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NOTES ON HISPANIOLAN HERPETOLOGY

8. THE FORMS RELATED TO ANOLIS HENDERSONI COCHRAN.

BY ERNEST E. WILLIAMS

In 1923 Doris Cochran described *Anolis hendersoni* from Petionville, Haiti. This long-headed species with a reduced dewlap was represented by a single adult male collected by J. B. Henderson and Dr. Paul Bartsch in 1917.

Ten years later, without making any reference to Anolis hendersoni, Noble and Hassler (1933) described the very similar Anolis baharucoensis from the mountains of Barahona peninsula to the east of the type locality of A. hendersoni. This new species was represented by 76 specimens. The series demonstrated marked sexual dichromatism, and there was for the first time information on the habits and habitat of the species. Noble and Hassler (1933, p. 12) reported collecting it between the altitudes of 1500 and 3700 feet and stated: "It is believed that the lower mountain sides are not humid enough for the species. It is much more terrestrial in its habits than the other species of Anolis in the same locality, being found on the ground and on low brush in coffee groves and forested areas. Its favorite habitat, however, was on low plants, leaves and trash along mountain streams and in humid ravines."

Since these two descriptions the only additional published information is in Cochran's (1941) "Herpetology of Hispaniola." She reported six additional specimens of hendersoni: one (USNM 82566) is a misidentified young coelestinus; the others are a Fond des Negres specimen (USNM 72629) collected by A. Wetmore and four specimens (MCZ 13792, 13794, 13795, 13797) collected at Port-au-Prince by G. M. Allen. Cochran recognized the strong resemblance between hendersoni and baharucoensis but retained the latter as a full species. She said: "A. hendersoni has a close ally in A. baharucoensis, as they are

both distinguished by the same elongated head and body. Although at first glance the immaculate dorsum of hendersoni does not suggest alliance with the heavily banded baharucoensis, other details of coloration are more suggestive of the relationship. The lips are spotted in a nearly identical manner. The white lateral line, so striking a feature of hendersoni, is developed in a slighter degree in baharucoensis. The peculiarly crowded appearance of the scales just behind the mentals and their extreme convexity which makes them appear to be ridged without actually being keeled, is duplicated exactly in both species. ferences are equally distinct and set them off in the same way that chlorocyanus and coelestinus are differentiated. The very fine body granules of baharucoensis and its rather square snout are not to be confused with the coarser scales and more rounded profile of hendersoni¹." No additional material of baharucoensis was recorded.

Recent collections (1959-61) in Haiti have greatly increased our knowledge of Anolis hendersoni and have permitted recognition of a third member of the hendersoni complex from the western tip of the southwestern peninsula. This new form is recognizable on the color pattern and probably on head length of the adult male, but the wealth of new material appears to show that there are no consistent squamation differences between any of the members of the complex, and, therefore, despite the absence of any clear and positive instance of intergradation, I regard these three as subspecies of a single species. This problem is further discussed below.

We may now redefine $Anolis\ hendersoni$ as a polytypic species of Anolis belonging to the Hispaniolan radiation of Etheridge's alpha section and carolinensis series 2 (i.e. an Anolis without caudal transverse processes, with the lateral processes of the interclavicle in close contact with the expanded proximal parts of the clavicles, and with three parasternal chevrons attached to the dorsal ribs followed by a single chevron not so attached) and with the following diagnostic external characters. Head and body slender (head ca. $\frac{1}{3}$ or more snout-vent length), dewlap very reduced, not extensible. Dorsal scales small, ca. four middorsal rows slightly enlarged and distinctly keeled but grading into

¹ Cochran (1941, p. 187) was able to examine only a single paratype of baharucoensis.

² These terms (for present purposes sufficiently defined by the data within the parentheses above) are derived from the doctoral thesis of Richard Etheridge at the University of Michigan (available on microfilm).

granular flank scales. Ventral scales smooth, polygonal, sub-imbricate. Digital dilations moderate. About 19-21 lamellae under phalanges ii and iii of fourth toe. Tail not compressed nor with crest. Verticils obscure. Sexually dimorphic in size and color pattern. Anterior head scales smooth. Supraorbital semicircles separated by one scale row. Interparietal scale separated from semicircles by 4-6 scales. Loreal rows 6-7, canthals 6-7, supralabials to center of eye 6-7, suboculars in contact with supralabials. Mentals much longer than wide, throat scales medially deeply inserted between them. Three populations conform to this definition but differ strongly in male color pattern (and in one instance in the relative head length of the adult male).

TAXONOMIC DESCRIPTION

Anolis Hendersoni Hendersoni Cochran¹

Anolis hendersoni Cochran 1923. Jour. Washington Acad. Sci. 13:25. (Type locality: Petionville, Haiti) — Cochran 1941, p. 181.

Specimen list. Haiti. Departement du Nord: Citadelle MCZ 25484, 25486, W. J. Eyerdam, 1927. Departement du Ouest: Portau-Prince MCZ 13792, 13794, 13795, 13797, G. M. Allen, 1919. Petionville USNM 59210 (type), J. B. Henderson and P. Bartsch, 1917. Boutillier Road MCZ 59951-7, E. Williams and A. S. Rand. 1959; MCZ 62956-9, A. S. Rand and J. Lazell, 1960. Morne Decayette MCZ 62960-8, A. S. Rand and J. Lazell, 1960; MCZ 62969-75, 63443, L. Whiteman, 1960; MCZ 65635-46, L. Whiteman, 1961. Diquini MCZ 64824-40, L. Whiteman, 1961. Below Kenskoff MCZ 59950, L. Bonfil, 1959. Penault MCZ 63437-42, L. Whiteman, 1960. Furcy MCZ 64823, L. Whiteman, 1961. Marbial, 21 km NE Jacmel MCZ 65170-8, CM 3812-17, L. Whiteman, 1961. Croix Joseph, Marbial, 21 km NE Jacmel MCZ 65183-202, CM 37818 (16), L. Whiteman, 1961. Source Fleury, Mayerre, 8 km E Jacmel MCZ 65179-82, CM 37819-22, L. Whiteman, 1961. Departement du Sud: Butete near Miragoane MCZ 66029-62, CM 37919 (32), L. Whiteman coll. 13-viii-61. Mingrette near Miragoane MCZ 66063-79, CM 37920 (15), L. Whiteman coll.

¹ The following abbreviations have been used for the museums or collections from which specimens of anoles of this complex have been examined: AMNH. American Museum of Natural History; CM, Carnegie Museum; MCZ, Museum of Comparative Zoology; UMMZ. University of Michigan Museum of Zoology: USNM, United States National Museum; YPM, Yale Peabody Museum; AS-X, Albert Schwartz, personal collection,

1961. Risque near Miragoane MCZ 66080-85, L. Whiteman coll. 1961.

Diagnosis. Head length in adult male about 33 per cent of snout-vent length. Male coloration distinctive. (Head brown. Nape vermiculate, lighter on darker brown. Dorsum brown anteriorly, greenish posteriorly, without transverse saddles or other markings. Flank stripe extending to groin bordered above by intense black and below at sides of belly by black vermiculation. Belly bluish.)

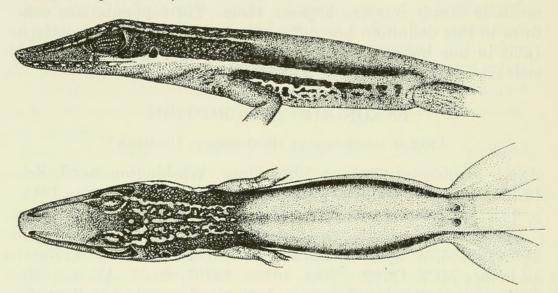


Figure 1. Anolis hendersoni hendersoni, MCZ 59949. Lateral and dorsal views. N. Strekalovsky del.

Color in life. Alive, hendersoni is quite spectacularly beautiful—especially the male. The differences between the two sexes are best shown by a tabular comparison of the descriptions of two specimens. I add a few remarks on color variation.

& from below Kenskoff

Head brown and anterior back brown merging into green at sacral region.

♀ from Boutillier Road

Head, nape and center of back dark brown, head somewhat mottled. The central dorsal area bordered by a cream line with an irregular boundary.

Nape with vermiculation behind interparietal which is white.

Nape without vermiculation. Interparietal white.

Blue spots on upper and lower labials. Limbs red brown. Tail with greenish tinge, becoming posteriorly.

marked with darker. Limbs and tail brown, obscurely mottled.

A broad blue-black band from behind eye over shoulder, becoming less well defined posteriorly.

A broad brown band from snout through eye along flanks, lighter in center, dark edged above and below.

Upper and lower labials obscurely

Below this a light line from upper labials to groin, white below eve, yellow from shoulder 34 of way to hind leg, beyond this with greenish tinge.

A light line from upper labials above shoulder to groin, nearly white below eye, yellow green in front of shoulder, purplish and indistinct on flanks.

Flanks below light line boldly mottled with black.

Flanks below light line darker, not mottled.

Throat yellow green.

Throat yellow green with two narrow dark longitudinal lines.

Belly blue green, some orange under base of tail.

Belly and underside of tail pale greenish.

Comments. The female, as the table indicates, is basically similar to the male in pattern but with duller colors and with frequently a light dorsal longitudinal band. The light flank stripe of the male is very brightly colored and brought into bold relief by the black mottling below it and the blue-black of the dark band above it. The same stripe is always obscure or absent posteriorly in females and may be very little evident anteriorly. The green of the hind quarters of the male is absent in the female and so also is the vermiculation on the nape. On the other hand, the two narrow black lines on the sides of the throat may be present or absent regardless of sex.

There is a striking consistency in pattern in the animals from well-separated localities (i.e. Diquini and Mayerre). Such variation as exists seems to be individual only. In the males this appears to be a matter of clarity of expression of various elements of the pattern; this has undoubtedly been influenced by vagaries of preservation. In the females, along with this same variability in the boldness or obscurity of pattern, there seems to be also real pattern variation in the dorsal zone from interparietal to sacral region. In the live specimen described above the impression is of a wide dark middorsal stripe bordered by a narrow light area on

each side. In numerous other females, however, the middorsal dark stripe is narrow, broken or irregular with usually a narrow light center and bordered on each side by a wide light area. This appears to be the more frequent of the two conditions.

This long-headed and slender form has until now been considered very rare. While nowhere as abundant as the ubiquitous species cybotes and distichus or even the two common green anoles, it is, as is often true of "rare" species, not really uncommon in certain restricted situations. It seems to be a bush anole of middle elevations and associated especially with certain bushy thickets. Its habits are thus similar to those which Noble and Hassler (1933, p. 14) reported for baharucoensis. Hendersoni is, however, apparently less restricted to humid situations than Noble and Hassler believed baharucoensis to be.

A. S. Rand made field notes (July 30, 1961) for this species at Morne de Cayette. "A. hendersoni were on stems and branches close to the ground, three or four feet up at most. They were crawling about in the bushes, jumping from branch to branch, seldom coming to the ground, though one did do so to catch an insect. They are very shy and escape by dodging away through the stems, neither climbing nor hiding. Relatively slow moving normally."

James Lazell, Jr. provides in Figure 4 sketches from life of female *hendersoni* from Boutillier Road (August 9, 1961). These show in excellent fashion the characteristic postures and attitudes of the species.

Anolis Hendersoni Baharucoensis Noble and Hassler

Anolis baharucoensis Noble and Hassler 1933. Amer. Mus. Novitates No. 652: 12. (Type locality: "Valley of Polo, Barahona Province, D. R.") — Cochran 1941: 184.

Specimen list. Haiti. Departement de Ouest: Road to Sal Trou, on south side of range of Mt. La Selle AMNH 50096, W. G. Hassler, 1935. Caroyé near Sal Trou MCZ 68693-714, USNM 146616-8, YPM 3704-13, UMMZ 123372-81, CM 38497 (11), G. Whiteman, 1962. Dominican Republic. Barahona Province: Vicinity of Polo AMNH 49516. Valle de Polo AMNH 51081-106, 51108-19, 51123-27, 51128 (type), 51129-52, 51154-56, MCZ 43822, 45952-53, 56138. Polo AMNH 50317, 50322-23. Palomino

¹ The records listed above for the vicinity of Sal Trou are the first for Haiti. At Caroyé, in addition to A. baharucoensis, George Whiteman obtained also the rare form, Chamaelinorops wetmorei.

Springs near Barahona AMNH 49840-42, 49884-85, MCZ 43827, 56137. Barahona AMNH 50263.1

Diagnosis. Head not more than 33 per cent of snout-vent length. Coloration of male distinctive. (Head green. Nape green spotted with brown. Dorsum with broad brown saddles on a green ground. Flank stripe extending to groin, not sharply defined, sometimes broken, bordered irregularly above and below. No black vermiculations on sides of belly. Belly cream tinged with brown and green.)

Color in life. Noble and Hassler (1933, p. 13): "In life the male is an extremely beautiful lizard. In its usual and brightest phase the dorsal surface of the head is an olive green; the neck a lighter green, spotted with brown. The back is a bluer green,

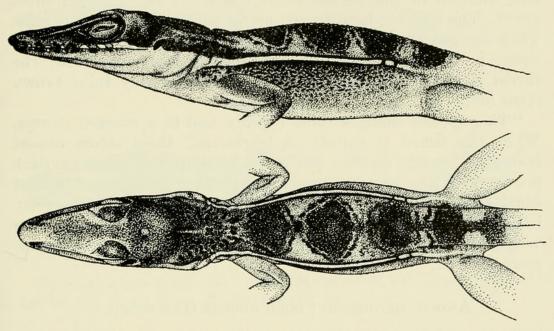


Figure 2. Anolis hendersoni baharucoensis, MCZ 68917. Lateral and dorsal views. N. Strekalovsky del.

1 Some confusion exists regarding the labelling of American Museum of Natural History specimens. Seventy-three paratypes of baharucoensis — AMNH 51081-127, 51129-56, all apparently from Valle de Polo, are listed above. (The specimens missing from the series are all presumably exchanged.) However, Noble and Hassler's text mentions specimens from five additional localities, only two of which are now accounted for by specimens so labelled in the American Museum collections. Thus, unrepresented in the extant collections, though mentioned by Noble and Hassler, is material from Maniel Viejo, from the coffee finca of Senor Luis E. Del Monte near Barahona, and from the property of Mr. G. Hermann near Paradis. In addition, some of the specimens now catalogued in the American Museum as baharucoensis from Polo are pulchellus, presumably from Puerto Rico or the Virgin Islands. Doubtless, as is known to have occurred with Hassler's and other material at this period, some of the lizards were kept alive for a period and only later and rather randomly catalogued.

Certain of the MCZ material (MCZ 43822, 43827) at present catalogued as paratypes, is listed as received in exchange from J. C. Armstrong and presumably was never at the American Museum and thus is not, in fact, paratypic. 1 Some confusion exists regarding the labelling of American Museum of Natural

while the four broad saddles or cross bars are a tone of burnt umber. The dorsal surface of the tail, for the anterior two-thirds, is a vellowish green with several dark brown bars. The posterior end of the tail is brown. The side of the head is greenish brown back to the eye. The upper eyelid may be vivid golden yellow. The posterior corner of the lower lid may be blue or purplish. Just posterior to the eye is a narrow patch of dark brown, followed by a crescent of light blue or white. Posterior to this the side of the head is a brownish green merging into the lighter green of the side of the body which is peppered and veined with brown. Extending from a point on the upper labials anterior to the eye along the sides of the body nearly to the hind leg is a slightly broken white or cream-colored line edged with brown and suffused in the region above the front leg with yellowish green. The legs are light brown above with slightly darker bars. They are nearly white beneath. The ventral surface of the abdomen is cream-colored, faintly tinged with brown and green. The throat is the same color with several rows of very faint brown spots along the side.

"This species changes color rapidly and to a marked degree. When the lizard is caught or frightened, these colors almost instantly become darker, the green changing to gray or dark brown with the brown cross bars growing darker and almost black-edged. The head becomes dark brown and the labials greenish. The pineal region becomes white and very conspicuous. The ventral surfaces turn greenish or yellowish and the spots become more distinct."

Anolis hendersoni dolichocephalus subsp. n.

Type: MCZ 64510, adult male, Place Negre near Jeremie, Departement du Sud, Haiti. Luc and George Whiteman coll. 12-xii-60.

Paratypes: Haiti. Departement du Sud. Place Negre near Jeremie MCZ 64507-9, 64511-36, Luc and George Whiteman coll. 12-xii-60. Les Platons above Carrefour Canon near Ducis MCZ 62976-82, A. S. Rand and J. Lazell coll. 4-viii-60. Carrefour Canon near Ducis MCZ 62983-92, A. S. Rand and J. Lazell coll. 4-5-viii-60. Tombeau Cheval MCZ 62993-7, A. S. Rand and J. Lazell coll. 7-viii-60. Mountains on road to Jeremie MCZ 56145, AMNH 49504, W. G. Hassler coll. 1935. About 8 miles from Camp Perrin AMNH 50098, W. G. Hassler, 1935. Five miles from Camp Perrin on Jeremie Road AMNH 50127, W.G. Hassler,

1935. Camp Perrin AS-X 2664, 2800-2802, 2923-25, A. Schwartz coll. 1962. 13 km N Cavaillon AS-X 3646, A. Schwartz coll. 1962.

Diagnosis. A subspecies of Anolis hendersoni differing in the greater elongation of the head in large males (more than 33 per cent snout-vent length) and in coloration. (Head brown, nape vermiculate lighter brown on darker. On dorsum of male a few small middorsal light-edged transverse bars at intervals, the widest just behind nape. Flank stripe extending only to midbody, narrowing and terminating rather abruptly. A narrow black border above the stripe and black vermiculations below it, both disappearing abruptly along with the stripe itself. The posterior flanks unpatterned. Belly yellowish.)

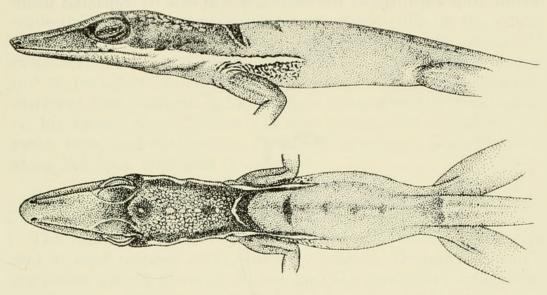


Figure 3. Anolis hendersoni dolichocephalus subsp. nov. Type, MCZ 64510. Lateral and dorsal views. N. Strekalovsky del.

Color in life. Description by W. G. Hassler of AMNH 50098 of from mountains on Jeremie road about 8 miles from Camp Perrin, 2000-3000 ft.: "Dark brown, striped with lighter brown or yellowish lines. Belly and throat yellowish. Belly spotted. No green."

A. S. Rand for specimens from Les Platons: "& Uniform light brown above, grayer on head and neck. Darker brown on side of neck. A yellow stripe, black bordered above and below from below eye to midbody. Below pale yellowish. Faint dark striping on throat. Dewlap area with greenish tint. Eye brown.

"\$\overline{\pi}\$ A middorsal stripe edged with light gray. Sides brown with white, black bordered stripe from below eye to mid body. Belly yellow. Throat and chin white."

A. Schwartz for specimens from Camp Perrin: "? Dorsal ground color yellow-tan with a fine pale hairline with brown suffusions on each side. Sides dark brown with a light lower line on sides. Upper labials cream, occipital creamy. Ventral ground color pale greenish yellow."

Comments. Again the color pattern is remarkably consistent in the several populations sampled. Males from the south side of the Massif de La Hotte (Les Platons etc.) differ from those from the vicinity of Jeremie only in the weaker expression of certain features, i.e. the vermiculation of the nape and the small middorsal transverse markings. The striking way, however, in which the flank stripe, the black line above it, and the vermiculation below stop abruptly at the same place is exactly repeated in all

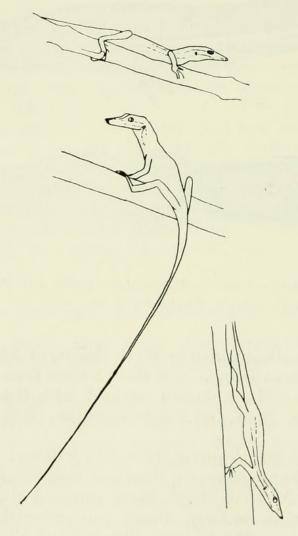


Figure 4. Anolis hendersoni hendersoni. A Boutillier Road female at the height of one foot above the ground. Characteristic poses. J. Lazell, Jr. del.

male specimens. The extreme long-headedness of fully adult males is again characteristic of all samples.

Female coloration is very like that of typical *hendersoni* except that in topotypic specimens from the vicinity of Jeremie the lateral light stripe fades rather abruptly at midbody, while in females from south of the Massif de La Hotte the stripe tends to continue very faintly to the groin as is usual in typical *hendersoni*.

Dolichocephalus at Tombeau Cheval (3000 ft. elevation) was captured along with Anolis monticola, A. distichus subsp., A. cybotes subsp. and A. coelestinus in the vicinity of a great heap of jagged limestone boulders overgrown with bushes and with much leaf litter — cool and shady. A. S. Rand reports that here while the monticola were found "around the cliffs on the rocks, roots, twigs, small branches and leaves close to the ground," dolichocephalus was "... up on small branches, vertical stems one to four feet up and to a less extent among the rocks. A. distichus was common on the larger trees and less frequently on big rocks. A coelestinus was seen and a few A. cybotes on rocks, trees, and bush stems. These last were much more common along the open trail and in coffee."

SPECIES OR SUBSPECIES

The three members of the *hendersoni* complex are allopatric and in most respects extraordinarily similar. Despite Cochran's statement quoted above, I do not find the structural differences between these three taxa at all clear. Abundance of material has reduced rather than strengthened any suggestion of shape or squamation difference.

The color differences, on the other hand, are very marked. What is the biological significance of such differences in anoles without a functional dewlap? There is no objective evidence. I have reduced baharucoensis to a subspecies and have described dolichocephalus at this level for the following reasons: While color is very important in Anolis and while the importance of pattern and color may be expected to be still more important in forms which lack a functional dewlap, anoles which do differ strongly in color and pattern (and even in structure) may intergrade (e.g. Lazell, 1962). Further, every sibling Anolis species of which I am aware is discovered to show at least average structural differences once the sample is adequate. The apparently contradictory case of A. alter newly described by me (Williams,

1962b) I believe to be an instance of inadequate sample size. The material of the *hendersoni* complex is now quite sufficient to demonstrate average differences, were they in fact present. It is true that the largest males of *dolichocephalus* are slightly but distinctly longer headed than any other members of the complex, but this is quite obviously not the sort of evidence that suggests species status.

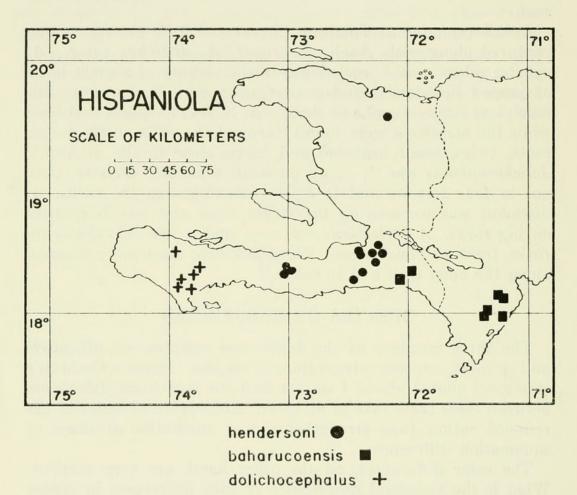


Figure 5. Map of the distribution of the races of A. hendersoni.

ZOOGEOGRAPHY

The two specimens from the Citadelle indicate that much is still to be found out about this group in Hispaniola. Rare as these forms have been in previous collections, they are abundant in some of the most recent. It is therefore impossible to reason on the basis of negative evidence that A. hendersoni is really absent in any part of Hispaniola north of the Cul de Sac — whether in Haiti or in the Dominican Republic.

It is thus too early to discuss the origin or history of the hendersoni complex. It is, however, worth calling attention to the tripartite division within what I have called (1961, 1962a) the "southern island"—Hispaniola south of the Cul de Sac. This singular pattern occurs in several other instances and will be discussed further in later papers of this series.

ACKNOWLEDGMENTS

I am indebted to A. S. Rand and J. D. Lazell, Jr. who first collected the new subspecies of hendersoni described herein and to Luc and George Whiteman of Port-au-Prince, Haiti, who obtained most of the other material reported here. I am grateful also to Dr. Doris M. Cochran and Mr. C. M. Bogert who permitted me to examine material in their charge and to Dr. Albert Schwartz who has allowed me to study material he has very recently collected. A grant from the American Philosophical Society and National Foundation Grant NSF G5634 have supported part of the collecting reported here. Work on these and other Haitian anoles has continued under NSF G16066.

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