viridigularis*, and *pacifica*) replace one another around the arctic except in Iceland and Greenland, where none occurs. Thus they might be thought of as forming a broken rassenkreis. The nominate form, *arctica*, ranges from the British Isles eastward across the northern parts of Eurasia and intergrades with *viridigularis* in Siberia. The latter form is found in western Siberia, largely south of the range of *pacifica*, and in parts of western Alaska. The widespread North American form, *pacifica*, also breeds in northeastern Siberia. Portenko (1939) and Bailey (1948) have shown that the breeding ranges of *pacifica* and *viridigularis* overlap in Anadyrland and western Alaska and reported no interbreeding. They concluded that the two were, therefore distinct species, an opinion followed by Vaurie (1965).

There are several reasons for doubting the specific status of *pacifica*. In the first place, those who have discussed the problem in the past have ignored one pertinent question: would *arctica* and *pacifica* interbreed if their ranges were to expand and meet? I think it likely that they would because the throat color is the same and the difference in size is less than that between *pacifica* and *viridigularis*. Secondly, there has been no thorough, detailed field study of *pacifica* and *viridigularis* in the area of overlap, and thirdly, there is evidence of interbreeding between the two forms.

Of the two forms, *viridigularis* is larger in all measurements, has a green (not purple) sheen on the throat, and a darker gray nape.

Green- or blue-throated individuals, otherwise indistinguishable from typically purple-throated individuals of *pacifica* are known to occur (Bailey, 1948: 140; Palmer, 1962: 45; Vaurie, 1965: 5), but whether this is a result of introgression with *viridigularis* or part of the normal range of variation of *pacifica* is unclear. To date, I have measured and examined 12 examples of *viridigularis* and approximately 270 of *pacifica* in breeding plumage. Of the latter, at least nine, or 3.3 percent have green or blue-green throats. All nine have measurements well within the range of *pacifica*. In addition, a male from Savoonga, St. Lawrence Island, Alaska (Colo. Mus. Nat. Hist. No. 26,769) labelled "*viridigularis*" has measurements well within the range of *pacifica*, although all above the means for males of that form. The nape is dark, like that of *viridigularis*, and it is either a very small example of that form or an intergrade. Two other green-throated birds may be intergrades: a male (Nat. Mus. Canada No. 8,816) from Barter Island, Alaska, has a nape intermediate in color between those of the two forms, a long wing (318 mm. or nearly 1.5 standard deviations above the mean for *pacifica*), a long tarsus (near the maximum for *pacifica*), but a small bill (below the mean for males of *pacifica*); and an unsexed bird (Amer. Mus. Nat. Hist. No. 348,959) from SE Victoria Island, Canada, has a light nape, long wing (321 mm.), a short tarsus (between the means for males and females of *pacifica*), a long bill (above the mean for males of *pacifica*) and a deeper bill than that of any *pacifica* I have measured. Two purple-throated males with long wings (323 and 325 mm.), long tarsi, and bills somewhat above the mean for males of *pacifica*, are also within the range of *viridigularis* in all these measurements and may be intergrades. While the sample of *viridigularis* which I have seen to date is too small to permit an accurate analysis of variation within that form, the presence of several probable intergrades suggests that interbreeding occurs between it and *pacifica*.

V. SUBSPECIES PROBLEMS

Gavia stellata squamata Portenko. — Vaurie (1965: 4) lists this subspecies as not well differentiated but warranting nomenclatural recognition, while Dement'ev and Gladkov (1968: 291) question its validity. I have examined 12 breeding adults from the range of this form from Franz Josef Land (3), Spitsbergen (7), and Bear Island (2), and I find that the plumage characters used to

differentiate this form from nominate *stellata* (Vaurie, *loc. cit.*) are not consistent within the population, and as Dement'ev and Gladkov (*loc. cit.*) pointed out, are found in some specimens from outside the range. On the evidence now available, I see no value in recognizing this subspecies.

Gavia arctica suschkini Zarudny. — Although this race, based on migrant individuals from Russian Turkestan, was recognized by Peters (1931: 34), it is generally considered a synonym of the nominate race by recent authors (e.g. Dement'ev and Gladkov, 1968: 297; Vaurie, 1965: 5). I have not seen the material on which this race was based and follow the above authors in not recognizing *suschkini*.

Gavia immer elasson Bishop. — This subspecies was also recognized by Peters (1931: 35), but not by Vaurie (1965: 7) and many other recent authors. This species varies greatly in size, wing lengths of adults ranging at least from 287 to 411 mm., but I have not collected sufficient data to work out the pattern of geographic variation, which appears to be largely clinal. While realizing the possibility that there may be recognizable subspecies within this species, I prefer to consider *immer* monotypic at least until a thorough revision can be made.

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SOUTH AMERICAN ANOLES: THE SPECIES GROUPS. 2. THE PROBOSCIS ANOLES (*ANOLIS LAEVIS* GROUP).

ERNEST E. WILLIAMS¹

ABSTRACT. The *Anolis laevis* group is known from three species represented by only nine specimens, all males, from four localities. All are distinguished by a soft multi-scaled proboscis and form a graded series from Peruvian *A. laevis* (proboscis minimally developed) through Brazilian *A. phyllorhinus* (proboscis of moderate size) to Ecuadorian *A. proboscis* (proboscis very long). Color in life and habitat are known only for *A. phyllorhinus*. The proboscis is interpreted as primarily an intraspecific social signal increasing the virtual size of the animals.

The most readily recognizable — at least in males — of all South American *Anolis* are the three species that have a nasal appendage or proboscis. The group may be described as follows:

Anolis laevis species group

Type species: *A. laevis* Cope 1876.

Definition: (Many possibly useful details are not determinable in *A. laevis* and hence are not mentioned here.) Alpha anoles of moderate size (60–97 mm snout-vent length) distinguished by a soft multi-scaled nasal appendage projecting forward *above* the rostral scale. Four to 10 scales across the snout between the second canthals. Supraorbital semicircles in contact or separated by as many as three scales. Loreal rows two to five. Interparietal of moderate to large size in contact with the supraorbital semicircles or separated by as many as three scales. Supralabials in contact with suboculars. Middorsal scales uniform or the median row raised into a crest of triangular scales. Tail crest single or double. Lamellae

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under fourth toes ranging between at least 17 and 26. Dewlap and postanals large in males. Females unknown.

Distribution: Widely disjunct: (1) trans-Andean Ecuador; (2) southern tributaries of the Amazon in central Amazonia; (3) western Amazonia.

INCLUDED SPECIES

Anolis laevis Cope 1876

(Fig. 1)

Scytomycterus laevis Cope, Jour. Acad. Nat. Sci. Phila., NS 8: 165.

Holotype. ANSP 11368, collected by Prof. James Orton.

Type locality. "Between Moyabamba and Balsa Puerto on the river Huallaga in eastern Peru."

Additional references: Boulenger, 1885: 56 (referred to the genus *Anolis* and placed between *A. tigrinus* and *A. punctatus*); Burt and Burt, 1933: 17 (listing only); Barbour, 1934: 154 (placed along with *A. tigrinus* as synonym of *A. transversalis*; both synonymies quite mistaken); Williams, 1965: 6-13 (discussed as member of the *punctatus* group *sensu lato*); Peters and Donoso-Barros, 1970: 57 (citation only); Malnate, 1971: 358 (listing of type in the Philadelphia Academy).

Anolis phyllorhinus Myers and Carvalho 1945

(Figs. 2 and 3)

Anolis phyllorhinus Myers and Carvalho, Bull. Mus. Nac. NS No. 43: 2.

Holotype. MN (Rio de Janeiro) 1804, adult male collected by Alexandre Parko on June 14, 1943.

Type locality. "Borba, lower Rio Madeira, State of Amazonas, Brasil."

Additional references: Williams, 1965: 8-13 (discussed as member of the *punctatus* group *sensu lato*, first mention of the second known specimen MZUSP 7118, Jacareacanga, Rio Tapajoz, Pará, Brasil¹); Peters and Donoso Barros, 1970: 63 (citation only).

Anolis proboscis Peters and Orcés 1956

(Figs. 4, 5, and 6)

Anolis proboscis Peters and Orcés, Breviora No. 62: 2.

¹Note that the region between the Madeira and Tapajoz is one of Haffer's (1974, p. 70) "distribution centers" for endemic Cis-Andean birds.

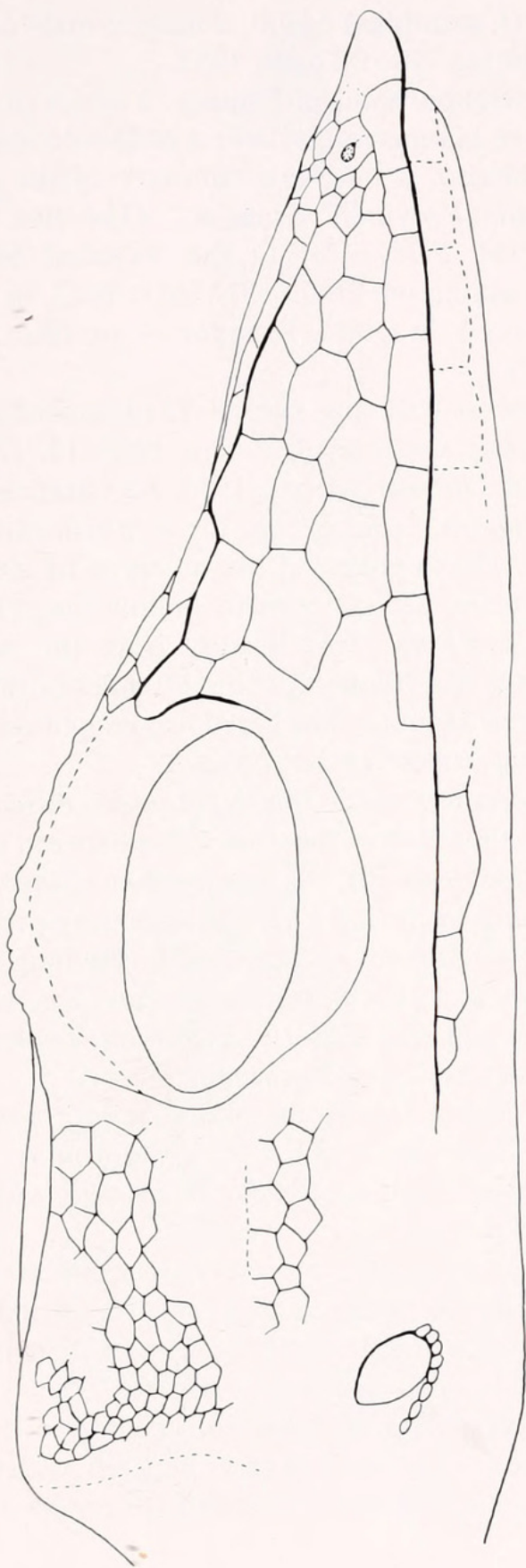


Figure 1. *Anolis laevis*, ANSP 11368. Lateral view of head of type.

Holotype. MCZ (Cambridge) 54300, a mature male collected by Antonio Proano during April 27–29, 1953.

Type locality. “Neighborhood of Cunuco, a small town at 1200 meters elevation, five kilometers northwest of Mindo, on the south bank of the Rio Mindo, a northern tributary of the upper Rio Blanco, in Pichincha Province, Ecuador.” (The five additional specimens — USNM 207671–73, in the National Museum of Natural History, Washington, D.C.; IPN 7611, 7612, in the collection of Gustavo Orcés V in Quito, Ecuador — are from Mindo or “region of Mindo.”)

Additional references: Williams, 1965: 8–13 (discussed as member of the *punctatus* group *sensu lato*); Peters, 1967: 13, 17 (key and citation); Peters and Donoso Barros, 1970: 63 (citation only).

Ecological information. None except for *A. phyllorhinus* Myers and Carvalho: “Mr. Parko collected the holotype of *Anolis phyllorhinus* in the capoeira (second growth or low jungle) that surrounds the town of Borba. This locality is in the Amazonian lowlands on the lower Rio Madeira, about 90 miles (airline) south-southeast of the city of Manaus. The lizard was caught on a low tree while Mr. Parko was collecting butterflies. . . .”

Distinguishing characters of the species. *A. laevis* differs from the two other species in the small number of scales between the second canthals (4, rather than 9 or 10), the low number of loreal rows (2, rather than 3 to 5) and in having a very rudimentary proboscis. *A. proboscis* has a crested dorsum and tail and a very long proboscis, while *A. phyllorhinus* lacks such crests and in fact has two rows of scales dorsally on the tail and a shorter proboscis. Table 1 lists the standard scale characters for each species.

Size. Snout-vent length: *laevis* 60 mm, *phyllorhinus* 73 mm, *proboscis* 74 mm. Tail: *laevis* 79 mm, *phyllorhinus* 153 mm, *proboscis* 97 mm. Hind limb length: *laevis* 39 mm, *phyllorhinus* 49 mm, *proboscis* 42 mm.

Color. *Laevis*: Cope reported the preserved specimen as follows: “Color above dark gray, below pigmented white (in spirits). The two colors are abruptly defined between the orbit and there are brown spots behind the axilla. Tail distinctly annulate.”

Phyllorhinus — Myers and Carvalho: “Color in alcohol (formalin-fixed) plain, dull, bluish gray above, lighter beneath, with no sign of a color pattern anywhere save on the toes and undersides of the legs.

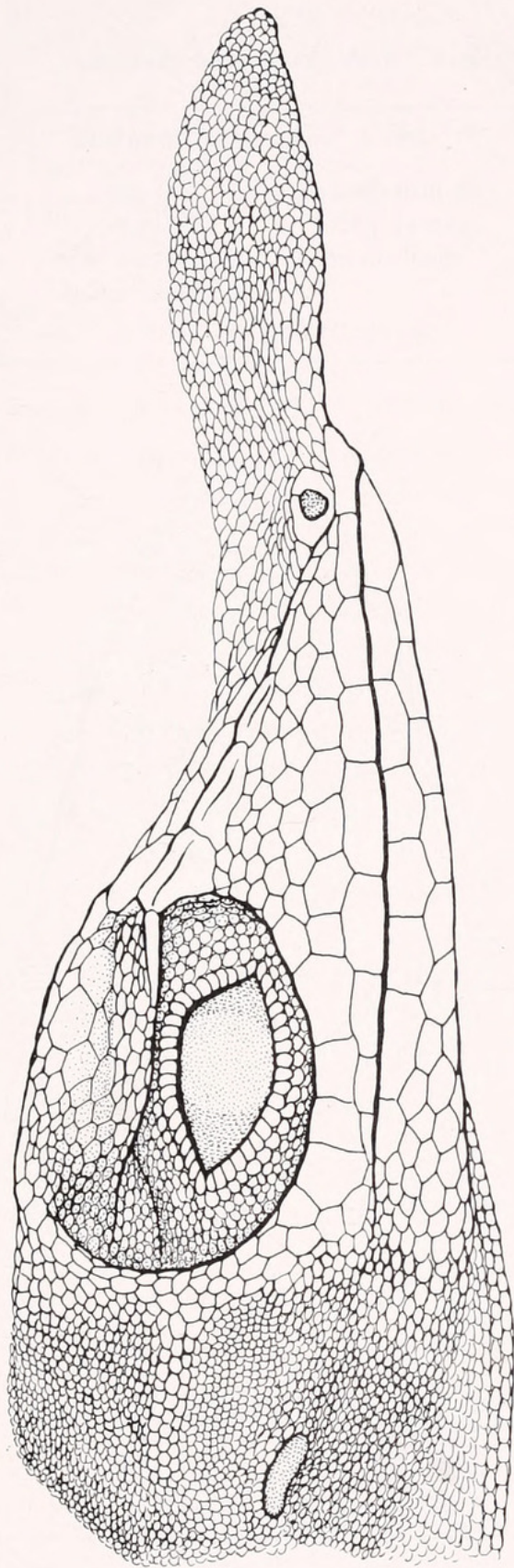


Figure 2. *Anolis phyllorhinus*, MZUSP 7118. Lateral view of head of São Paulo specimen.

Table 1. Scale counts and characters.

	<i>laevis</i> soft protuberance covered with ? small scales N = 1	<i>phyllorhinus</i> leaf-like laterally compressed with granular scales N = 2	<i>proboscis</i> leaf-like laterally compressed with elongate scales N = 6
scales between second canthals	4 (Cope)	10	9-10
scales between semicircles	0	0	1-3
scales between interparietal and semicircles	0	1-2	1-3
loreal rows	2	4-5	3-5
rows between suboculars and supralabials	0	0	0
labials to center of eye	?	6-7	9-12
sublabials in contact with infralabials	?	5-6	2-3
median gular scales in contact with mental between sublabials	?	4	2
middorsal rows enlarged	0	0	1 (crest of tri- angular scales)
tail crest	double row, no crest	double row, no crest	crest present
lamellae 4th toe	?	25-26	17-21

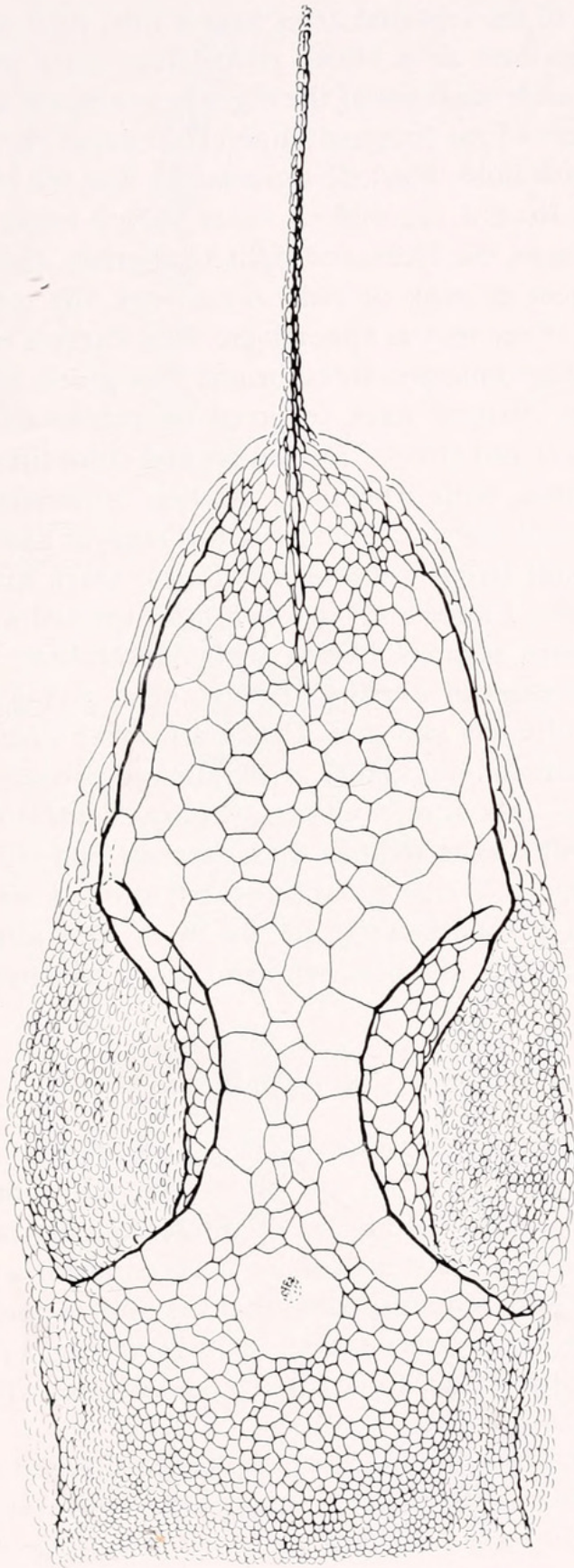


Figure 3. *Anolis phyllorhinus*, MZUSP 7118. Dorsal view of São Paulo specimen.

The undersurfaces of the legs and arms bear a fine, light mottling, perhaps better described as a bluish reticulation on a yellowish ground color. The undersurfaces of the digital expansions are dark. The superior surfaces of the toes and fingers (but not of the feet and hands) are light, with bold, blackish crossbands. The tail gradually becomes brownish toward the end. A color sketch made by Mr. Parko from life shows the creature bright blue-green, the dewlap yellowish, with traces of pink or red on the toes, the top of the snout, and the end of the rostral appendage." Mr. Parko's notes say the beast immediately changed from bright blue-green to brown when captured, but changed back to green on preservation.

Proboscis — Peters and Orcés: "Dorsal ground color (in alcohol) a dull gunmetal blue, with irregular, parallel, horizontal black streaks along vertebral margin. These streaks vaguely line up and form a pair of lateral bands between the limbs. Dark brownish-black spot at shoulder. Limbs and lateral surfaces spotted with light yellowish white; limbs vaguely barred with darker blue; skin in interstices between scales of dorsum of digits light, giving appearance of banding on fingers and toes. Dorsum of head unicolor, as back; temporal region and lips lighter, with faint reddish or purplish tinge and a marked light spot over ear opening. Ventral surfaces generally lighter, with vague reddish tints on chest and chin; belly stippled with light spots. Venter of limbs heavily spotted with white proximally, becoming totally white on the foot. Tail alternately barred with gunmetal blue and blackish bands approximately equal in width."

TAXONOMY AND NOMENCLATURE

The single recognition character — the proboscis — differs considerably in the three known species, which are abundantly distinct. The extent of the differences might reasonably raise the issue of parallel evolution, but the proboscis is so singular a feature that it seems subjectively more probable that the known species are the relicts of a once much larger radiation. It is also very possible that there are more species still to be discovered, perhaps with quite restricted distributions.

It is clear that the first adumbrations of a proboscis are found in *A. punctatus* and some of its relatives. In these the rostral scale and rostral area are produced to overhang the lower jaw. In *laevis* there

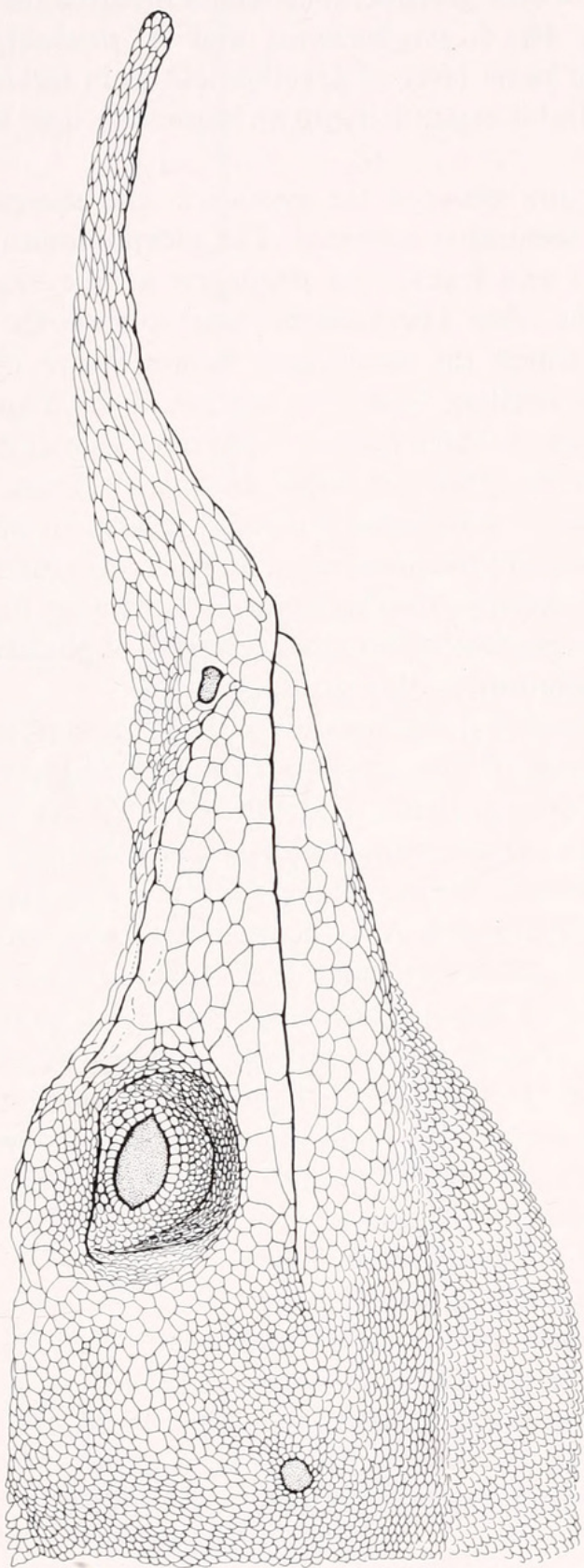


Figure 4. *Anolis proboscis*, USNM 207672. Lateral view of head.

appears to be a soft protuberance which involves the smaller post-rostral scales. In *A. phyllorhinus* and *A. proboscis* the rostral remains at the same level of development as in *laevis* but the area above the rostral is expanded into an impressive nose leaf, longest in *A. proboscis*.

The distinction between the *proboscis* and *punctatus* group is thus perhaps somewhat artificial. The morphological sequence is, however, clear and leads from *proboscis* at one extreme back to *punctatus* at the other. I find it convenient to make the distinction at the point at which the scales and tissues above the rostral are involved in the swelling. Since the relation of this area to the rostral is very similar in the three species, it provides greater plausibility for the contention that this is a single lineage. It is not, on the other hand, clear that *A. punctatus* is directly related to the species that mimic it by means of the presence of a projecting rostral in the male. However, any decision on this point is necessarily tentative, and I emphasize convenience rather than certainty of phyletic affinity as a basis for recognition of this group.

Nothing is known of the function of the proboscis (see below) and all nine specimens of this group thus far collected have been males. This has raised (e.g. Peters and Orcés, 1956) the issue that the proboscis anoles might be the males of species already described on the basis of females. However, there are few described species still known only from females. Also the other external characters of each of the proboscis anoles are such that it would require a degree of sexual dimorphism beyond anything known in lizards to make any of the three proboscis species possibly conspecific with any other described anoles. In the case of *A. punctatus* and the other species with projecting rostrals, this and the presence of a dewlap, enlarged postanal scales and sometimes minor differences in color distinguish the males. Scale counts and other aspects of morphology do *not* significantly differ between the sexes.

Only *A. proboscis* is known from series (the type, three newly collected specimens given to the United States National Museum by Orcés, and two in the Orcés collection in Quito). *A. phyllorhinus* is represented by only two specimens, the type and a badly preserved second specimen. *A. laevis* is still known only from the type, which is now in extremely poor condition.

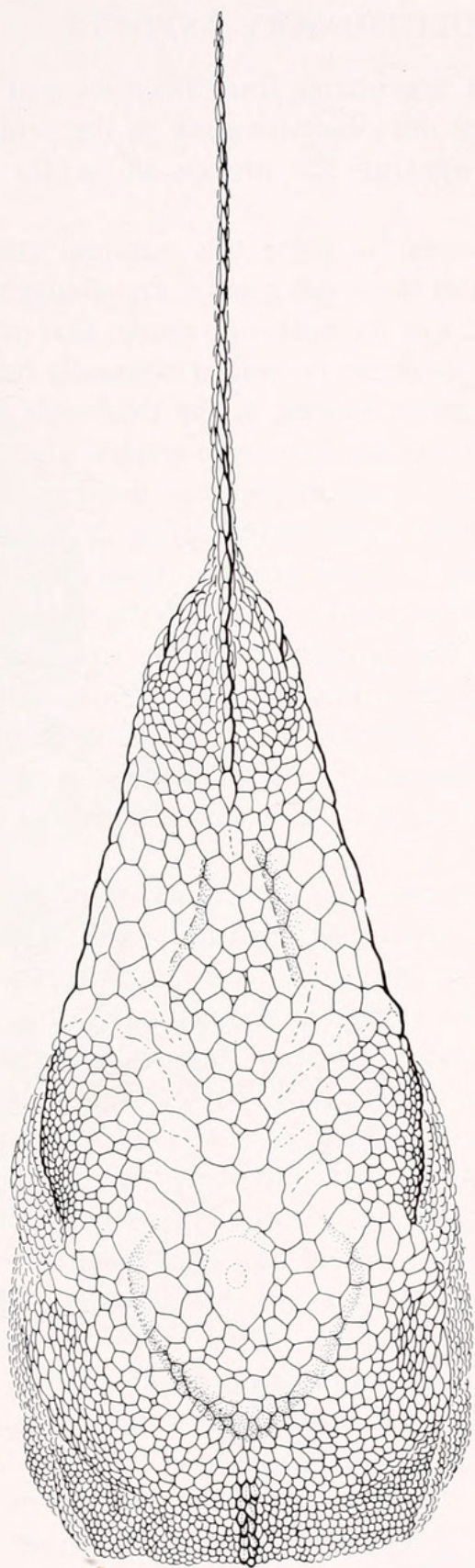


Figure 5. *Anolis proboscis*, USNM 207672. Dorsal view of head.

EVOLUTIONARY ASPECTS

Three species, nine specimens, four localities and one note on habitat are the sum of our objective data on the proboscis anoles. They provide little opening for discussion or for evolutionary speculation.

It is possible, however, to place this minimal amount of data against a background of the much greater knowledge of anoles as a whole. It is a peculiarity of the proboscis anoles that in no other way are they known to be different or indeed especially interesting. The single aspect that appears striking is the proboscis itself.

Other bizarre structures are known in anoles. The dewlap would be bizarre were it less common and less familiar. High tail fins supported by heightened caudal neural spines occur in a number of distantly related species. Casque heads — heads enlarged by crests and ridges — occur in several *Anolis* and in the related anole genera *Phenacosaurus* and *Chamaeleolis*. All these structures — dewlap, tail fin, casque head and proboscis — have the effect of increasing the apparent size of the animals that bear them. In the case of the dewlap, there is evidence of use in agonistic encounters, and evidence (Rand 1967) that larger animals usually win in such encounters.

Trivers (1976) has shown the importance of sexual selection for size in one species of *Anolis*; he has inferred the generality of the rule. There are, however, aspects of increase in real size that make the course of evolution complex. A real increase in size with its implied increase in weight can carry with it functional restrictions that compel changes in the life style of the species that exercises this option. Sometimes such changes are realized within the ontogeny of a single species. Sometimes we see them as the alternative strategies utilized by sympatric species (Schoener, 1970; Williams, 1972). Virtual changes in size — unreal but visually effective — are still another alternative. Virtual size has the advantage of introducing few if any functional problems.

I have called attention to elongation of the head in many crown anoles (Williams, 1965). It is probable that this initially has a (still undefined) functional explanation. However, there are side effects: the change of head shape probably has its species-recognition aspects and the size of the head has its agonistic advantage aspects. Yet if these latter aspects have too much effect, the bony structure of



Figure 6. *Anolis proboscis*, USNM 207672. Lateral view.

the head is elongated beyond its functional optimum. There will therefore again be a premium on virtual rather than real change of head shape. We see the beginning of such a phenomenon in *Anolis punctatus* and in some related species where (in males) only the rostral scale is enlarged. *A. laevis* carries this process a slight step further. *A. phyllorhinus* and *A. proboscis* have gone much further.

It is significant that the probosces in *A. phyllorhinus* and *A. proboscis* are not similar in detail. One would expect this if there were functional aspects to the structure *per se*. On the contrary, it appears a similar visual effect may readily be achieved by only broadly comparable means. This corresponds with species recognition devices and intra-species display where there is no requirement that structures be similar; rather the requirement is that they be different. (In view of the wide allopatry of the known proboscis anoles, there could be no selection for striking difference *now*, but perhaps it has existed in the past.)

Within the Iguanidae, the basiliscines would seem to be quite parallel cases. Head casques — very different in structure — are present in all three genera; in *Basiliscus*, dorsal and tail fins are present, different and wonderfully conspicuous in three species, very reduced in a fourth. (Once a bizarre structure has been adopted as an intra- and interspecies signal, an option open to a new member of a group is to abandon the structure: absence of a signal is itself a signal.) The absence of a dewlap is a strategy adopted by two species in the very complex anole fauna of Cuba; the dewlap is consistently retained in the simplest faunas and is reduced only in the fauna almost as locally complex as Cuba, that of Hispaniola (Williams and Rand, 1977).

Outside the Iguanidae, a number of species in the closely related family Agamidae show parallels to the proboscis anoles: *Ceratophora* (Ceylon, three species, see M. Smith, 1935 and Taylor, 1953); *Harpesaurus* (Java, Sumatra, Nias, five species *fide* Wermuth, 1967); *Lyriocephalus* (Ceylon, one species, Taylor, 1953) and *Cophotis* (Ceylon and Sumatra, De Roois, 1915). The probosces in these are all soft structures but considerably more variable in shape, number and squamation than those of the proboscis anoles. (Figs. 7–9 show the differences within the genus *Ceratophora*.) For chameleons Rand (1961) has already discussed the function of the ornamentation that is so remarkably developed in the montane

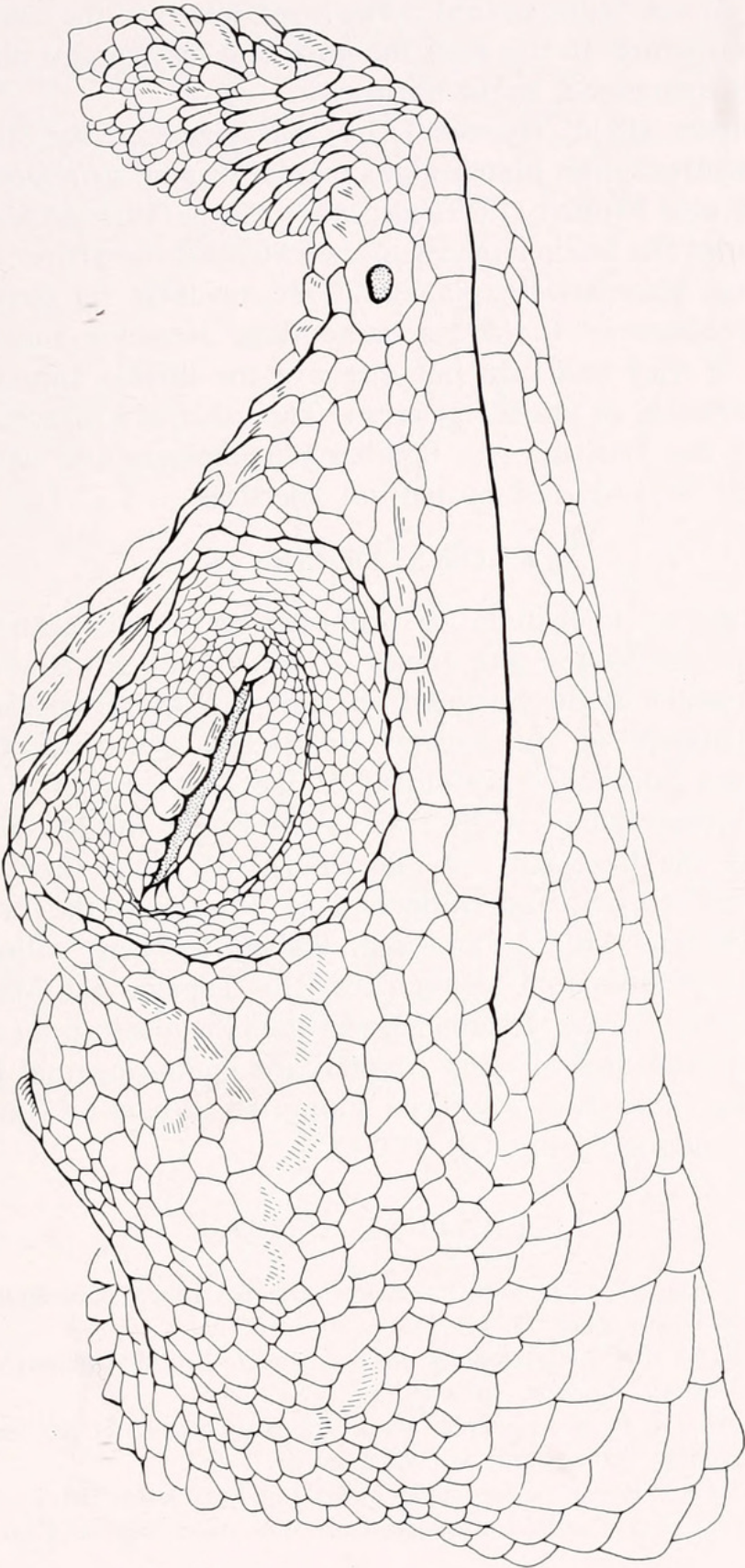


Figure 7. *Ceratophora tennentii*, MCZ 136187. Side view of head.



Williams, Ernest E. 1979. "South American Anoles: the species groups. 2. The proboscis anoles (*Anolis laevis* group)." *Breviora* 449, 1–19.

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