STUDIES ON THE FAUNA OF CURAÇAO AND OTHER CARIBBEAN ISLANDS: No. 173

SYSTEMATICS AND EVOLUTION IN THE WEST INDIAN IGUANID GENUS CYCLURA

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Throughout the Greater Antilles, the Virgin Islands, the Cayman Islands, the Bahama Islands, and the Turks and Caicos islands occurs a group of moderate to very large lizards of the iguanid genus Cyclura. These ground iguanas form a conspicuous element of the herpetofaunas of their respective islands. In some areas, the ground iguanas are still very abundant, in others somewhat less so, and in still others they have either become recently extinct or are known only from fossils. Fourteen species are currently recognized, with the largest percentage occurring in the Bahamas Islands. There has been no recent taxonomic treatment of the genus. That of BARBOUR & Noble (1916) was the only systematic study, and these authors were very greatly hampered by far from adequate material of many taxa. They examined a total of 22 specimens and named four species, each on the basis of a single individual. We on the other hand have examined 378 preserved specimens. As might be presumed, the characteristics which BARBOUR & NOBLE employed to distinguish species are not always confirmed when longer series of specimens are studied. Accordingly, diagnoses of species of Cyclura may not easily be made solely on the basis of absolute differences in head scutellation or other scale features - the amount of variation in any series is often so great that we have found it impossible to maintain several currently recognized species on absolute scale differences. Rather, scale modalities have been used in part to diagnose taxa. In addition, color and pattern of both adults and juveniles (especially the latter) reveal relationships which would perhaps be more obscure if these data were not available. Nevertheless, there are many problems remaining within the genus, and we feel that our treatment of the various taxa may well be modified as more material is accumulated. We have adhered to a via media in our taxonomic treatment; we have described no new subspecies (although in some cases there are differences which in other iguanid genera suggest subspeciation) but on the other hand we have maintained all names presently in use (although in some cases the subspecies remain rather poorly defined). We have not hesitated to express our opinions in the soundness of our own interpretations in these cases.

We have been able to examine such a large quantity of specimens only through the cooperation of the curatorial personnel at several museums, both in the United States and abroad. There exist many other specimens of *Cyclura* in American collections which we deliberately did not choose to examine; these specimens are often with imprecise locality or other data and are lizards that died in public or private collections and were later preserved. Much of the material we have examined is in the collection of the senior author (Albert Schwartz Field Series – ASFS); specimens formerly in the collection of the junior author have now been catalogued in the ASFS. Between us, we have seen living examples of all but four taxa which we recognize herein.

We have borrowed specimens from the following collections: American Museum of Natural History (AMNH); British Museum (Natural History) (BMNH); Carnegie Museum (CM); Field Museum of Natural History (FMNH); Museum of Zoology, Louisiana State University (LSUMZ); Museum of Comparative Zoology (MCZ), collection of Richard Thomas (RT); Florida State Museum, University of Florida (UF/FSM); Museum of Zoology, University of Michigan (UMMZ); National Museum of Natural History, Smithsonian Institution (USNM). For the loans of these large lizards, we wish to thank Richard G. Zweifel, George W. Foley, Alice G. C. Grandison, Neil D. Richmond, Clarence J. McCoy, Robert W. Inger, Hymen Marx, Douglas A. Rossman, Richard Thomas, Donald W. Buden, Ernest E. Williams, Walter A. Auffenberg, Charles F. Walker, the late James A. Peters, and George R. Zug. Fossil material from the Department of Vertebrate Paleontology at Harvard University was lent through the courtesy of Farish Jenkins.

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Photographs of type-material in the British Museum (Natural History) and the Muséum National d'Histoire Naturelle have been supplied to us by Miss Grandison and Jean Guibé. John C. Briggs at the University of South Florida arranged for payment of shipping charges between northern collections and Tampa. Bruce R. Sheplan made counts on many specimens on our behalf. We have had access to Recent skeletal material and Kodachrome transparencies of living iguanas in the collection of Lewis D. Ober. We are in the debt of these persons and others, since without their assistance our work would have been more arduous and expensive, and surely less comprehensive.

We wish also to thank those people who were instrumental in the field in securing material for us or who acted as field assistants: Donald W. Buden, Gary A. DARLING, JOHN R. FEICK, DANNY C. FOWLER, WILLIAM A. GEHRMANN, Jr., MICHAEL W. Hucks, Ronald F. Klinikowski, David C. Leber, John K. Lewis, Dennis R. PAULSON, BRUCE R. SHEPLAN, RICHARD THOMAS, PETER J. TOLSON, and C. RHEA WARREN. The illustrations of dorsal and lateral views of Cyclura heads are the work of CHRISTOPHER L. LANE. We salute the endeavors of all these men. Finally, without the capable help of RONALD I. CROMBIE, our literature search would have been virtually impossible.

We are aware of 24 trivial names proposed for members of the genus Cyclura. These are, in the order of their proposals,

cornuta Bonnaterre, 1789 carinata Harlan, 1824 cychlura Cuvier, 1829 nubila Gray, 1831

harlani Duméril & Bibron, 1837 ricordii Duméril & Bibron, 1837

macleayi Gray, 1845

collei Grav, 1845 lophoma Gosse, 1848 baeolopha Cope, 1861

onchiopsis Cope, 1885

nigerrima Cope, 1886

rileyi Steineger, 1903

caymanensis Barbour & Noble, 1916 inornata Barbour & Noble, 1916 nuchalis Barbour & Noble, 1916 steinegeri Barbour & Noble, 1916

pinguis Barbour, 1917 mattea Miller, 1918

portoricensis Barbour, 1919 cristata Schmidt, 1920 figginsi Barbour, 1923

bartschi Cochran, 1931 lewisi Grant, 1940

Of these 24 taxa, two (mattea, portoricensis) are known only from fossil remains, the former from St. Thomas, the latter from Puerto Rico. We have dealt very little with these two fossil forms, although we have examined the extant material associated with these two names.

Of the living (or very recently extinct) forms, the above listed trivial names have been proposed in association with several genera: Lacterta (cornuta), Cyclura (carinata), Iguana (cychlura), and Aloponotus (ricordii). In addition, the generic names Metapoceros Wagler, 1830, and Hypsilophus Fitzinger, 1843, have been used for members of the genus. No one recently has seriously questioned the placement of all the Antillean ground iguanas in a single genus, Cyclura. Yet among them, at least C. ricordi and C. pinguis stand apart externally, both from each other and the balance of the species. Avery & Tanner (1971), in their discussion of the anatomy and presumed history of the iguanine genera (including Cyclura) did not divide the genus; on the other hand they examined specimens of the taxa carinata, cornuta, macleayi, and nuchalis only, and all of these may with propriety be grouped together as rather "typical" ground iguanas. Perhaps their conclusions as to the integrity of the genus Cyclura might have been somewhat changed had they studied specimens of C. ricordi or C. pinguis.

METHODOLOGY

BARBOUR & NOBLE (1916) used a complex of relationships of the head scales to each other as partially diagnostic for the species that they recognized. We have utilized their characters and in addition have proposed others in an effort to determine scutellar differences between the various populations of Cyclura. Some populations are extremely distinct (at the species level), but we are less able to differentiate many other taxa, even at the subspecific level, despite (or perhaps because of) far more material than was available to earlier workers. There is additionally the problem of the two fossil forms, mattea and portoricensis. The only extant Cyclura from Greater Puerto Rico is C. pinguis on remote Anegada Island, the northeasternmost of the Virgin Islands. C. pinguis is a very distinctive lizard. Considering the cohesive relationships between the faunas of the Virgin Islands and Puerto Rico, it would not seem unreasonable to consider the three Greater Puerto Rican taxa (mattea, portoricensis, pinguis) conspecific.

We have taken the following data in our analysis of variation in *Cyclura*. Most characters are self-explanatory, but in those which may lead to confusion we have defined the terms and the method of taking data.

1) Sex. Determined from extruded hemipenes or dissection of the proximal portion of the tail. – Mature males of most species are readily recognized by the generally "jowly" appearance of the head, due to the enlarged and bulky masseters, and the better developed longitudinal fold of skin at the throat. (We deliberately avoid the use of the word "dewlap" for this longitudinal gular fold; although

the former is more concise, it has connotations within the genus *Anolis* which do not apply in *Cyclura*.)

- 2) Snout-vent length in millimeters.
- 3) Tail length in millimeters.
- 4) Head length, from tip of snout to anterior margin of auricular opening, in millimeters.
 - 5) Head width, just behind the eyes, in millimeters.
- 6) Number of scale rows between the prefrontal shields and the frontal scale.
- 7) Number of scale rows between the frontal scale and the interparietal scale.
- 8) Number of azygous scales in the suture between the paired prefrontals.
 - 9) Number of scales between the anteriormost canthal scales.
 - 10) Number of scales bordering the frontal scale.
 - 11) Number of scales bordering the interparietal scale.
 - 12) Whether the first prefrontal is in contact with the precanthal.
- 13) Number of rows of scales between the supraorbital semicircles and the interparietal scale.
 - 14) Number of vertical rows of loreal scales.
 - 15) Number of lorilabial rows, counted vertically, below eye.
 - 16) Number of supralabials to center of eye.
 - 17) Number of superciliary scales.
 - 18) Number of subocular scales to the auricular opening.
 - 19) Number of infralabials to center of eye.
 - 20) Number of sublabials to center of eye.
- 21) Number of rows of scales between the infralabials and the sublabials.
 - 22) Number of postmental scales.
- 23) Total number of femoral pores, counted separately on each hindlimb.
 - 24) Number of fourth toe subdigital scales.
 - 25) Number of subdigital scales distal to comb, on second toe.
 - 26) Number of subdigital scales between combs, on third toe.
- 27) Number of enlarged dorsal crest scales between occiput and shoulder.

- 28) Number of enlarged dorsal crest scales between shoulder and sacrum.
- 29) Number of enlarged dorsal crest scales between sacrum and first caudal verticil.
- 30) Are the occiput-shoulder crest scales higher than the shoulder-sacrum crest scales?
- 31) Are the shoulder-sacrum crest scales higher than the post-sacral crest scales?
- 32) Total number of dorsal crest scales between occiput and first caudal verticil.
 - 33) Number of scales in fifth caudal verticil around tail.
 - 34) Number of middorsal scales in fifth caudal verticil.
- 35) Number of dorsolateral scales in nostril to eye distance, taken by laying off the nostril-eye distance by calipers on the upper side and counting longitudinally.
 - 36) Number of scale rows between rostral scale and nasal scale.
 - 37) Number of scale rows between prefrontal scales.
 - 38) Number of scales composing comb on third toe.
 - 39) Number of scales between nasal scales.

Several of these counts, because of the very limited variation, were not utilized in our final analysis; we have, rather, emphasized those relationships and scale counts which have maximal variability between populations and have discarded counts which add little or nothing to the variation within and between species.

Cyclura Harlan, 1824

Cyclura Harlan, 1824. J. Ac. Nat. Sci. Phila. 4: 242, 250. Type-species - Cyclura carinata.

Metapoceros Wagler, 1830. Natür. Syst. Amph., p. 147. Type-species - Cyclura cornuta.

Aloponotus Duméril & Bibron, 1837. Erp. gén. 4: 190. Type-species - Cyclura ricordii.

Definition. – A genus of iguanid lizards which are moderate to large (maximum 745 in males, 623 in females) in snout-vent length, tail slightly shorter to slightly longer than snout-vent length (modally tail and snout-vent length about equal); usually a median se-

ries of enlarged dorsal crest scales, interrupted at the shoulders and at the sacrum; tail usually strongly verticillate, the verticils made more obvious in some species be very large and spinose scales, in others these scales less weakly differentiated or even virtually indistinguishable from other caudal scales; from 2 to 9 scale rows between the prefrontal shields and the frontal scale but these scale rows absent in three species; 3 to 15 scale rows between the frontal scale and the interparietal scale but these rows absent in three species; azygous scales present (two species) or absent (six species) in the prefrontal suture; 3 to 17 scales between the anteriormost canthal scales (not applicable in one species); 3 to 29 scales bordering the frontal (not applicable in three species); 6 to 19 scales bordering the interparietal scale (not applicable in one species); first prefrontal in contact with the first precanthal in one species, rarely so in one species, never in all other species; 1 to 6 scale rows between the supraorbital semicircles and the interparietal (not applicable in one species); loreal rows usually well defined and varying between 3 and 13; lorilabial rows 1 to 8 (not applicable in two species); 5 to 11 supralabial scales to eye center; 7 to 17 superciliary scales; 9 to 20 subocular scales to tympanum; 5 to 10 infralabials to eye center; 0 to 6 rows of scales between infralabials and sublabials (not applicable in one species); 1 to 6 postmental scales; femoral pores usually in 1 row, interrupted medially, but occasionally in 2 or 3 rows, varying between 26 and 80, the high counts from that species (C. cornuta) with double or triple rows of pores, but femoral pores of variable occurrence and even absent in one species (C. collei); fourth toe subdigital scales 27 to 45; subdigital scales to comb on second toe 11 to 19 (not applicable in three species); 1 to 5 scales between combs on third toe (not applicable in three species); 33 to 93 scales around tail in fifth caudal verticil, 2 to 7 middorsal scales in fifth caudal verticil; 6 to 44 dorsolateral body scales in naris-eve distance; medial dorsal crest scales variable in expression and relative heights on three regions (neck-body-tail), total number of median crest scales varying between 51 and 123, but the tail (= postsacral) portion of the series much reduced and uncountable in two populations (= subspecies); sclera of eyes red (except in C. cornuta).

Cyclura nubila Gray, 1831

- Iguana (Cyclura) Nubila Gray, 1831. In Griffith's Animal Kingdom, p. 39. Holotype – BMNH 1946.8.29.88.
- Cyclura harlani Duméril & Bibron, 1837 (partim). Erp. gén. 4: 218. Syntypes MNHN (Muséum National d'Histoire Naturelle) A661, MNHN 2367; 2367; MNHN A661 herein selected as lectotype. Type-locality "Caroline."
- Cyclura Macleayi Gray, 1845. Cat. lizards Brit. Mus., p. 190. Holotype BMNH 1946.8.4.28. Type-locality Cuba.
- Cyclura caymanensis Barbour & Noble, 1916. Bull. Mus. Comp. Zool. 60: 148. Holotype - MCZ 10534. Type-locality - probably Cayman Brac, Cayman Islands
- Cyclura macleayi lewisi Grant, 1941. Herp. Cayman Is., p. 35. Holotype BMNH 1939.2.3.68. Type-locality Battle Hill, east end of Grand Cayman, Cayman Islands.

Type-locality. "South America?" Here restricted to Cuba.

DEFINITION. - A species of Cyclura characterized by the combination of very large size (males to 745, females to 623 snout-vent length), 3 to 8 (modally 5) scale rows between the frontal and interparietal scales, azygous scales usually present (modally 3) in the prefrontal suture, 4 to 11 (modally 6) scales between the anterior canthal scales, 6 to 16 (modally 10) scales bordering the frontal, first prefrontal rarely in contact with precanthal, 4 to 13 (modally 5 and 7) vertical rows of loreals, 10 to 16 (modally 13) suboculars to anterior border of tympanum, 5 to 14 (modally 8) sublabials to eye center, 2 to 6 (modally 3) rows of scales between infralabials and sublabials (Fig. 7), 1 to 6 (modally 3) postmentals, 33 to 50 femoral pores in a single row, dorsal crest scales 9 to 22 between occiput and shoulder, 20 to 53 ($\bar{x} = 40.2 + 1.2 - twice standard$ error of mean) between shoulder and sacrum, 6 to 24 between sacrum and first caudal verticil, total dorsal crest scales between occiput and first caudal verticil 52 to 85 ($\bar{x} = 69.2 + 1.5$), dorsal crest scales on neck always higher than body crest scales, body crest scales usually higher than postsacral crest scales, 35 to 93 scales around tail in fifth caudal verticil, 14 to 31 dorsolateral body scales in naris-eye distance, rostral scale always in contact with nasals. Adults variable (in part by population) in coloration, the body dark grayish to blackish and patternless or virtually so, with dense pale buffy flecking to give a more or less dark-and-pale stippled effect, head either generally buffy to tan or bright blue to greenish, in one population the body with a greenish wash in some individuals, and at times with remnants of the dark fuvenile pattern greatly obscured and persisting as a series of vague dark diagonal lateral bars; juvenile pattern strongly chevronate with about five to 10 pale chevrons, their apices pointed anteriorly, which break up laterally into buffy ocelli or a series of ovate fragments, all black-bordered, the chevron interspaces stippled with black, the middorsal portion of each pale chevron expanded to give a series of middorsal subrectangular or subcircular pale blotches, the dark chevron borders persisting onto the venter to the midline either as entire dark lines or as series of more or less circular or ovate black-bordered pale spots. Tail in adults tan, in juveniles streaked with black and grays or vaguely ringed, the rings not corresponding to the caudal verticils. Scale count variation in Tables 3–5.

DISTRIBUTION. — Cuba and the Isla de Pinos, including the Archipiélago de los Canarreos, the Jardines de la Reina, and the Archipiélago de Sabana-Camagüey, and presumably many more off-shore cays and islets; also the Cayman Islands (Grand Cayman, Little Cayman, Cayman Brac); introduced on Isla Magueyes off the southwestern coast of Puerto Rico.

Cyclura nubila nubila Gray

DEFINITION. – A subspecies of *C. nubila* reaching very large size (males to 745, females to 623 snout-vent length), modally 3 scales between the prefrontal shields and the frontal scale, modally 5 scale rows between the frontal and the interparietal, modally 6 scales between the anteriormost canthals, first prefrontal rarely in contact with precanthal, vertical loreal rows modally 5, supralabials to eye center modally 7, superciliary scales 9 to 15, subocular scales 10 to 16, total dorsal crest scales (occiput to first caudal verticil) 52–85, modally 5 scales middorsally in fifth caudal verticil, and dorsolateral scales in naris-eye distance 14 to 31. Adults dark gray to black dorsally, much dotted or stippled with buffy to tan; head and tail buffy to tan, the sides at times with vague diagonal remnants of the dark chevronate juvenile pattern; head never blue or

orange. Juveniles strongly chevronate black and pale with between 5 and 10 pale chevrons, their apices directed anteriorly, which break up into lateral series of pale locelli or ovate fragments, all black-bordered, the dark pattern extending to the ventral midline as a series of diagonal dark lines; interspaces between pale chevrons stippled or marbled with black; throat blotched with various shades of gray, tail longitudinally streaked with black and gray or vaguely ringed, the rings not corresponding to the caudal verticils; upper surface of hindlimbs dark with scattered pale circular ocelli, this condition persisting into adults of some local populations.

DISTRIBUTION. - Cuba and the Isla de Pinos, including the Archipiélago de los Canarreos, the Jardines de la Reina, and the Archipiélago de Sabana-Camagüey, and presumably many other off-shore cays and islets.

VARIATION. – The largest male (ASFS 7841) has a snout-vent length of 745, the largest female (ASFS 7477) 623; unfortunately, these two specimens are no longer available and the measurements recorded were taken in the field. There is little reason to doubt their accuracy, however, since we have examined other individuals of *C. n. nubila* which approach these in size. The smallest specimen (CM 702) has a snout-vent length of 110. The longest head in males measures 110.9 (AMNH 78187) and in females 86.1 (AMNH 81400); maximum head breadth in males is 58.7 (AMNH 78183) and in females 44.2 (AMNH 81400).

For convenience of discussion, we have divided the series of C. n. nubila into three sections: 1) the sample primarily from the Península de Guanahacabibes in extreme western Pinar del Río Province (including one other specimen from this province), 2) the sample from the balance of Cuba, between Habana and Oriente provinces, and 3) the sample from the Isla de Pinos. These samples comprise 18, 14, and 22 specimens, respectively. Modalities in various scale counts vary among the samples. For example, the Pinar del Río and Isla de Pinos samples modally have 5 scale rows between the frontal and the interparietal, the general Cuban sample 6. Although one might generalize that the Pinar del Río and Isla de Pinos samples are similar in modalities in many counts (and this is expected since the Isla de Pinos is close to extreme western Cuba),

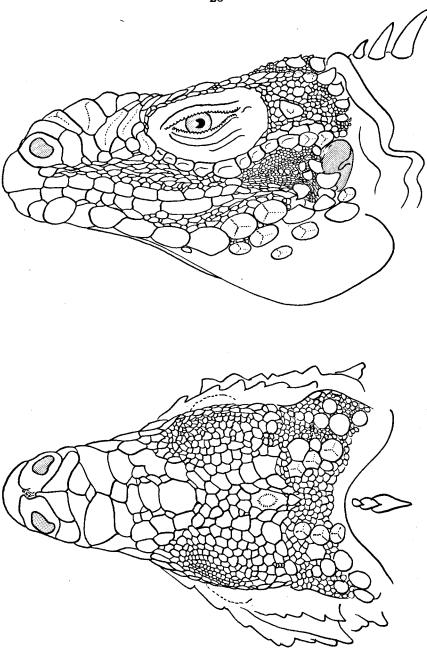


Fig. 7. Lateral and dorsal view of the head of Cyclura nubila (AMNH 81399); the subspecies is C. n. nubila from Cayo Matías, Archipiélago de los Canarreos, Habana Province, CUBA; snout-vent length unrecorded; male.

still there are exceptions to this generalization. However, in no count do the Isla de Pinos lizards differ consistently and strikingly from their Cuban relatives.

The most intriguing variation in relationships of head scales in C. n. nubila is that involved with contact between the first prefrontal and the precanthal. These two scales do not touch as a strong modality in C. nubila, and this is true bilaterally of all specimens examined from Habana-Oriente and the Isla de Pinos. It is in the Pinar del Río sample that there is a high number of contacts. In 10 lizards, the contact is unilateral, and in four lizards bilateral. Counting each side separately, there are thus 18 series (= sides) with contact and 18 series without contact. In the two remaining subspecies of C. nubila, contact between the first prefrontal and precanthal occurs very rarely (one unilateral contact in C. n. caymanensis, one unilateral contact in C. n. lewisi). No other single feature of scutellation or coloration and pattern seems to distinguish these Pinar del Río lizards. Were the percentage of lizards with contact between these two scales higher or more consistent or bilateral, we would be prone to distinguish them nomenclatorially. However, we feel that they represent a local deme or demes which have slightly different head scutellation in contrast to the rest of both the species and subspecies.

In general, C. n. nubila is a gray lizard, much stippled or mottled with tan, a tan head and tail, and with adults having indications of the contrasting juvenile pattern (although old or large adults lack any indications of this pattern whatsoever). In some adults, the sides are greenish, and the light stippling or mottling in creamyellow rather than tan. There is never any striking blue coloration. The juvenile pattern, which is exceptionally contrasting and bold, is composed of a series of five to 10 pale chevrons which are expanded middorsally to give a longitudinal series of subcircular or subrectangular pale blotches. These pale chevrons break up laterally into diagonal series of ocelli or pale longitudinal fragments, bordered with black, which extend onto the venter. Between these pale dorsal chevrons are black chevrons which form the margins of the lateral pale pattern. The tail is streaked with grays and black, and the pattern is not oriented to the verticils as a series of rings.

The hindlimbs are dark with clearly marked and well separated circular pale (tan) ocelli; this condition persists into some adults, most especially those from the Isla de Pinos. In most adults, however, the ocelli become increasingly obscure and the hindlimbs become grayish or blackish, irregularly mottled or stippled with tan.

In adults, a conspicuous feature is the very high dorsal crest scales. Usually the nuchal crest scales are very high, higher than those on the body. The height of the body crest scales is variable in their relationship to the postsacral crest scales, and it is not unusual to have the postsacral crest scales even higher and more stout than those on the body. However, the body crest scales are more often slightly lower than the postsacral crest scales.

REMARKS. - Our use of nubila Gray rather than macleayi Gray for the Cuban iguana and its subspecies is due to our examination of the holotype of the former name. BARBOUR & NOBLE (1916: 143) dismissed the name nubila by saying that it is "based upon a young specimen without locality" and that the "description given by Gray is worthless," Both statements are true. But despite its small size (snout-vent length 135) the specimen shows the typical head-scale configuration of Cuban and Caymanian Cyclura, including the lack of contact between the first prefrontal and the precanthal and the presence of azygous scales between the two pairs of transversely much enlarged prefrontals. Another possibility is that the specimen is from the Bahama Islands, but the population there (to which we apply the name cychlura Cuvier) characteristically has the first prefrontal and precanthal in contact (four exceptions unilaterally in 85 specimens). We obviously have no doubt that nubila is the appropriate name for the Cuban and Caymanian Cyclura.

The situation with *harlani* Duméril & Bibron is slightly more complex. This name is based upon two syntypes, one of which is a preserved adult (MNHN 2367) and the other a poorly mounted specimen (MNHN A661). The preserved specimen, of which we have examined photographs, shows the head scutellation typical of the Bahamian *Cyclura*, whereas the photograph of the mounted lizard, although in fairly poor condition, can be associated with the Cuban specimens. Since MNHN 2367 is unquestionably Bahamian in ori-

gin, we have selected MNHN A661 as the lectotype of harlani. But the situation of the names is even more complex, in that MNHN 2367 is also the holotype of Iguana cychlura Cuvier, and this is the prior name applicable to those Bahamian lizards which have been previously associated with the names baeolopha, figginsi, and inornata. Accordingly, this complex of Bahamian taxa we regard as subspecies of C. cychlura, which name replaces baeolopha Cope.

C. n. nubila is moderately abundant in Cuba and on the Isla de Pinos, as well as upon many archipelagos of islets, islands and cays which surround the two major islands. Although primarily a denizen of xeric and rocky situations (beaches with a backing of diente de perro limestone are preferred habitats which support large populations), individuals occasionally are encountered in more mesic (but nonetheless rocky) situations, as near San Vicente in Pinar del Río Province. Large adults are abundant upon the grounds of the United States Naval Base at Guantanamo Bay and form an attractive adjunct for visitors there. C. n. nubila has also been successfully introduced on Isla Magueyes off the southwestern coast of Puerto Rico.

SPECIMENS EXAMINED. - Cuba, Pinar del Río Province, northeast coast, Ensenada de Corrientes (AMNH 78179-92); north shore, Ensenada de Corrientes, 45 km W Cayuco (AMNH 82939-41); 4.5 km W San Vicente (AMNH 78193); Habana Province,



Fig. 8. Cuba and Isla de Pinos; solid circles indicates localities from which specimens of *Cyclura nubila nubila* have been examined. In this and all other maps, we have indicated only those localities from which we have examined material, despite published or verbal records from other sites; see text and Schwartz & Thomas, 1975 (Carn. Mus. N.H. Spec. Publ. 1, 216 pp.) for further details of distribution.

3.2 km E Boca de Jaruco (AMNH 82942, AMNH 81392-94); Matanzas Province, Punta Hicacos (AMNH 96043); Las Villas Province, Punta Casilda, nr. Trinidad (AMNH 78194); Cayo Bahía de Cádiz, Archipiélago de Sabana-Camagüey (AMNH 81397); Camagüey Province, Cayo Cachiboca, at lighthouse (AMNH 78195); large key, 3 km NW Cayo Cachiboca lighthouse, on southernmost point (AMNH 78196-98); Oriente Province, Cabo Cruz (ASFS 7388); Aguadores (ASFS 7477); 27 km E Siboney (ASFS 7851); 13.8 km E Imías (ASFS 8477-78); U.S. Naval Base, Guantánamo Bay, west side, Girl Scout Camp (ASFS V15049, ASFS V16324); U.S. Naval Base, Guantánamo Bay, east side, Windmill Beach (ASFS V16353). - Isla de Pinos, Playa de Rocas, between Bibijagua and Júcaro (AMNH 81395); Playa de Herradura, just N Bibijagua (AMNH 81396); Punta del Este (AMNH 81398); no locality other than "Isla de Pinos" (CM 698-703, CM 989-990, CM 42534-37); Cayo Matías (AMNH 81399 - 2 specimens); Cayo Hicacos (AMNH 81400 - 2 specimens); Cayo Avalos (AMNH 82936); key just off NW tip of Cayo Largo (AMNH 82937-38); no locality other than "South America?" (BMNH 1946.8.29.88 - holotype of Cyclura nubila). - Puerto Rico, Isla Magueyes (ASFS V26926).

Cyclura nubila caymanensis Barbour & Noble

Definition. - A subspecies of C. nubila reaching moderate size (males to 483, females to 405 snout-vent length), modally 4 scales between the prefrontal shields and the frontal scale, modally 5 scale rows between the frontal and the interparietal, modally 10 scales between the anteriormost canthals, first prefrontal very rarely in contact with precanthal, vertical loreal rows modally 8, supralabials to eye center modally 8, superciliary scales 11 to 14, subocular scales 12 to 16, total dorsal crest scales 64 to 82, and dorsolateral scales in naris-eye distance 20-29. Adults dorsally combinations of tan and gray (or black) mottling or stippling, with diagonal dark bars on sides indicated, hindlimbs ocellate creamy to light greenish; no blue or orange on head. Juveniles with 5 to 10 pale chevrons which break up laterally into ocelli or fragments, all black-bordered, this ocellate pattern extending onto the venter as far as the midline; interspaces pale and without so much dark interchevron pigment as in juvenile C. n. nubila, the general aspect being paler gray and without a strongly contrasting pattern; venter occasionally without ocellate pattern and, rather, longitudinally streaked with grays.

DISTRIBUTION. - Cayman Brac and Little Cayman, Cayman Islands; recently introduced on Grand Cayman (see beyond).

Variation. – The largest male (ASFS V16974) has a snout-vent length of 483 and is from Little Cayman; the largest female (ASFS V26915) has a snout-vent length of 405 and is also from Little Cayman; maximally sized individuals from Cayman Brac (from which more specimens have been examined) are 460 and 390 respectively. The smallest juveniles (ASFS V16892–93) are from Little Cayman and have snout-vent lengths of 97. The longest head in males measures 102.3 (ASFS V26919) and in females 76.7 (ASFS V26916); maximum head breadth in males is 46.9 (ASFS 17046) and in females 42.1 (ASFS V26916).

Comparing scale counts of 12 lizards from Cayman Brac and seven from Little Cayman, the counts and relationships of the head scales are similar. In some counts, however, there are different modalities. For instance, Cayman Brac lizards modally have 4 scale rows between the frontal and interparietal, Little Cayman lizards modally have 5. The number of scales between the anterior canthals is modally 10 on Cayman Brac and modally 6 and 8 on Little Cayman; the means of these counts are 8.9 on Cayman Brac and 7.7 on Little Cayman. A strongly modal difference is in the number of rows of scales between the supraorbital semicircles and the interparietal, where the mode is 1 on Cayman Brac and 2 on Little Cayman, Lorilabial rows are modally 3 on Cayman Brac, 4 on Little Cayman. Infralabials to eye center are modally 8 on Cayman Brac, 7 on Little Cayman, whereas sublabials to eye center are modally 8 on Cayman Brac and 7 on Little Cayman. In counts of femoral pores, fourth toe subdigital scales, partial and total dorsal crest scales, the two populations are very comparable in both means and extremes.

In color, adult *C. n. caymanensis* are mottled or marbled tans and grays without either greenish or blue tints. Black diagonal lateral juvenile bars are often indicated in adults, and if there are remnants of the pale middorsal areas of juveniles, they are shown as pale series of dorsal crest scales on the body. The hindlimbs are ocellate, the ocelli creamy to light greenish. The throat may be rusty, and the belly is gray, with the underside of the tail buffy. Specimens from Little Cayman did not differ in life in color or pattern from Cayman Brac material. The juveniles have 5 to 10 pale

chevrons which are expanded middorsally to give a middorsal series of pale subcircular or subrectangular blotches. The dark chevrons which alternate with the pale chevrons are solid and more broad than in *C. n. nubila*, and the hindlimbs are usually less clearly ocellate, being rather marbled or mottled. The tail is banded rather than streaked. The dark dorsal chevrons extend into the venter as series of hollow isolated dark blotches, but one juvenile lacks this feature and the venter is longitudinally streaked with darker grays.

COMPARISONS. - In scutellation, C. n. nubila differs from C. n. caymanensis in the following modalities (in each case, the modality for nubila is listed before that of caymanensis): scale rows between prefrontal shields and frontal scale (3, 4); azygous scales in prefrontal suture (3, 2); scales between anterior canthals (6, 10); vertical loreal rows (5, 8); lorilabial rows (2, 3); supralabials to eye center (7, 8); superciliaries (10, 12 and 13); suboculars to tympanum (13, 14); sublabials to eye center (8, 7); scale rows between infralabials and sublabials (4, 3); postmentals (3, 2). Postsacral crest scales are more in caymanensis (13 to 23) than in nubila (6-22). Although there in considerable overlap of total dorsal crest scales between nubila (52-85) and caymanensis (64-82), means for the three segments of C. n. nubila (63.2, 69.2, 68.3) are lower than those for the two populations of C. n. caymanensis (72.5, 73.5). The same is true of dorsolateral body scales in naris-eye distance; the range of this count in C. n. nubila is 14 to 31 (means of three samples 18.6, 20.0, and 19.0), whereas in C. n. caymanensis the range is 20 to 29 (means 23.0 and 26.3).

The much larger size of *C. n. nubila* is readily apparent when compared with *C. n. caymanensis*. Adults of the two subspecies are comparable in coloration and pattern, both with basically variegated patterns of grays or black and tans, with vestiges of the juvenile contrasting pattern at times evident. Some *C. n. nubila* have a greenish wash, a condition not observed in *C. n. caymanensis*. Juveniles of the two subspecies are similar, but young *caymanensis* are much paler and much less contrastingly patterned than those of *nubila*. In addition, the hollow dark-bordered ovals which are the

ventral extensions of the pale dorsolateral chevrons are absent in young C. n. nubila and are a regular feature of young C. n. caymanensis.

The nuchal crest scales are regularly higher than the body crest scales, and the body crest scales are regularly higher than the post-sacral crest scales in *C. n. caymanensis*. This same condition is generally true in *C. n. nubila*, but the details are more variable.

REMARKS. – C. n. caymanensis is abundant on both Little Cayman and Cayman Brac. Like its Cuban relative, caymanensis inhabits areas of sandy substrate with rocks or adjacent cliffs to offer retreat and sanctuary. The interior raised platform with its steep and eroded margins on Cayman Brac offers ideal opportunities for ground iguanas, but individuals were encountered away from this optimum habitat in piles of lumber and building materials and even within a partially completed cottage on Little Cayman.

C. n. caymanensis has been recently introduced on western Grand Cayman; since C. n. lewisi, the resident Grand Cayman subspecies, appears to be absent or very rare in this area, no competition between the two subspecies is likely. However, we regard with some scepticism the movement by man of individuals of one subspecies into the range of another, most especially when the resident subspecies is extremely localized and uncommon.

SPECIMENS EXAMINED. — Cayman Islands, Cayman Brac, West End, north shore (ASFS 16729); 9.6 km NE West End (ASFS V16730); West End (ASFS V16992–94); The Creek, 12.8 km NE West End (ASFS 16966–67); 1.6 km NE West End (ASFS 17046); no other locality (ASFS V26924–25, ASFS V26917, ASFS V26919). — Little Cayman, Blossom Point (ASFS 16892–94, ASFS 16974); no other locality (UF/FSM 21736, ASFS V26915–16).

Cyclura nubila lewisi Grant

DEFINITION. – A subspecies of *C. nubila* reaching large size (males to 515, females to 410 snout-vent length), modally 4 scales between the prefrontal shields and the frontal scale, modally 4 scales between the frontal and interparietal, modally 5 scales between the anteriormost canthals, first prefrontal very rarely in contact with

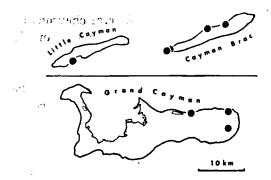


Fig. 9. Little Cayman and Cayman Brac, showing localities for Cyclura nubila caymanensis. Grand Cayman, showing localities for C. n. lewisi. Note that C. n. caymanensis has been introduced on the western portion of Grand Cayman.

precanthal, vertical loreal rows modally 7 and 8, supralabials to eye center modally 8, superciliary scales 11 to 17, subocular scales 14 to 16, total dorsal crest scales 72 to 80, modally 4 scales middorsally in fifth caudal verticil, and dorsolateral scales in nariseye distance 16 to 23. Adults dorsally bluish gray to bright blue anteriorly, black posteriorly; head bright blue in males to pale greenish in females; subadults (no small juveniles known) grayish with darker areas forming chevrons, head blue-green, alternating with a series of six to eight buff-colored black-bordered vertebral spots (= pale chevron remnants); hindlimbs ocellate dorsally.

DISTRIBUTION. - Grand Cayman, Cayman Islands.

Variation. – The largest male (ASFS 17111) has a snout-vent length of 515, the largest female (UF/FSM 20526) 410. The smallest specimen (LSUMZ 22150) has a snout-vent length of 171. The largest head in males measures 123.8 (ASFS V26914) and in females 88.3 (UF/FSM 20526); maximum head breadth in males is 56.4 (ASFS V26914) and in females 44.6 (UF/FSM 20526).

In scutellation, C. n. lewisi differs in the modes of several counts from the subspecies nubila and caymanensis; in the following comparisions, the mode of lewisi is listed first, followed by those of caymanensis and nubila. C. n. lewisi has modally less azygous

scales in the prefrontal suture (1, 2, 3) than do the other subspecies; number of scales between the anterior canthals are modally fewer (5, 10, 6), with a striking difference between lewisi and geographically adjacent caymanensis. C. n. lewisi modally has 9 scales bordering the frontal (10 in both nubila and caymanensis), and the first prefrontal is rarely in contact with the precanthal (one of 10 sides). In lewisi, there are modally 2 rows of scales between the supraorbital semicircles and the interparietal, whereas the modes are 1 in both nubila and caymanensis. Note, however, that on Little Cayman (which is that island closest to Grand Cayman) there also is a strong local mode of 2 in caymanensis. Like caymanensis, lewisi has a mode of 7 or 8 in vertical loreal rows, in contrast to 5 in nubila. Lorilabial rows are modally lower in lewisi (1, 3, 2). Number of superciliaries in lewisi is modally high (15, 12 and 13, 10). Like caymanensis, lewisi modally has 3 rows of scales between the infralabials and the sublabials, in contrast to 4 in nubila. C. n. lewisi modally has 3 or 4 postmentals (with one even higher count of 6), whereas the modes are 2 in caymanensis and 3 in nubila; only four other specimens of C. nubila have counts about 3, whereas half of the *lewisi* have counts above 3 postmentals. C. n. lewisi resembles C. n. caymanensis in the relative heights of the three segments of the dorsal crest scales, and in total number of dorsal crest scales, lewisi has a higher mean (75.0) than do either nubila (63.2, 69.2, 68.3 in three samples) or caymanensis (72.5 and 73.5 in two samples), although it is approached closely by adjacent caymanensis. The low mean of scales around the tail in the fifth caudal verticil in lewisi (49.5) stands in contrast to this mean in caymanensis (58.1, 53.2 in two samples) and nubila (58.3, 52.0, 52.8 in three samples). Indeed, the extremes in the three subspecies in this count show that lewisi (35-57) has markedly less scales than either caymanensis (46-67) or nubila (38-93). Like caymanensis, lewisi has modally 4 middorsal scales in the fifth caudal verticil, in contrast to 5 in nubila. Finally, dorsolateral scales in naris-eye distance are less (16-23; $\bar{x} = 20.2$) in lewisi than in caymanensis (20-29; $\bar{x} = 23.0$ and 26.3 in two samples); on the other hand, the dorsolateral scales are of comparable size in nubila (14-31; $\bar{x} = 18.6, 20.0, 19.0 \text{ in three samples}$.

Surely the most distinctive feature of C. n. lewisi is the bright blue color in adults of both sexes. One's impression of adults, most especially adult males, is that they are basically blue lizards. Field notes on an adult female (ASFS 17092) state that the head is pale greenish, the body anteriorly bright blue, lighter along the middorsal area, the posterior half black, the jowls and chin pale blue. The blue color of the jowls continues onto the throat and chest. A mature male (ASFS 17111) was even more brightly and uniformly blue than the female described above. Color notes taken by DONALD W. BUDEN on LSUMZ 22150, the smallest specimen of this subspecies known to us, are: "dorsum predominantly gray, dark areas forming a series of chevrons; head blue-green; a series of buffcolored black-bordered vertebral spots [which are the remnants of pale chevrons typical of the species and are in this specimen eight in number] extending from the neck to form light brown bands on the distal hald of the tail. Venter grayish mottled black and white, 'dewlap' pale yellow-green, mottled gold; iris yellow, 'white' of eye orange." Another young specimen (LSUMZ 22151) of about the same size (the head is damaged and no accurate snout-vent length can be taken) has the remnants of six pale dorsal chevrons. In both specimens the hindlimbs are ocellate. Although there are no really small juvenile C. n. lewisi in collections, the pattern remnants on these two small individuals are quite similar to those of comparably sized nubila and caymanensis. It should also be noted that even in young individuals, there is already indication of the bright coloration of the adults.

Neither of the Caymanian subspecies of *C. nubila* appears to reach the very large size of the nominate subspecies. Although one's impression of *lewisi* males is that they are larger and more bulky than are male *caymanensis*, the two subspecies differ very little in snout-vent length in both sexes.

REMARKS. - Peculiarly, C. n. lewisi appears to be rare on Grand Cayman. Most specimens were taken at or near the type-locality, an area of sandy and rocky scrub, ideal for these large lizards. However, D. W. Buden secured a single young individual at Old Man Bay, a locality at about mid-length of Grand Cayman from

east to west. It seems certain that the species should be looked for in areas other than the extreme eastern end of the island, since suitable habitats occur elsewhere.

SPECIMENS EXAMINED. - Cayman Islands, Grand Cayman, Battle Hill (ASFS 17092, ASFS 17111, ASFS V26914, LSUMZ 22151); 4.8 km NW East End (UF/FSM 20526); Old Man Bay (LSUMZ 22150).

Cyclura cychlura Cuvier, 1829

Iguana cychlura Cuvier, 1829. Règne animal 2: 45. Holotype – MNHN 2367.
 Cyclura baeolopha Cope, 1861. Proc. Ac. Nat. Sci. Phila. 13: 123. Holotype – Acad. Nat. Sci. Philadelphia 8120. Type-locality – Andros Island, Bahama Islands.
 Cyclura inornata Barbour & Noble, 1916. Bull. Mus. Comp. Zool. 60: 151. Holotype – MCZ 11062. Type-locality – U Cay of Allan's Harbour, near Highborn Cay, Bahama Islands.

Cyclura figginsi Barbour, 1923. Proc. New England Zool. Club 8: 108. Holotype – MCZ 17745. Type-locality – Bitter Guana Cay, near Great Exuma Cay, Exuma Cays, Bahama Islands.

Type-locality, "Caroline." Here restricted to Andros Island, Bahama Islands.

Definition. – A species of *Cyclura* characterized by the combination of large size (males to 411, females to 4651) snout-vent length), 2 to 4 (modally 5) scale rows between the frontal and interparietal scales, azygous scales often present (modally 1) in the prefrontal suture, 3 to 7 (modally 4) scales between anterior canthal scales, 6 to 12 (modally 8) scales bordering the frontal, first prefrontal almost always in contact with precanthal, 4 to 9 (modally 6) vertical rows of loreals, 9 to 17 (modally 16) suboculars to anterior border of tympanum, 5 to 9 (modally 7) sublabials to eye center, 1 or 2 (modally 2) rows of scales between infralabials and sublabials, 1 to 4 (modally 1) postmentals (Fig. 10), 33 to 48

¹⁾ In this and a few other cases, our recorded maximum snout-vent lengths for females exceed those given for males. We regard this anomalous situation as a sample artifact. For instance, in the case of *C. c. inornata*, the junior author handled in the field but did not retain or preserve a male with a snout-vent length of 410 mm, in excess of all specimens later examined by us. Thus, all "maximum" snout-vent lengths are to be treated with some mistrust; still, we feel that all taxa of *Cyclura* are obviously not identical in size and there are species or subspecies which are larger or smaller than others.

femoral pores in a single row, dorsal crest scales 13 to 30 between occiput and shoulder, 37 to 83 ($\bar{x} = 62.1 \pm 1.7$) between shoulder and sacrum, 10 to 22 between sacrum and first caudal verticil, total dorsal crest scales between occiput and first caudal verticil 67 to 118 ($\bar{x} = 96.4 + 2.0$), dorsal crest scales on neck always higher than body crest scales, body crest scales usually higher than postsacral crest scales, 40 to 74 scales around tail in fifth caudal verticil, 16 to 26 dorsolateral body scales in naris-eye distance, rostral scale always in contact with nasals. Adults variable in coloration (in part by population), either black with extensive bright orange markings on the lower sides, head and dorsal crest scales, or black with cream mottling dorsally and no body vermiculations, or dull gray-brown dorsally with white dorsal crest scales and head scales black with vague orange suffusions; juvenile pattern composed of between five and seven pale chevrons with their apices pointed anteriorly, alternating with dark chevrons, the pale chevrons becoming obscured laterally by dark stippling or dotting, the dark chevrons extending to the ventral midline or not, the lateral dark chevrons not strongly diagonal, the dorsal crest scales and heads pale (presumably some shade of orange) in one population. Scale count variation in Tables 3-5.

DISTRIBUTION. – The Bahama Islands, where known from Andros Island and the Exuma Cays (with the exception of White Cay which is occupied by *C. rileyi*); for details of Bahamian distributions of the subspecies, see beyond.

Cyclura cychlura Cuvier

Definition. – A large (males to 411, females to 465 snout-vent length) subspecies of C. cychlura with modally 2 rows of scales between the prefrontal shields and frontal scale, modally 0 azygous scales in the prefrontal suture, modally 4 scales between the anterior canthal scales, modally 9 superciliaries, modally 13 suboculars to anterior border of tympanum, modally 2 postmentals, total dorsal crest scales 84 to 108 ($\bar{x} = 96.5$), 42 to 74 ($\bar{x} = 52.6$) scales around tail in fifth caudal verticil, and modally 3 middorsal

scales in fifth caudal verticil; adults dark gray to black with extensive bright orange blotching on head, face, and lower sides, and dorsal crest scales bright orange.

DISTRIBUTION. - Andros Island, Bahama Islands.

Variation. – The largest male (UF/FSM 20616) has a snout-vent length of 411, the largest female (USNM 64650) 465. The smallest specimen (UMMZ 118320) has a snout-vent length of 203. The longest head in males measures 117.7 (USNM 49772) and in females 43.5 (USNM 64650).

Although we have not collected specimens of *C. c. cychlura* ourselves, the senior author has examined a living individual at Drigg's Hill on south Andros and has had the opportunity to examine Kodachrome slides of a large male from Andros. In general terms, the lizards are dark brown to black, heavily blotched or spotted about the head and anterior third of the body with deep orange; the dorsal crest scales are also orange. The smallest specimen studied (UMMZ 118320) has dorsally a six chevronate pattern with about five dark chevrons, separated middorsally by pale areas; the sides have five diagonal dark bars with the interspaces between the bars marbled dark and light grays. The lateral pattern continues onto the venter. The hindlimbs are not ocellate.

REMARKS. - Our use of cyclura Cuvier instead of baeolopha Cope for the Andros Cyclura requires comment. BARBOUR & NOBLE (1916: 144) noted the existence of the CUVIER name and commented that CUVIER had used the name for "l'iguane de la Caroline." These authors suggested that the original specimen probably had been brought to the Carolinas (presumably South Carolina) and that CUVIER has mistakenly attributed the specimen to the continent rather than from the adjacent Bahama Islands. BARBOUR & NOBLE (loc. cit.) also stated that: "Which Bahaman species he had it is impossible to decide from his meagre descriptions. So unless the type is still in existence and sufficiently well preserved, which is improbable, it will not be possible to more than surmise that Cuvier probably had a specimen of C. baeolopha." Contrary to these

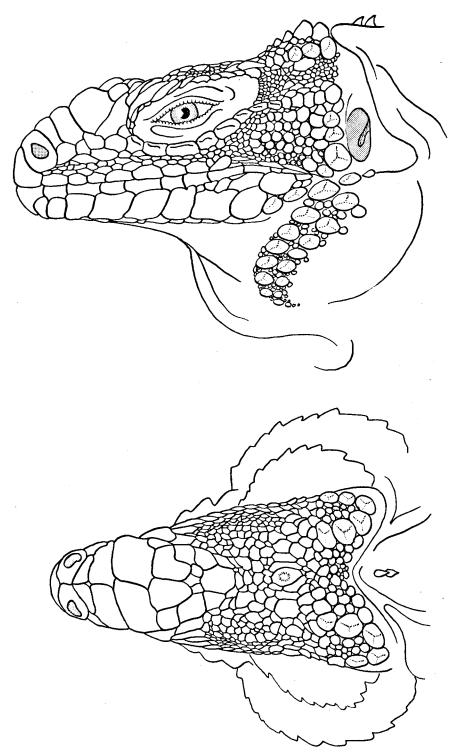


Fig. 10. Lateral and dorsal views of the head of Cyclura cychlura (UMMZ 118318); the subspecies is C. n. cychlura from Long Bay on Pot Cay Creek, Andros Island, Bahama Islands; snout-vent length 394 mm; male.

authors' suspicions, the holotype (MNHN 2367) is in excellent condition; we have examined photographs of the dorsal view of the entire animal, and dorsal and lateral views of the head. The presence of azygous scales between the prefrontals eliminates all other taxa except *C. nubila* from consideration. Other scale counts and relationships suggest strongly that *cychlura* is the prior name for Bahamian iguanas.

The problem further resolves itself into which (of the three subspecies we here associate with each other) Bahamian population should bear the tautonym. We confess to being subjective in this matter to some extent, but we have been swayed primarily in selecting the Andros population as the source of the holotype because of the proximity of that island to the southeastern United

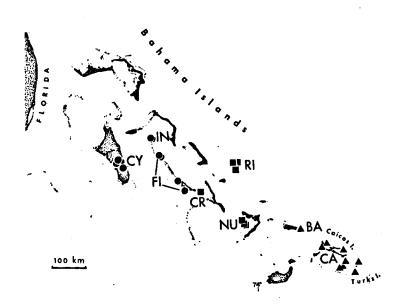


Fig. 11. The Bahama Islands and the Caicos and Turks Islands, showing the distribution of three species of Cyclura as follow: Solid circles = C. cychlura; solid squares = C. rileyi; solid triangles = C. carinata. Subspecies as follow: CY = C. c. cychlura; IN = C. c. inornata; FI = C. c. figginsi; RI = C. r. rileyi; CR = C. r. cristata; NU = C. r. nuchalis; CA = C. c. carinata; BA = C. c. bartschi. Some localities for C. c. figginsi have not been mapped but are in the Exuma Cays.

States (in contrast to the more remote areas within the Bahamas where *Cyclura* occurs) and the likelihood that the original specimen might most probably have been brought from Andros to South Carolina than from elsewhere in the Bahamian archipelago.

Comparison of C. cychlura with C. nubila shows that the two species are fairly closely related; the similarities of having azygous snout scales (if nothing else) tends to affirm this relationship. One feature (aside from radical differences in pattern and color) that differentiates them is the number of dorsal crest scales. The crest scales between the shoulder and sacrum in C. nubila range between 20 and 52 ($\bar{x} = 40.2 \pm 1.2$) and in C. cychlura between 37 and 83 ($\bar{x} = 62.1 \pm 1.7$). Although there is considerable overlap, the means are obviously quite distinct and statistically significant. The number of specimens involved in these computations (including all subspecies) are 73 C. nubila and 70 C. cychlura. Total number of dorsal median scales shows the same situation in these two species. In C. nubila these scales vary between 52 and 85 ($\bar{x} = 69.2 \pm 1.5$) and in C. cychlura between 67 and 118 ($\bar{x} = 96.4 \pm 2.0$).

SPECIMENS EXAMINED. — Bahama Islands, Andros I., no other locality (USNM 31968, USNM 49772, USNM 49775, USNM 64596, USNM 64650, USNM 64917, MCZ 15524); Long Bay Cay on Pot Cay Creek, South Bight (UMMZ 118318-20); Mangrove Cay (MCZ 6947, MCZ 6979); east tip of Fever Cay, North Bight (UF/FSM 19066, UF/FSM 20615-16); west tip of Fever Cay, North Bight (UF/FSM 20617, FMNH 131935).

Cyclura cychlura inornata Barbour & Noble

DEFINITION. – A small (males to 307, females to 220 snout-vent length) subspecies of C. cychlura with modally 4 rows of scales between the prefrontal shields and frontal scale, modally 1 azygous scale in the prefrontal suture, modally 6 scales between the anterior canthal scales, modally 9 superciliaries, modally 14 suboculars to anterior border of tympanum, modally 2 postmentals, total dorsal crest scales 83 to 110 ($\bar{x} = 104.5$), 40 to 55 ($\bar{x} = 45.9$) scales around tail in fifth caudal verticil, and modally 3 middorsal scales in fifth caudal verticil; adults black dorsally, mottled with

cream, the dorsal crest scales not contrasting conspicuously with dorsal body color.

DISTRIBUTION. – U Cay (= Southwest Allan's Cay) and Leaf Cay, Allan's Cays, at the northern extreme of the Exuma Cays, Bahama Islands.

Variation. – The largest male (ASFS V26920) has a snout-vent length of 307 and is from U Cay, and the largest female (AMNH 80089) has a snout-vent length of 220 and is from Leaf Cay. The smallest specimen (AMNH 80096) has a snout-vent length of 124 and is from Leaf Cay. The longest head in males measures 64.4 (ASFS V26920) and in females 61.9 (MCZ 11062); maximum head breadth in males is 35.7 (ASFS V26920) and in females 32.9 (MCZ 11062).

The senior author examined an adult male (ASFS V10734) and a juvenile (ASFS V10735) from U Cay in life. In both these specimens the dorsal ground color was black, mottled with cream dorsally and without any body vermiculations. No orange, so bold and prominent in C. c. cychlura, was noted on living U Cay C. c. inornata, nor are the dorsal crest scales brightly or differently colored in inornata as they are in cychlura. However, the junior author noted that living Leaf Cay lizards had much pink and orange on the head. Preserved juveniles resemble the single preserved cychlura juvenile, except that there are about seven pale chevrons and five dark chevrons dorsally and extending onto the sides, with the interspaces marbled with pale and dark gray. The venter is dark with no chevron remnants or pattern. The pale neck chevrons are more prominent than in juvenile cychlura. As in the latter subspecies, the hind-limbs are not ocellate.

COMPARISONS. – Aside from the apparent color and pattern differences between cychlura and inornata, the two subspecies differ in several other ways. Apparently cychlura is a much larger lizard than is inornata, with both sexes reaching greater snout-vent lengths (cychlura males and females maximally 411 and 465; inornata males and females 307 and 220). The scale rows between the prefrontal shields and the frontal scale are modally 2 in cychlura and 4 in inornata. Modally cychlura has 0 azygous scales in the prefrontal

suture (with a range of 0-4 to very many small scales), whereas inornata modally has 1 azygous scale (with a range of 1-5). The number of scales between the anteriormost canthals is modally 4 (range 6-10) in cychlura, and modally 6 (range 4-7) in inornata; the mean in cychlura is 4.5, in inornata 5.6. In number of suboculars to tympanum, cychlura modally has 13, inornata 14. C. c. cychlura has a mean of 96.5 (range 84-108) total dorsal crest scales, whereas in C. c. inornata the mean is 104.5 (range 83-110). The scales in the fifth caudal verticil average 52.6 in cychlura, 45.9 in inornata; in this count there is great overlap (42-74 in cychlura; 40-55 in inornata), but the trend toward greater number of scales in cychlura is obvious.

REMARKS. - C. c. inornata is known only from two cays (U Cay, Leaf Cay) of the Allan's Cays which lie at the northern end of the Exuma chain of cays. The species is not uncommon there, and both cays support populations consonant in size with those of the islets. One of the northern Exuma Cays (Ship Channel Cay) also supports an endemic subspecies of Ameiva auberi Cocteau; it seems probable that the history of this small group of islets has been in some way different from that of the balance of the Exuma Cays. In general, we feel that C. c. inornata is fairly well characterized, but it surely does not merit specific status as proposed by its original describers.

SPECIMENS EXAMINED. - Bahama Islands, U Cay (= Southwest Allan's Cay) (ASFS V10734-35, UF/FSM 22908, MCZ 11062 - holotype, ASFS V26920); Leaf Cay (AMNH 80087-96, ASFS V26923).

Cyclura cychlura figginsi Barbour

DEFINITION. — A small (males to 315, females to 285 snout-vent length) subspecies of *C. cychlura* with modally 3 rows of scales between the prefrontal shields and frontal scale, modally 1 azygous scale in the prefrontal suture, modally 4 scales between the anterior canthal scales, modally 10 superciliaries, modally 13 suboculars to anterior border of tympanum but subocular series incomplete in almost half of the specimens, modally 1 postmental, total dorsal

crest scales 67 to 118 ($\bar{x} = 92.7$), 41 to 66 ($\bar{x} = 49.4$) scales around tail in fifth caudal verticil, and modally 4 middorsal scales in fifth caudal verticil; adults somewhat variable by population but generally dull gray-brown above with white crest scales, head scales black with vague orange suffusions on snout and infralabials.

DISTRIBUTION. – The Exuma Cays (Guana Cay, Prickly Pear Cay, Allen Cay, Guana Cay off north end of Normans Pond Cay, Ozie Cay?, Bitter Guana Cay, and Gaulin Cay), Bahama Islands.

Variation. – The largest male (UF/FSM 19256) has a snout-vent length of 315, the largest female (ASFS V26921) 285. The smallest specimen (UMMZ 117398) has a snout-vent length of 94. The longest head in males measures 70.5 (UF/FSM 19256) and in females 56.0 (ASFS V26921); maximum head breadth in males is 40.0 (UF/FSM 19256) and in females 30.8 (ASFS V26921).

We have grouped together all specimens of Cyclura from the central and southern Exuma Cays (with the exception of the isolated specimens from White Cay at the southern end of the chain) as C. c. figginsi, despite at least some pigmental differences between adults of the various populations involved. The longest series (26 lizards) is from Bitter Guana Cay (including Gaulin Cay) and these specimens are topotypes or near-topotypes. Adults from Bitter Guana are dull gray-brown above in life, with white dorsal crest scales. The head scales are black with vague orange suffusions on the snout scales and infralabials, but there was no prominent cream, yellow, or orange blotching as is present in C. c. cychlura. Specimens from Guana Cay (= 2.2 km SE Jewfish Cay) were pale bluish gray in life and showed some diffuse pale whitish or pale grayish spotting. Specimens examined in life by the junior author from this same cay had the dorsal crest scales magenta. It seems likely that each islet inhabited by C. cychlura in this region of the Exumas has a local deme which has differentiated pigmentally to some extent from its neighbors. But to assign each population to a separate subspecies on the basis of the limited material available from most islets involved would be foolish. Even distinguishing figginsi, as distinct from both cychlura and inornata, is difficult. Of the three subspecies of C. cychlura, certainly figginsi seems to us the least distinctive; this may be due principally to the local deme variation within its range.

One factor that has swayed us in retaining figginsi as an entity is the distinctive juveniles, of which we have a good series. In them, the dorsum is boldly crossbarred with about seven black bands which become slightly diagonal and which alternate with pale gray bands, all heavily dotted with small pale dots. The venter is longitudinally streaked, and there is no trace of a lateral pattern.

Comparisons. – Like inornata, figginsi appears to be a smaller lizard than cychlura; adult males reach a maximum size of 315. adult females 285, in contrast to 411 and 465 in male and female cychlura. Such a difference may be a sample artifact, but on the other hand we have examined 52 figginsi in contrast to only 17 cychlura and 16 inornata. In scutellation, the following differences occur. C. c. figginsi modally has 3 rows of scales between the prefrontal shields and the frontal scale (mode 2 in cychlura, 4 in inornata). Like inornata (but in contrast to cychlura), figginsi modally has 1 azygous scale in the prefrontal suture (range 0-8). Like cychlura (but in contrast to inornata), figginsi has 4 scales between the anteriormost canthal scales. In contrast to both cychlura and inornata (both with modes of 9), figginsi has a mode of 10 superciliaries. In contrast to inornata (which has a mode of 14) but like cychlura, figginsi modally has 13 suboculars to the tympanum. Again, like cychlura (but unlike inornata with a mode of 2), figginsi has a mode of 1 postmental scale; the mode of 2 postmentals in inornata is strong (eight of 16 specimens). In total dorsal crest scales, figginsi averages less (92.7; range 67-118) than either cychlura (96.5; range 84-108) or inornata (104.5; range 83-110). In number of scales in the fifth caudal verticil, the mean in figginsi (49.4) is intermediate between that of cychlura (52.6) and inornata (45.9). Finally, of the three subspecies, figginsi has a mode of 4 scales in the fifth caudal verticil dorsally, whereas both cychlura and inornata have strong modes of 3 in this position.

The series from the various islets are generally too short for any fine analysis of variation between populations of *figginsi*. But there is one obvious difference which is noteworthy. Of the total series

of figginsi studied, 11 specimens have the infralabial series to the center of the eye incomplete or irregularly broken. Of these 11, seven (of eight specimens) are from Prickly Pear Cay, and four (of 12 specimens) are from Guana Cay; in all these specimens, the incomplete infralabial row is bilateral. The long series of figginsi from Bitter Guana Cay and Gaulin Cay shows no irregularities.

REMARKS. – Judging from the experience of the senior author, C. c. figginsi is quite abundant on Bitter Guana Cay, where tail-drags and half-eaten fruit were encountered both along the strand and in the rocky interior; the latter situation doubtless serves as a retreat for these lizards. The very fact that our series contains a large number of juvenile specimens suggests that C. c. figginsi is breeding successfully, and that it is in little danger of immediate extinction.

SPECIMENS EXAMINED. — Bahama Islands, Guana Cay, near Great Exuma Cay (UMMZ 117397-400, UMMZ 118312-17); Ozie Cay (= Guana Cay?), off north end of Norman Pond Cay (ASFS V26921-22); Prickly Pear Cay (UF/FSM 14358, UF/FSM 19251-57); Allen Cay (UF/FSM 3595-97); Guana Cay (= 2.2 km SE Jewfish Cay) (ASFS V23968-70); Bitter Guana Cay (MCZ 17745 — holotype); Gaulin Cay, Bitter Guana Cay (ASFS V11490-500, CM 41068, ASFS V20442-44, ASFS V23967, UF/FSM 22009, UF/FSM 22909, UF/FSM 23439-42, UF/FSM 24516-17).

Cyclura cornuta Bonnaterre, 1789

Lacerta cornuta Bonnaterre, 1789. Tableau encycl. Erpét., p. 40. Holotype – unknown (not in MNHN).

Cyclura ochiopsis COPE, 1885. Amer. Nat. 19: 1006. Syntypes - USNM 9977, USNM 12239, MCZ 4717. Type-locality - Navassa Island.

Cyclura nigerrima Cope, 1886. Proc. Am. Phil. Soc. 23: 264. Holotype – USNM 9974. Type-locality – Navassa Island.

Cyclura stejnegeri Barbour & Noble, 1916. Bull. Mus. Comp. Zool. 60: 163. Holotype – USNM 29367. Type-locality – Isla Mona.

Type-locality. "Sainte-Domingue ... dans les mornes de l'hôpital, entre l'Artibonite & les Gonaïves."

Definition. – A species of *Cyclura* characterized by the combination of large size (males to 463, females to 510 snout-vent length), with three to five scales (frontal + one or two pairs of prefrontals)

enlarged on the snout, 11 to 13 (modally 10) scale rows between the frontal and interparietal scales, azygous scales between prefrontals absent, 8 to 17 (modally 13) scales between the anterior canthal scales, 13 to 29 (modally 18) scales bordering the frontal, first prefrontal never in contact with precanthal, no obvious rows of vertical loreal scales, 10 to 16 (modally 12) suboculars to anterior border of tympanum, 6 to 18 (modally 12) sublabials to eye center, 3 to 6 (modally 4) rows of scales between infralabials and sublabials (Fig. 12), 1 to 4 (modally 3) postmentals, 32 to 80 femoral pores usually in two (occasionally in one or three partial) rows, dorsal crest scales 14 to 25 between occiput and shoulder, 40 to 56 $(\bar{x} = 47.4 \pm 1.4)$ between shoulder and sacrum, 12 to 23 between sacrum and first caudal verticil, total dorsal crest scales between occiput and first caudal verticil 70 to 97 ($\bar{x} = 84.4 \pm 2.3$), dorsal crest scales on neck never higher than body crest scales, body crest scales almost never higher than postsacral crest scales, 33 to 51 scales around tail in fifth caudal verticil, 13 to 44 dorsolateral body scales in naris-eye distance, rostral scale in contact with nasals or separated from then by 1 or 2 rows of scales, and 3 to 7 (modally 4) scale rows between prefrontal scales. Adults patternless dark gray, gravish brown, to black. Juveniles very dark and virtually patternless but with about nine vague and faint pale crossbars on the sides separated by dark gray areas (often series of gray blotches) which extend onto the venter; hindlimbs not ocellate. Scale count variation in Tables 3-5.

DISTRIBUTION. – Hispaniola (including the satellite islands of Isla Beata, Ile de la Petite Gonâve, Ile de la Tortue, and Ile Grande Cayemite), Navassa Island, and Isla Mona. Also reported from Ile Petite Cayemite, Isla Saona, and from Isla Cabritos in Lago Enriquillo, República Dominicana.

Cyclura cornuta cornuta Bonnaterre

Definition. – A subspecies of *C. cornuta* characterized by the combination of modally 2 rows of scales between the prefrontal shields and the frontal scale, modally 3 rows of scales between supraorbital semicircles and interparietal, modally 8 supralabials

to eye center, modally 12 sublabials to eye center, 32 to 66 ($\bar{x}=46.2$) femoral pores, 30 to 37 ($\bar{x}=33.1$) fourth toe subdigital scales, middorsal scales in fifth caudal verticil modally 4, dorsolateral body scales in naris-eye distance 13 to 26, scale rows between rostral and nasals modally 1; adults dark grayish brown to black and without pattern, juveniles like adults but with vague indications of about nine paler crossbars.

DISTRIBUTION. — Hispaniola, including Isla Beata, Ile de la Petite Gonâve, Ile de la Tortue, and Ile Grande Cayemite; probably on other satellite islands but unknown by specimens; reported from Ile Petite Cayemite, Isla Saona, and Isla Cabritos in Lago Enriquillo.

Variation. – The largest male (ASFS X1300) has a snout-vent length of 404 and the largest female (MCZ 28595) a snout-vent length of 510. The smallest juvenile (MCZ 3597) has a snout-vent length of 80. The longest head in males measures 136.5 (USNM 65139) and in females 106.4 (MCZ 28596); maximum head breadth in males is 71.7 (USNM 54139) and 57.5 (MCZ 28595) in females.

The adults in general are some shade of very dark brown to dark gray or even black, with the venter somewhat less heavily pigmented than the dorsum. Bright colors are entirely absent, and the lizard is quite drab in comparison with other species (and quite different in aspect from C. ricordi with which it is partly sympatric and syntopic). Juveniles are dark and virtually patternless, with vague indications of about nine paler crossbars that are quite faint. The femoral pores are usually in two series on each leg, but occasionally they may be in one or three rows; these multiple rows of femoral pores account for the high counts of femoral pores in C. cornuta in contrast to those in other species.

C. c. cornuta is widespread in Hispaniola where it favors the most xeric areas such as the Cul de Sac-Valle de Neiba plain and the Península de Barahona. In such situations it is often very abundant. In addition, the subspecies occurs along rocky coastlines and on rocky islets (Ile de la Petite Gonâve) and appears to be exceptionally common on Isla Beata, at least along the northern coast. In some xeric areas, notably the western Valle de Cibao in northern República Dominicana, the species seems to be uncommon. Its apparent absence from at least partially very arid Ile de

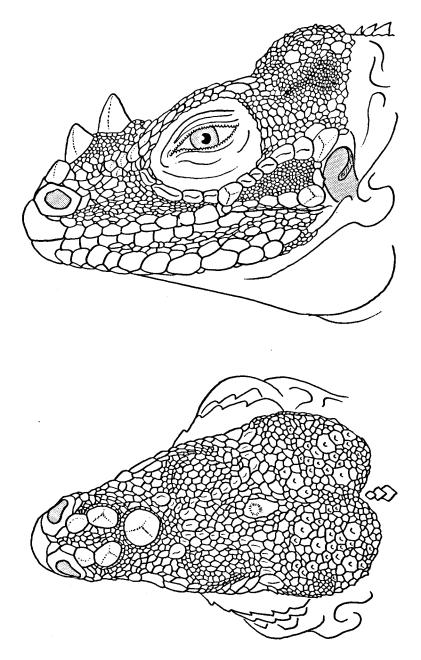


Fig. 12. Lateral and dorsal views of the head of Cyclura cornuta (ASFS V2785); the subspecies is C. c. cornuta from Isla Beata, República Dominicana; snout-vent length unrecorded; questionably female.

la Gonâve is puzzling and should not be construed as fact. It may be that the species occurs there in some numbers, perhaps locally, but remains uncollected due to the bulk of the lizards as far as preservation and transportation is concerned.

Since C. cornuta lacks azygous scales in the prefrontal suture, it is easily differentiated from both C. nubila and C. cychlura. On the other hand, the three to five enlarged snout scales (frontal + one or two pairs of prefrontals) into peaked cones which are often high in adults (and from which the common name "rhinoceros iguana" has been derived) distinguish C. cornuta from the Cuban species and C. cychlura. The dorsal crest scales in C. cornuta vary between 40 and 56 ($\bar{x} = 47.4 \pm 2.4$) in contrast to 20-53 ($\bar{x} = 40.2 \pm 1.2$) in C. nubila and 37-83 ($\bar{x} = 62.1 \pm 1.7$) in C. cychlura. C. cornuta is thus intermediate both in range and mean in this count between the two geographically adjacent species. In total number of median dorsal scales C. cornuta shows the same relationship. These scales vary between 70 and 97 ($\bar{x} = 84.4 \pm 2.3$) in C. cornuta, between 52 and 85 ($\bar{x} = 69.2 \pm 1.5$) in C. nubila, and between 67 and 118 $(\bar{x} = 96.4 \pm 2.0)$ in C. cychlura. In all cases, there is no overlap of twice the standard error of the means, despite considerable overlap in actual counts.

SPECIMENS EXAMINED. – Haiti: Dépt. de l'Ouest, Mirebalais (ASFS X1300); Dépt. du Sud, Jérémie (MCZ 3597); Cap St. Georges (ASFS V26014); Ile de la Petite Gondve (FMNH 14801-03, MCZ 25568, USNM 80395, USNM 80397-98, USNM 82107, USNM 84033, USNM 63112); Ile de la Tortue (USNM 59455); Ile Grande Cayemite (USNM 60599-601). – República Dominicana: Independencia Province, Jaragua (ASFS X9782-83, RT 744); 6 km W Duvergé (ASFS V13804); 5 km E Duvergé (ASFS V13803); ? 5 km E Duvergé (ASFS V14944); Azua Province, Barreras (ASFS V21271); Pedernales Province, Oviedo (viejo) (USNM 65139); Isla Beata (ASFS V2785-86, MCZ 28594-97, MCZ 33410).

Cyclura cornuta stejnegeri Barbour & Noble

DEFINITION. - A subspecies of *C. cornuta* characterized by the combination of modally 3 rows of scales between the prefrontal shields and the frontal scale, modally 3 rows of scales between the supraorbital semicircles and the interparietal, modally 8 supralabi-

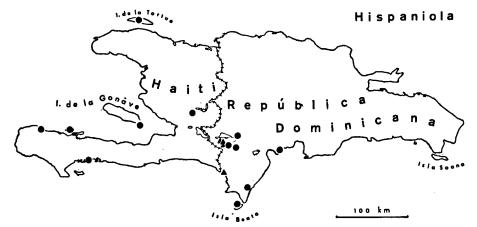


Fig. 13. Hispaniola, showing the distribution of Cyclura cornuta cornuta (solid circles) and C. ricordi (solid triangles). The total range of C. c. cornuta is more extensive than indicated, and two other subspecies (stejnegeri, onchiopsis) occur, respectively on Isla Mona and Navassa Island, to the east and west of Hispaniola.

als to eye center, modally 8 sublabials to eye center, 40 to 80 ($\bar{\mathbf{x}} = 59.8$) femoral pores, 32 to 39 ($\bar{\mathbf{x}} = 34.4$) fourth toe subdigital scales, middorsal scales in fifth caudal verticil 3 to 5 (no mode), dorsolateral body scales in naris-eye distance 17 to 21, scale rows between rostral and nasals modally 0, adults (as preserved) dark and patternless, juveniles like those of $C.\ c.\ cornuta$ with a faint pattern consisting of about eight pale crossbars which are poorly defined and become more or less diagonal on the sides, separated by dark gray areas which often form blotch series.

DISTRIBUTION. - Isla Mona.

Variation. – The largest male (AMNH 13775) has a snout-vent length of 463 and the largest female (MCZ 35602) a snout-vent length of 470. The longest head in males measures 117.1 (AMNH 13775) and in females 98.3 (MCZ 35602); maximum head breadth in males is 66.9 (AMNH 13775) and in females 55.7 (MCZ 35602). The smallest juvenile (UMMZ 124822) has a snout-vent length of 115.

In color and pattern, adult C. c. stejnegeri do not appear to differ from C. c. cornuta; both are basically drab brownish to black liz-

ards. Juvenile stejnegeri are like juvenile cornuta, in that they have a faint dorsal pattern consisting of about eight pale crossbars which are poorly defined and which become more or less diagonal on the sides, separated by dark gray areas which, in contrast to cornuta, may include series of blotches. The dark lateral areas continue onto the venter. The hindlimbs are not ocellate. Judging from the juvenile pattern of stejnegeri (which is somewhat more bold than that of the nominate subspecies), one can suggest that the pattern is like a much diluted or obscured C. nubila pattern. The two species differ, both as juveniles and adults, as far as pattern is concerned, in that nubila has ocellate hindlimbs, a feature absent in all subspecies of C. cornuta.

Comparisons. - C. c. steinegeri differs from C. c. cornuta in the following ways. In steinegeri, there are modally 3 scale rows between the prefrontal shields and the frontal scale (= unpaired "horn"), whereas the mode in cornuta is 2; of 58 cornuta, only four have 3 rows of scales in this position, whereas of 18 steinegeri, only three have 2 rows of scales. In steinegeri, subocular scales to the tympanum are either 12 or 14 (= two bimodes) whereas in cornuta the mode is 11. A striking difference between the two subspecies is the mode of 8 sublabial scales to the eye center in steinegeri and a mode of 12 in cornuta. The total number of femoral pores in stejnegeri varies between 40 and 80 ($\bar{x} = 59.8$) whereas in cornuta the range is 32 to 66 ($\bar{x} = 46.2$). C. c. steinegeri seems to have a higher incidence of double or triple rows of femoral pores than does cornuta, and this accounts for the higher number of pores in the former. In number of scale rows between the rostral scale and the nasal scales, cornuta modally (66 per cent) has 1, whereas in steinegeri the rostral and nasals are most often (75 per cent) in contact (= no interposed scale rows). Contact between rostral and nasals does not occur in 20 of 58 cornuta, and 1 row of scales occurs in four of 16 steinegeri, so that each subspecies does show some incidence of that character modally typical of the other.

REMARKS. – C. c. stejnegeri, although represented in collections by relatively few specimens (11), appears to be very common on

Isla Mona between Puerto Rico and Hispaniola. This island is basically xeric and presents fairly optimal conditions for these ground iguanas. However, human disturbance and indescriminate killing of these large lizards for "sport" may already have endangered what was once a thriving population.

SPECIMENS EXAMINED. – Isla Mona (MCZ 11145, MCZ 35602-03, AMNH 13775, AMNH 31887, AMNH 60659, USNM 29365, USNM 29367 – holotype); Anclaje Sardinero (ASFS V6554); middle of north side (MCZ 49741); near beach on eastern side (UMMZ 124822).

Cyclura cornuta onchiopsis Cope

DEFINITION. – A subspecies of C. cornuta characterized by the combination of modally 2 rows of scales between the prefrontal shields and the frontal scale, 4 and 6 scale rows between the supraorbital semicircles and the interparietal (no mode), 7 supralabials to eye center in all specimens, 6 to 10 (no mode) sublabials to eye center, 33 to 38 ($\bar{\mathbf{x}}=36.3$) femoral pores, 38 to 41 ($\bar{\mathbf{x}}=38.6$) fourth toe subdigital scales, middorsal scales in fifth caudal verticil 7 in all specimens, dorsolateral body scales in naris-eye distance 30 to 44, scale rows between rostral and nasals 1 or 2; adults as preserved dark and patternless, juveniles unknown.

DISTRIBUTION. - Formerly Navassa Island, now generally conceded to be extinct.

VARIATION. – We have examined three specimens of C. c. on-chiopsis: one female (USNM 9977) with a snout-vent length of 378, one male (MCZ 4717) with a snout-vent length of 420, and one small individual (USNM 12239) with a snout-vent length of 130. These three specimens are the syntypes of Cyclura onchiopsis Cope, and USNM 9974 (which we have not seen) is the holotype of C. niger-rima Cope, 1886. As far as we are aware, these four lizards are the sole representatives of the Navassa population in collections. There is no evidence that the species is still extant since such recent visitors as Thomas (1966) neither observed nor collected the species. Presumably the fate of the Navassa lizards was sealed with the introduction on that islet of cats or goats by the lighthouse-keepers

and their families. The adult male (MCZ 4717) has the head length 100.1 and the head breadth 54.8; the female (USNM 9977) has the head length 98.2 and the head breadth 49.6.

COMPARISONS. - Since there is such a very limited number of specimens available, we can say little with any degree of security concerning the differences between onchiopsis, cornuta, and steinegeri. Judging only by our material, the following appear to be significant. Like cornuta (but unlike stejnegeri), onchiopsis modally has 2 scale rows between the prefrontal shields and the frontal scale. Both cornuta and stejnegeri modally have 3 rows of scales between the semicircles and the interparietal, whereas one onchiopsis has 4 rows of scales, and two have 6 rows of scales in this position. C. c. onchiopsis has 7 supralabials to the eye center, whereas both cornuta and steinegeri modally have 8. The number of femoral pores in onchiopsis varies between 33 and 38 ($\bar{x} = 35.3$), whereas this count in cornuta is 32-66 ($\bar{x} = 46.2$) and in steinegeri 40-80 ($\bar{x} = 59.8$); onchiopsis has strikingly fewer femoral pores than either of the other subspecies. On the other hand, onchiopsis has between 38 and 41 $(\bar{x} = 38.6)$ fourth toe subdigital scales, whereas this count in cornuta is 30-37 ($\bar{x} = 33.1$) and in steinegeri 32-39 ($\bar{x} = 34.4$). There is virtually no overlap in this count, although increased data on onchiopsis would doubtless show it.

Only one onchiopsis has a tail complete enough to take a count of median dorsal scales in the fifth caudal verticil; the count is 7 scales in this specimen, whereas in cornuta the count ranges from 4 to 6 (mode 4) and between 3 and 5 in steinegeri (no mode). Like cornuta (and in contrast to steinegeri) the rostral and nasal scales are not in contact in onchiopsis; it may be recalled, however, that separation of the rostral and nasals is a modal condition only in cornuta, whereas all onchiopsis have these scales separated bilaterally.

Perhaps the most striking difference between *onchiopsis* and both *cornuta* and *stejnegeri* is the size of the dorsolateral scales. In nariseye distance, the dorsolateral scales in *cornuta* vary between 13 and 26 ($\bar{x} = 18.6$), in *stejnegeri* between 17 and 21 ($\bar{x} = 19.3$), and in *onchiopsis* between 30 and 44 ($\bar{x} = 39.3$). The smaller size of these

scales in *onchiopsis* is apparent even to the eye and without resorting to use of calipers. It is even conceivable that *onchiopsis* should be considered a species distinct from *C. cornuta* on the basis of this single character (plus perhaps other modalities), but to do so would obscure its obvious affinities with the latter species.

REMARKS. — We have used the name onchiopsis Cope for that lizard which has been customarily been called C. nigerrima or C. cornuta nigerrima Cope. Both names (onchiopsis and nigerrima) were used by Cope in the 1885 paper, but only onchiopsis was diagnosed at that time. The diagnosis of nigerrima was made in 1886. In effact, nigerrima is a nomen nudum, which was validated the following year. Since there is no question that Navassa supported but a single species of Cyclura, nigerrima must stand in the synonymy of onchiopsis.

We have already pointed out that *C. c. onchiopsis* is almost certainly extinct. For discussions of the history of Navassa and its fauna, see Turner (1960) and Thomas (1966).

SPECIMENS EXAMINED. - Navassa Island, USNM 9977, USNM 12239, MCZ 4717).

Cyclura collei Gray, 1845

Cyclura Collei Gray, 1845. Cat. lizards Brit. Mus., p. 190. Holotype - BMNH 1936.12.3.108.

Cyclura lophoma Gosse, 1848. Proc. Zool. Soc. London, p. 99. Holotype – BMNH 47.12.27.101. Type-locality – between Spanishtown and Passage-fort, Jamaica.

TYPE-LOCALITY. Jamaica.

DEFINITION. – A species of *Cyclura* characterized by the combination of moderate size (males to 428, females to 378 snout-vent length), frontal scale not conspicuously enlarged and set off from balance of head scales, azygous scales between prefrontal shields absent, canthals not set off from balance of head scales, first prefrontal never in contact with precanthal, 3 or 4 (modally 4) poorly defined vertical rows of loreals, 13 or 14 (modally 14) suboculars to

anterior border of tympanum, 5 or 6 (modally 6) sublabials to eye center, 2 or 3 (modally 2) rows of scales between infralabials and sublabials (Fig. 14), 1 to 3 (modally 2) postmentals, 35 to 41 femoral pores in a single row but femoral pores absent in three of five specimens, dorsal crest scales 16 to 20 between occiput and shoulder, 49 to 59 ($\bar{x} = 53.4$) between shoulder and sacrum, 13 to 21 between sacrum and first caudal verticil, total dorsal crest scales between occiput and first caudal verticil 81 to 98 ($\bar{x} = 88.2$), dorsal crest scales on neck equal in height to those on body, body crest scales higher than postsacral crest scales, 47 to 85 scales around tail in fifth caudal verticil, 20 to 24 dorsolateral body scales in naris-eye distance, rostral scale always separated from nasal scales by 1 row of scales or very many granules. Adults (fide BARBOUR & Noble, 1916: 160, and Gosse, 1848: 99-100) green dorsally, grading into slaty blue with some oblique lines of dark olive-green on shoulders, and three broad triangular patches from the dorsal crest scales to the venter, with dark olive-brown zigzag spots, dorsal crest scales on body brighter bluish green than body, to muddy dorsally, top of snout and sides of head washed with green, dorsal and lateral body surfaces blotched with straw, the blotches breaking up into groups of small spots, less tinged with green; juvenile color and pattern unknown. Scale count variation in Tables 3-5.

DISTRIBUTION. - Jamaica, including Goat Island and Little Goat Island.

Variation. – We can add nothing to the color and pattern data given above since *C. collei* is now quite rare or extinct. Recently, a dried carcass was found on the southern shore of the Hellshire Hills, which suggests that there may be a small residual population of these lizards still extant in that area, but no specimens have reached collections for many years. The largest male (USNM 103688) has a snout-vent length of 428 and the largest female (MCZ 21892) has a snout-vent length of 378. The longest and broadest heads of the series of five specimens pertain to the same individuals: male – head length 111.1, breadth 59.9; female – head length 84.4, breadth 44.8, There are no juveniles in the lot, the smallest lizard (MCZ 21894) having a snout-vent length of 333.

The characters given in the species definition will suffice to dis-

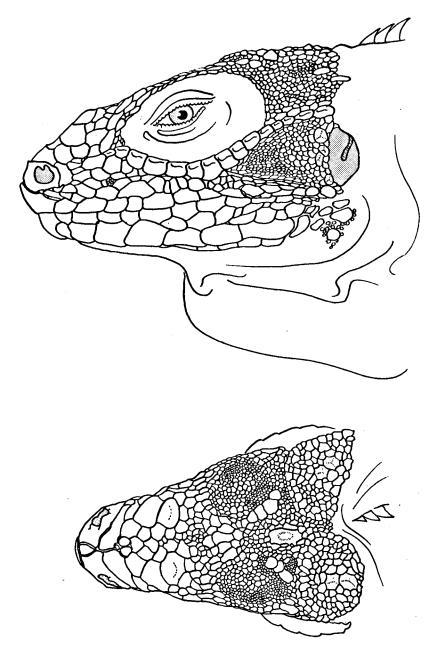


Fig. 14. Lateral and dorsal views of the head of Cyclura collei (MCZ 21892) from Goat Island, Jamaica; snout-vent length 378 mm; female.

tinguish $C.\ collei$ from all other species. The number of dorsal crest scales between the shoulder and the sacrum is moderate (49-59; $\bar{x}=53.4$) and intermediate between the means of this count in nubila and cornuta on one hand and cychlura on the other. The total dorsal median scale count likewise is intermediate (81-98; $\bar{x}=88.2$) but is closest in mean to that of cornuta (84.4) rather than that of cyclura (96.4) or nubila (69.2).

A peculiarity of the series of *C. collei* is the absence of femoral pores in three of five specimens; these three specimens include one adult male (MCZ 21893) and two adult females (MCZ 21892, MCZ 21894), so that the condition does not seem to be extreme atrophy of the regularly smaller femoral pores in female *Cyclura* in general. No other species has this condition. These three specimens are from Goat Island; a fourth specimen from Goat Island has the femoral pores well developed. Although the separation of the rostral scale from the nasal scales is customarily by a single row of scales, one specimen (MCZ 9397) has a great many tiny granules in this position; we construe this condition as extreme fragmentation of the more normal single row of scales in this position.

Remarks. – Although C. collei seems now to be extremely rare if not extinct on Jamaica itself (due to the introduction of the mongoose in 1872), it persisted in some numbers on Goat Island and Little Goat Island until World War II, when these islets were manned by service personnel who shot the lizards for "sport." Even so, earlier reports (Gosse, 1851; Grant, 1940) suggest that C. collei was never widespread in Jamaica, and that the lizard occurred only along the southern xeric coast. Along these lines it is perhaps pertinent to note the type-locality of C. lophoma (i.e., between Spanishtown and Passage-fort), a locality in southern Jamaica.

Specimens examined. – Jamaica, Goat Island (MCZ 21892-94); Goat Island, Old Harbour (MCZ 9397); Little Goat Island (USNM 103688).

Cyclura pinguis Barbour, 1917

Cyclura pinguis Barbour, 1917. Proc. Biol. Soc. Wash., 30: 100. Holotype - MCZ 12082.

TYPE-LOCALITY. Anegada Island, British Virgin Islands.

Definition. - A species of Cyclura characterized by the combination of large size (males to 539, females to 476 snout-vent length), 6 or 7 scales (no mode) between the frontal and interparietal scales, azygous scales absent in the prefrontal suture, 10 to 12 (modally 10 and 11) scales between the anterior canthal scales, 7 to 9 (no mode) scales bordering the frontal, first prefrontal never in contact with precanthal, 3 to 10 (modally 4) vertical rows of loreals, 12 to 14 (modally 13) sublabials to eye center, 2 or 3 (modally 2) rows of scales between the infralabials and sublabials, 1 to 6 (modally 2 and 3) postmentals (Fig. 5), 38 to 58 femoral pores in a single row, dorsal crest scales 9 to 15 between occiput and shoulder, 31 to 40 $(\bar{x} = 35.0)$ between shoulder and sacrum, 9 to 12 between sacrum and first caudal verticil, total dorsal crest scales between occiput and first caudal verticil 54 to 63 ($\bar{x} = 58.8$), dorsal crest scales on neck very low and rather inconspicuous, never higher than body crest scales, body crest scales usually equal to postsacral crest scales, 37 to 40 scales around tail in fifth caudal verticil, 6 to 8 large dorsolateral scales in naris-eye distance, rostral scale separated from nasal scales by 1 or 2 (modally 2) rows of smaller scales. Adults generally brown to gray dorsally with vertical rows of turquoise dots; juvenile coloration and pattern unknown but presumably like adults. Scale count variation in Tables 3-5.

DISTRIBUTION. - Known only from Anegada Island, B.V.I.

VARIATION. – The largest male (ASFS V14254) has a snout-vent length of 539, the largest female (ASFS V14253) a snout-vent length of 476. The smallest specimen (ASFS V14236) has a snout-vent length of 230 and is subadult. The longest head in males (ASFS V14254) measures 135.6, in females (ASFS V14253) 93.2; maximum

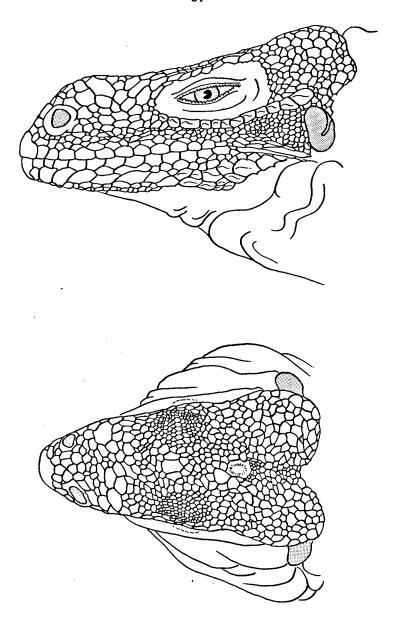


Fig. 15. Lateral and dorsal views of the head of $\it Cyclura\ pinguis$ (ASFS V14262) from Sand Path, Anegada Island, Virgin Islands; snout-vent length 400 mm; female.

head breadth in males (ASFS V14254) is 61.7, in females (ASFS V14253) 47.9.

Adults are generally brown to gray dorsally with vertical rows of turquoise dots. Detailed color notes on the largest male (ASFS V14254; snout-vent length 539) taken by the junior author, reflect the details of the color and pattern in this sex. Head brown, darker in area of temporals, labials, and nasals. Throat and "dewlap" lighter brown. Nuchal region brown with a column of turquoise dots extending posteriorly to rump and downward to lateral fold. Below fold, turquoise reticulated with brown, fading to blue-tan on venter. Tail turquoise above at base, brown posteriorly, blue, fading to cream, below. Forelimbs reddish turquoise above: feet same with toes a bit darker, tan flecked with brown below. Hindlimbs turquoise and brown above; feet and toes darker; below tan, flecked with brown. An adult female (ASFS V14258; snout-vent length 426) was recorded by the junior author as "Essentially like the male (described above) except much more gray in the nuchal and shoulder regions and forefeet more brown." In the color notes taken on the entire series, "turquoise" as a color name appears repeatedly, usually in reference to rows or columns of dots on the body, or as the base (or an ancillary color) on the limbs, feet, or tail. Since the color and pattern between adults of the two sexes are very comparable, differing perhaps only in intensity (the males being somewhat darker in general than the females), we imagine that young specimens are colored and patterned much like adults. Carey's color notes on the two smallest specimens available (ASFS V14235 - snout-vent length 290; ASFS V14236 - snout-vent length 230) state that these lizards were "essentially like" the adults except that neither of them had the darkened supra- and infralabials and mental present as in some adults, and that only the rostral was darker. The dorsal crest scales were light tan, not brown. Turquoise was present on all limbs and feet, tail, and as rows of dots from the dorsal crest scales down the sides to the lateral fold.

REMARKS. - C. pinguis is perhaps (aside from C. ricordi) the most distinctive of the species of Cyclura. Aside from its color and pattern, the low and inconspicuous nuchal crest scales and the very

large dorsolateral body scales distinguish it at once from all other species. As far as dorsal crest scales between the shoulder and sacrum are concerned, *C. pinguis* has a lower mean (35.0) than any other species, being most closely approached by *C. ricordi* (39.1) and *C. nubila* (40.2). The same holds true for total dorsal crest scales, where the mean in *C. pinguis* is 58.8, approached most closely by *C. ricordi* (63.4) and *C. nubila* (69.2).

The very large size of the dorsolateral body scales is easily apparent even upon the most casual examination. In *C. pinguis*, there are between 6 and 8 scales included in the naris-eye distance, whereas in all other species combined, these counts vary between 13 and 44 (both counts in *C. cornuta*).

We have already noted the fact that two other nominal species, both known from skeletal remains only, have been named from islands on the Puerto Rico Bank: mattea Miller and portoricensis Barbour. Cyclura is otherwise unknown from these islands, and it seems possible - perhaps even probable - that both mattea and portoricensis are synonymous with (or at best should be regarded as subspecies of) C. pinguis. We have examined skeletal material of all three taxa and find no trenchant differences between them: however, we known nothing regarding ontogenetic change or sexual differences in skeletal proportions or fine structure in these taxa, and thus we pro tem retain mattea and portoricensis as distinct species. We wish also to point out that, although there is a great community of herpetofaunas between Puerto Rico and the Virgin Islands - all islands on the Puerto Rico Bank - this community of faunas is not an identity. There are several species (Anolis roosevelti Grant; Amphisbaena fenestrata Cope; Sphaerodactylus parthenopion Thomas) which occur on the Virgin Islands but not on Puerto Rico. Thus we cannot assume out-of-hand that C. pinguis is conspecific with C. mattea or C. portoricensis.

C. pinguis is locally common on Anegada. We will not comment further on ecological or other data for this species, since these have been already very thoroughly treated by CAREY (1975).

SPECIMENS EXAMINED. – B.V.I., Anegada I., Sand Path (ASFS V14195); Sand Path, Cooper Rock (ASFS V14262); Low Key (ASFS V14196); Windberg Key (ASFS V14235–37, ASFS V26913); Citron Bush (ASFS V14253–54).

Cyclura ricordi Duméril & Bibron, 1837

Aloponotus ricordii Duméril & Bibron, 1837. Erp. gén. 4: 190. Holotype - MNHN 8304.

TYPE-LOCALITY. "Sainte-Domingue."

DEFINITION. - A species of Cyclura characterized by the combination of moderate size (males to 440, females to 365 snout-vent length), 7 to 11 (modally 8) scale rows between the frontal and interparietal scales, azygous scales in prefrontal suture absent, 9 to 17 (modally 12) scales between anterior canthal scales, frontal scale not conspicuously enlarged, first prefrontal never in contact with precanthal, 7 to 13 (modally 10) vertical rows of loreals, 16 to 20 (modally 17) suboculars to anterior border of tympanum, 9 to 15 (modally 12) sublabials to eye center, no distinct rows of scales between infralabials and sublabials (Fig. 16), 1 or 2 (modally 2) postmentals, 28 to 46 femoral pores in a single row, dorsal crest scales 11 to 21 between occiput and shoulder, 31 to 43 ($\bar{x} = 39.1 \pm 1.9$) between shoulder and sacrum, 7 to 18 between sacrum and first caudal verticil, total dorsal crest scales between occiput and first caudal verticil 51 to 78 ($\bar{x} = 63.4 \pm 3.8$), dorsal crest scales on neck always higher than body crest scales, body crest scales always higher than postsacral crest scales, 56 to 89 scales around tail in fifth caudal verticil, 20 to 33 dorsolateral body scales in naris-eye distance, rostral scale always in contact with nasal scales. Adult and juvenile patterns identical (except that in adults the juvenile pattern is slightly diluted and less contrasting than in juveniles): juvenile pattern consisting of five or six bold pale gray chevrons alternating with dark gray to black chevrons of which five continue as bold but narrow lines diagonally onto venter. In adults, these same pattern elements persist, but the dark chevrons become less black and more gray ventrolaterally, although it is not unusual for the dark chevrons to maintain their juvenile intensity dorsally. Scale count variation in Tables 3-5.

DISTRIBUTION. - Hispaniola, where known bij specimens only from the Valle de Neiba in the República Dominicana and the Península de Barahona south of the Sierra de Baoruco, and seen on Isla Cabritos in Lago Enriquillo by junior author;

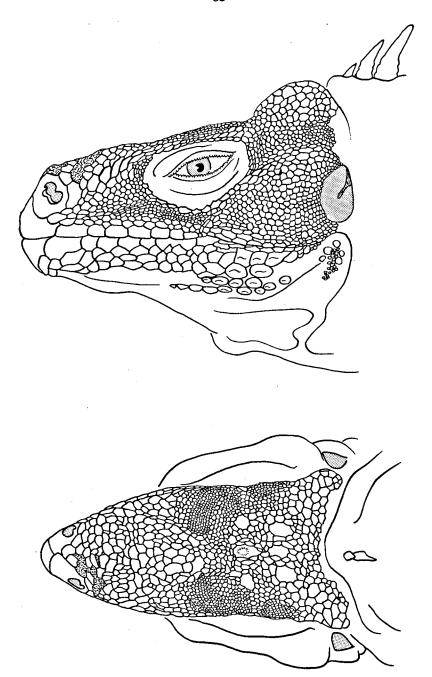


Fig. 16. Lateral and dorsal views of the head of *Cyclura ricordi* (ASFS V21091) from 14 km W Duvergé, Independencia Province, República Dominicana; snoutvent length 440 mm; male.

presumably also occurring in the Haitian Cul de Sac plain which is continuous with the Dominican Valle de Neiba but as yet unknown by specimens from Haiti.

Variation. – The largest male (ASFS V21091) has a snout-vent length of 440 and the largest female (ASFS V13802) a snout-vent length of 365. The smallest juvenile (ASFS V13806) has a snout-vent length of 85. The longest head in males (ASFS V21091) measures 81.8 and in females (ASFS V13802) 59.8; maximum head breadth in males is 39.2 (ASFS V13798) and in females 35.5 (ASFS V13802).

C. ricordi shows very little variation in coloration and pattern, nor does it demonstrate any striking ontogenetic change in these features. Juveniles are strongly and contrastingly patterned with five or six bold pale chevrons, alternating with dark gray to black chevrons which extend onto the sides: five of the black chevrons continue onto the venter as bold but narrow diagonal black lines. This pattern persists in adults, although in most full-grown individuals the pattern is usually not so intense as it is in juveniles; nevertheless the pattern elements are clearly visible in these duller specimens.

The most obvious "key character" which will distinguish C. ricordi from all other species of Cyclura is the presence of greatly enlarged and spinose scales at each caudal verticil. These scales are obvious in even the smallest juvenile, and their appearance is not ontogenetic. In general, C. ricordi resembles Ctenosaura in the very spinose tail.

REMARKS. - The distribution of *C. ricordi* seems to be limited to the very arid Valle de Neiba in the República Dominicana (including Isla Cabritos in Lago Enriquillo) and on the xeric portion of the Península de Barahona south of the Sierra de Baoruco. There are no specimens available from the Haitian Cul de Sac plain, but we expect the species to occur there. Judging from our experience, we feel that *C. ricordi* and *C. c. cornuta* occur in about equal numbers in the Valle de Neiba; the two species are widely sympatric and probably widely syntopic as well. They are brought in by native collectors at any locality in about equal numbers. On the Península de Barahona, however, *C. c. cornuta* seems to be the

more abundant of the two; although we have only limited material of both species from the Península de Barahona, the senior author has observed living and road-killed Cyclura there, both on the road between Pedernales and Oviedo, and between Cabo Rojo and Aceitillar; all such individuals were C. cornuta and not C. ricordi. Since the latter species does not seem to be especially secretive in the Valle de Neiba, it is likely that C. ricordi is less common than C. cornuta on the Peninsula. Although one has the impression that C. c. cornuta is the larger member of the pair, we call attention to the fact that our largest male C. c. cornuta has a snout-vent length of 404, whereas the largest C. ricordi male has a snout-vent length of 440. The discrepancy in female size, however, is very marked, with the largest female C. c. cornuta having a snout-vent length of 510, the largest female C. ricordi a snout-vent length of only 305. In the field, the two species can easily be identified by the dark and unpatterned dorsum and sides of C. c. cornuta in contrast to the diagonally barred back and sides of C. ricordi.

C. ricordi, in relation to other species of Cyclura, has less dorsal crest scales (31–43; $\bar{\mathbf{x}}=39.1$) than C. cychlura (37–83; $\bar{\mathbf{x}}=62.1$) and C. cornuta (40–56; $\bar{\mathbf{x}}=47.4$). C. ricordi resembles C. nubila in number of dorsal crest scales between the shoulder and sacrum, at least as far as mean is concerned (30–53; $\bar{\mathbf{x}}=40.2$ in C. nubila), but the variation (= range) in C. ricordi is less (31–43) than in C. nubila. In total median crest scales, C. ricordi has a lower mean (63.4) than C. nubila (69.2) and C. cychlura (96.4), but the range of these scales (51–78) in C. ricordi is almost completely enclosed within the range in C. nubila (52–85).

SPECIMENS EXAMINED. – República Dominicana, Independencia Province, 10 km NW Duvergé (ASFS V13798–802, ASFS V14943, ASFS V13805–07, ASFS V26911); 14 km W Duvergé (ASFS V21091); 13.1 km NW Duvergé (ASFS V30679–703); Pedernales Province, 5 km E Pedernales (ASFS V2538).

Cyclura carinata Harlan, 1824

Cyclura carinata Harlan, 1824. J. Ac. Nat. Sci. Phila. 4: 250. Holotype – unknown; not in Academy of Natural Sciences of Philadelphia.

Cyclura carinata bartschi Cochran, 1931. J. Wash. Ac. Sci. 21: 39. Holotype – USNM 81212. Type-locality – Booby Cay, east of Mayaguana Island, Bahama Islands.

TYPE-LOCALITY, "Turk's Island."

Definition. - A species of Cyclura characterized by the combination of small size (males to 350, females to 285 snout-vent length), no enlarged frontal scale, azygous scales in prefrontal suture absent, 7 to 13 (modally 9) scales between the anterior canthal scales, first prefrontal never in contact with precanthal, 6 to 11 (modally 9) vertical rows of loreals, 11 to 17 (modally 15) suboculars to anterior border of tympanum, no clearly demarcated sublabials, 1 to 4 (modally 2) postmentals (Fig. 17), 26 to 48 femoral pores in a single row, dorsal crest scales 11 to 20 between occiput and shoulder, 39 to 71 ($\bar{x} = 49.1 \pm 1.4$) between shoulder and sacrum, 6 to 15 between sacrum and first caudal verticil, total dorsal crest scales between occiput and first caudal verticil 61 to 101 ($\bar{x} =$ = 75.9 ± 1.9), dorsal crest scales on neck usually higher than body crest scales, body crest scales usually higher than postsacral crest scales, 46 to 74 scales around tail in fifth caudal verticil, 16 to 25 dorsolateral body scales in naris-eye distance, rostral scale always in contact with nasals. Adults gray dorsally, variegated with dull tan on back and sides or with paler gray to cream on head and neck, venter bluish, greenish, or dirty gray, dorsal crest scales of males blue-gray; juveniles drab gray with between four and six anterior brown crossbars which do not extend onto sides but form an obscure series of inconspicuous bars which fade laterally, venter unpatterned and unstreaked but stippled or mottled dark gray. Scale count variation in Tables 3–5.

DISTRIBUTION. – Booby Cay off Mayaguana Island, Bahama Islands; Turks Islands (Big Sand Cay and Long Cay); Caicos Islands (Pine Cay, Ft. George Cay, North Caicos, Big Iguana Cay off East Caicos, Long Cay off South Caicos, Big Ambergris Cay and Little Ambergris Cay).

Cyclura carinata carinata Harlan

DEFINITION. - A subspecies of *C. carinata* with modally 2 postmentals and modally 1 scale separating the nasal scales.

DISTRIBUTION. - The Turks and Caicos islands.

Variation. - The largest male (MCZ 15528) has a snout-vent length of 350 and is from Pine Cay in the Caicos Islands, whereas the largest female (AMNH 80100) has a snout-vent length of 242 and is from Long Cay in the Caicos Islands. None of 27 specimens from the Turks Islands reaches so large a size in either sex as do the Caicos Islands specimens; the largest male (ASFS V27329) from the Turks Islands has a snout-vent length of 313 and is from Big Sand Cay, whereas the largest Turks Islands female (ASFS V23651) has a snout-vent length of 219 and is from Long Cay. The smallest juvenile C. c. carinata (UMMZ 117401) has a snout-vent length of 75 and is from Long Cay, Turks Islands; the smallest Caicos Islands juvenile (AMNH 80106) has a snout-vent length of 83 and is from Long Cay. Maximum head measurements, as might be expected, are all from Caicos Islands specimens. The longest head in males (MCZ 15529) measures 69.0, in females 45.3 (AMNH 80100); maximum head breadth in males is 39.4 (LSUMZ 22152) and in females 25.7 (AMNH 80100).

C. c. carinata is an exceptionally drab lizard. Adults are gray dorsally, variegated with dull tan on the back and sides, or with paler gray to cream on the head and neck; the venter is bluish, greenish, or dirty gray, and the dorsal crest scales on males may be blue-gray. Juveniles are drab gray with between four and six anterior brown crossbars which do not extend onto the sides but form an obscure series of inconspicuous bars which fade laterally; the venter is unpatterned and unstreaked but may be stippled or mottled with dark gray. As far as our very limited color notes are concerned, there seem to be very few, if any, differences in coloration and pattern between individuals from various islands. This is most especially surprising since C. c. carinata has a range including a large number of islands (unquestionably more than mentioned

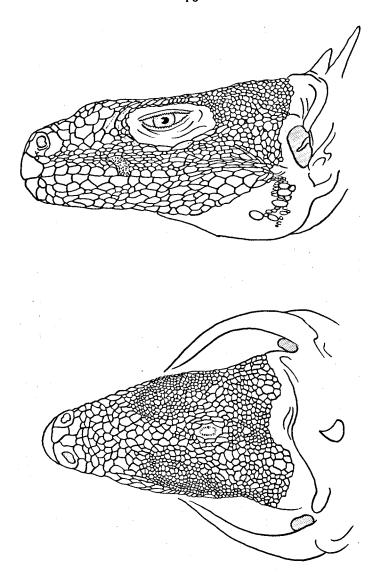


Fig. 17. Lateral and dorsal views of the head of *Cyclura carinata* (ASFS V10612); the subspecies is *C. c. carinata* from Ambergris Cay, Caicos Islands; snout-vent length 340 mm; male.

here in the distribution from which we have examined material); one might expect that, as in C. c. figginsi, local island demes might vary somewhat on these details, but such does not seem to be the case.

In addition to uniformity in color and pattern, the modes and means of the Caicos Islands and Turks Islands samples are remarkably similar. In both samples of *C. c. carinata*, there are modally 9 scales between the anteriormost canthals, 3 scale rows between the semicircles and the interparietal, 9 vertical loreal rows, 8 supralabials to eye center, and 2 postmentals. The mean numbers of femoral pores in the two subsamples are 38.9 and 37.1, in fourth toe subdigital scales 34.6 and 33.1, in occiput-shoulder crest scales 15.6 and 16.5, in sacrum-first caudal verticil scales 10.9 and 10.4. One difference between the two subsamples is that Caicos Islands specimens modally have 1 scale between the nasals, whereas the mode in Turks Islands lizards is 2.

Within the members of the genus thus far discussed, C. carinata ranks moderately in mean number of dorsal crest scales between the shoulders and the sacrum ($\bar{x}=49.1$; range 39–71); the low count is from a Turks Islands lizard, the high from a Caicos Islands specimen. In general, the Turks Islands C. carinata have less shoulder-to-sacrum scales (39–53; $\bar{x}=43.9$) than do those from the Caicos Islands (41–71; $\bar{x}=51.2$). In total median dorsal scales, C. carinata is lower in mean (75.9) than the species cychlura (96.4), cornuta (84.4), collei (88.2), and higher than nubila (69.2), ricordi (63.4) and pinguis (58.8).

REMARKS. -C. c. carinata has a broad geographic distribution in the Turks and Caicos islands, where it occurs on a large number of islands and cays - probably far more than those whence we have examined specimens. It is locally abundant, most especially on smaller islands with herbaceous to shrub stage growth.

SPECIMENS EXAMINED. - Turks Islands, Long Cay, 3.2 km SE Grand Turk Island (ASFS 10925-26, ASFS V23651-58, MCZ 11902, USNM 81785-93, UMMZ 118321-25, UMMZ 117401); Big Sand Cay (ASFS V27328-29). - Caicos Islands, Pine Cay (ASFS V19455-56, UMMZ 118326, LSUMZ 22151-53, MCZ 15528-29); Ft. George Cay (ASFS V27278-81); North Caicos I., Kew (ASFS V27231); Big Iguana Cay off

East Caicos (USNM 81219-33, USNM 81776-80; Long Cay off South Caicos (ASFS V10681, AMNH 80100-06); Big Ambergris Cay (ASFS V27388-89); Little Ambergris Cay (ASFS V27392); "Amergris Cays" (ASFS V10612, MCZ 11904, MCZ 42315-16).

Cyclura carinata bartschi Cochran

DEFINITION. – A subspecies of *C. carinata* with modally 3 postmentals and modally 0 scales separating the nasal scales.

DISTRIBUTION. - Booby Cay, off Mayaguana Island, Bahama Islands.

VARIATION. – The largest male (ASFS V11336) has a snout-vent length of 335, the largest female (ASFS V11339) 285. The longest head in males measures 68.1 (ASFS V11336) and in females 49.9 (MCZ 42357); maximum head breadth also occurs in these two specimens, with the male having a head breadth of 38.0 and the female 29.1. The smallest individual (ASFS V11340) has a snout-vent length of 163.

The adults in life are gray above, mottled with paler gray to cream on the head and neck; the iris is golden. Juveniles have about six dorsal brown crossbars which are faint and become even more obscure with increasing age. These crossbars do not extend onto the venter, which is dark, stippled or mottled, and unpatterned. Neither adults nor juveniles have the hindlimbs ocellate.

COMPARISONS. — We retain the name bartschi with some misgivings. We have examined nine specimens, of which seven were collected by C. Rhea Warren and were examined in life by the senior author. In general, their body colors seem to be somewhat paler (tending towards creams to pale grays) than those of nominate carinata (gray to dull tan), although the latter subspecies does have cream to pale gray mottling on the head and neck. In size, bartschi seems to be intermediate between Caicos Islands and Turks Islands carinata, at least in males; the largest female bartschi is larger (snout-vent length 285) than any female carinata examined by us (242). The two scale differences which seem most pertinent

are the modal occurrence of 3 postmental scales in bartschi (in contrast to 2 postmentals in both subsamples of carinata), and in modally having the nasals in contact (nasals separated by 1 or 2 scales modally in both carinata subsamples). Neither of these differences is absolute, however. The postmental range in bartschi is 1-4 with a mode of 3; of nine lizards, seven (78 per cent) have 3 or 4 postmentals. The postmental range in Caicos Islands carinata is 1-3, with a mode of 2; of 46 lizards, 26 (56 per cent) have 1 or 2 postmentals. The postmental range in Turks Islands lizards is 1-3 with a mode of 2; of 25 specimens, 20 have 1 or 2 postmentals (80 per cent). Thus less than 3 postmentals occurs with very low frequency in bartschi (two of nine specimens) but is much more frequent in C. c. carinata, with the Turks Islands lizards showing a higher percentage than those from the Caicos Islands.

In regards to the nasal contact, six of nine bartschi have the nasals in contact, whereas one has 1 row of scales separating the nasals and two have 2 rows in this position. The same range (0-2) occurs in Caicos Islands lizards, but the mode of 1 row of scales (24 of 43 lizards) is strong; eight lizards have the nasals in contact and 11 have 2 rows of scales in this position. Combining data for both subsamples of C. c. carinata shows that 88 per cent of C. c. carinata have 1 or 2 rows of scales between the nasals and 12 per cent have the nasals in contact, whereas in C. c. bartschi, 33 per cent have 1 or 2 rows of scales between the nasals and 67 per cent have the nasals in contact.

A third reason for our accepting bartschi as a subspecies distinct from C. c. carinata is the fact that it occurs outside the Caicos-Turks area. C. c. bartschi seems to be an outlier population of a species which otherwise has a compact distribution; it would seem likely that bartschi has been long isolated from its parent population. It is however striking that, considering the relative stability of characteristics in both subsamples of C. c. carinata, C. c. bartschi has diverged to a somewhat greater degree.

REMARKS. -C. c. bartschi seems to be common on Booby Cay off the eastern end of Mayaguana Island. Warren noted that there were reports of occasional lizards on Mayaguana itself, but there is

no known established population on that island. Since the channel separating Booby Cay from Mayaguana is on 0.4 km across, it does not seem unlikely that occasional iguanas reach Mayaguana by swimming from Booby Cay.

SPECIMENS EXAMINED. - Bahama Islands, Booby Cay (ASFS V11336-42, MCZ 38182, MCZ 42357).

Cyclura rileyi Stejneger, 1903

Cyclura rileyi Stejneger, 1903. Proc. Biol. Soc. Wash. 16: 129. Holotype – USNM 31969.

Cyclura nuchalis Barbour & Noble, 1916. Bull. Mus. Comp. Zool. 60: 156. Holotype - Acad. Nat. Sci. Philadelphia 11985. Type-locality - Fortune Island, Bahama Islands.

Cyclura cristata Schmidt, 1920. Proc. Linn. Soc. N.Y. 33: 6. Holotype – AMNH 7238. Type-locality – White Cay (north of Watling's Island), Bahama Islands; later corrected (Schmidt, 1936: 128) to White Cay, Exuma Cays, Bahama Islands.

Type-locality. Watling's Island (= San Salvador Island), Bahama Islands.

DEFINITION. - A species of Cyclura characterized by the combination of small size (males to 306, females to 254 snout-vent length), 4 to 7 (modally 4) scale rows between the frontal and interparietal scales, azygous scales in prefrontal suture absent, 5 to 11 (modally 7) scales between the anterior canthal scales, 3 to 9 (modally 7) scales bordering the frontal, first prefrontal never in contact with precanthal, 3 or 4 (modally 3) vertical rows of loreals, 10 to 15 (modally 13) suboculars to anterior border of tympanum, 5 to 7 (modally 6) sublabials to eye center, 2 or 3 (modally 2) rows of scales between infralabials and sublabials (Fig. 18), 1 to 3 (modally 2) postmentals, 35 to 50 femoral pores in a single row, dorsal crest scales 13 to 25 between occiput and shoulder, 60 to 81 ($\bar{x} = 68.7$ ± 1.4) between shoulder and sacrum, 18 to 27 between sacrum and first caudal verticil, total dorsal crest scales between occiput and first caudal verticil 104 to 123 ($\bar{x} = 115.4$), but postsacral scales not enlarged and thus not counted in two populations (rileyi. nuchalis), dorsal crest scales on neck always higher than body

crest scales, body crest scales almost never higher than postsacral crest scales, 40 to 48 scales around tail in fifth caudal verticil, 18 to 25 dorsolateral body scales in naris-eye distance, rostral scale always in contact with nasals. Adults dorsally variable (by subspecies) from orange with pale blue-green markings and fine black vermiculations, bluish gray marbled with orange-brown or blackish, or gray with brown to orange-brown vermiculations; juvenile color and pattern pale brown with a middorsal pale zone often including about seven vague darker areas, and in one populations with a tendency toward general overall dorsal longitudinal pale and dark streaking. Scale count variation in Tables 3–5.

Cyclura rileyi rileyi Stejneger

Definition. – A subspecies of C. rileyi with modally 5 rows of scales between the prefrontal shields and the frontal scale, modally 7 scales between the anterior canthals, 5 to 7 ($\bar{x} = 6.4$; modally 7) scales bordering the frontal, modally 4 vertical loreal rows, modally 5 lorilabial rows, modally 6 supralabials to eye center, modally 10 superciliaries, modally 6 sublabials to eye center, modally 2 rows of scales between infralabials and sublabials, postsacral crest scales poorly defined, caudal verticils poorly defined, modally 1 scale row between prefrontals; adults dorsally orange with pale blue-green markings and fine black vermiculations; head and ventral ground color pale blue-green, tail mostly grayish green with irregular black blotches which form bands distally; uppersides of hindfeet blackish, remainder of limbs pale blue-green above with orange markings.

 $\label{eq:Distribution.} \mbox{ - San Salvador Island (= Watling's Island), Bahama Islands, including Man Head Cay and Green Cay.}$

Variation. – The largest male (ASFS V10620) has a snout-vent length of 306, the largest female (ASFS V2392) 254. The longest head in males measures 57.3 (ASFS V10620) and 43.2 in females (ASFS V2392); these same two specimens have the maximum head breadths – 32.5 in males and 24.6 in females. The smallest juvenile (ASFS V2334) has a snout-vent length of 80.

An adult male from Man Head Cay was described in life as dorsally orange with pale blue-green markings and fine black vermiculations. The head and venter were pale blue-green, with orange markings on the labials, throat, and chest. The iris was brown. The tail was mostly grayish green with irregular black blotches, these forming bands distally. The upper surfaces of the hindfeet were blackish and the rest of the limbs pale blue-green with orange markings dorsally. Five young individuals (snout-vent lengths 80–118) were dorsally pale brown, somewhat darker middorsally, the dorsal crest scales alternating dark and light, and with a middorsal pale line and a pair of paravertebral dark lines, slightly paler dorso-laterally and darker again laterally; the venter was unmarked. All young specimens had dark markings on the nape, the largest lizard having a mottled head as well as assuming a greenish tinge over the entire body.

A series of adults from near Cockburn Town was described as basically colored like the adult female described above; the hands and feet were conspicuously dark, and the dorsal crest scales were bright orange in one male. A female with a snout-vent length of 228 was somewhat differently colored in that there was no orange in the dorsal pattern; rather, the back was pale blue-gray with darker brown markings.

As preserved, juveniles lack dorsal chevrons or pale diagonal markings; rather, the back is either unicolor dark with a pale (grayish) middorsal zone or stripes, or with at times about seven vague darker areas included on the dorsal crest area.

In dorsal crest scales between shoulder and sacrum, C. rileyi most closely approaches C. cychlura in mean (68.7 in rileyi versus 62.1 in cychlura), although the amount of variation in cychlura (37-83) totally embraces that in rileyi (60-81). The same is true for total median dorsal scales, although the data here are much less reliable, since two of the subspecies of C. rileyi (rileyi, nuchalis) have the postsacral scales so inconspicuous and reduced that meanningful counts cannot be taken; therefore, the median dorsal scale counts here used for C. rileyi are in effect those of C. r. cristata, in which subspecies the median postsacral scales are well developed. Using this count alone for C. rileyi, the mean (115.4) exceeds that

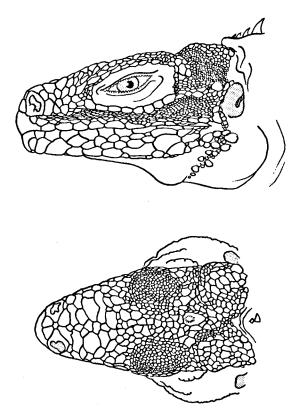


Fig. 18. Lateral and dorsal views of the head of *Cyclura rileyi* (ASFS 10620); the subspecies is *C. r. rileyi* from Green Cay, San Salvador, Bahama Islands; snout-vent length 306 mm; male.

of all other species and is most closely approached by that of *C. cychlura* (96.4). Although there is some overlap in the counts between these two species (37–118 in *cychlura*; 104–123 in *rileyi*), there is not total overlap. It is perhaps pertinent that the highest median dorsal counts (67–118) in *C. cychlura* are in *C. c. figginsi*, that subspecies that occurs closest to *C. r. cristata* (both are in the Exuma Cays). In some ways, *C. r. cristata* appears to bridge the gap, both geographically and morphologically, between *C. cychlura* and *C. rileyi*. But its resemblances (most notably juvenile pattern)

are so like that of C. rileyi that we prefer to associate it nomenclatorially with that species rather than with C. cychlura.

REMARKS. – C. r. rileyi is abundant on the island of San Salvador. PAULSON (1966) reported the occurrence of the species in cormorant (*Phalacrocorax olivaceus* Humboldt) rookeries on that island. It is apparently less common elsewhere on San Salvador but does occur on Man Head Cay and Green Cay in some numbers.

SPECIMENS EXAMINED. – Bahama Islands, San Salvador (no other locality) (UF/FSM); 4.0 km SE Cockburn Town, island in Great Lake (ASFS V2391-95); Man Head Cay off northeast end of San Salvador (ASFS V2329-35); Green Cay (ASFS V10620-24).

Cyclura rileyi nuchalis Barbour & Noble

Definition. – A subspecies of C. rileyi with modally 4 rows of scales between the prefrontal shields and the frontal scale, modally 7 scales between the anterior canthals, 3 to 8 ($\bar{x} = 6.4$; modally 6) scales bordering the prefrontal, modally 3 vertical rows of loreals, modally 5 lorilabial rows, modally 6 supralabials to eye center, modally 8 superciliaries, modally 6 sublabials to eye center, always 2 rows of scales between the infralabials and the sublabials, postsacral crest scales poorly defined, caudal verticils poorly defined, modally 1 scale row between the prefrontals; adults dark blackish to bluish gray, marbled with orange-brown to blackish, venter grayish with orange-brown marbling on chest.

DISTRIBUTION. - Fortune Island, Fish Cay, and North Cay, Crooked-Acklin's group, Bahama Islands.

VARIATION. – The largest male (ASFS V8943) has a snout-vent length of 263, the largest female (ASFS V8942) 240. The longest head in males measures 56.2 and in females 44.3; the maximum head breadth is 29.4 in males and 25.8 in females; all head measurements are from the specimens cited above as having the greatest snout-vent lengths. The smallest juvenile (MCZ 125171) has a snout-vent length of 121.

Adult C. r. nuchalis were described in life as dark blackish with a gray venter (ASFS V8722); dark bluish gray dorsally, marbled with orange-brown or blackish. Venter grayish with orange-brown marbling on chest; iris blackish brown (ASFS V8942-48). In general, adult C. r. nuchalis are comparable in color and pattern to C. r. rileyi in that both are more or less reticulate orange on a dirty gray to brown background dorsally. Juvenile C. r. nuchalis are very similar in both coloration and pattern to juvenile C. r. rileyi with a darker middorsal zone in the dorsal pale band. The dorsal colors in life of juvenile nuchalis are dirty tan and black; the head is dirty brownish, the venter gray, and the gular area dirty yellow. Juveniles do not show the vermiculations and brighter oranges found in adults.

COMPARISONS. – Differences between C. r. rileyi and C. r. nuchalis are of the same modal nature as in other subspecies. In scale rows between the prefrontal shields and the frontal scale, rileyi has a mode of 5, nuchalis a mode of 4. C. r. rileyi modally has 7 scales bordering the frontal, whereas C. r. nuchalis modally has 6. In rileyi, there are modally 10 superciliaries, whereas in nuchalis the mode is 8. C. r. rileyi appears to reach a larger size (males to 306, females to 254) than does C. r. nuchalis (males to 263, females to 240). The two subspecies are similar in that they (in contrast to C. r. cristata) have clearly defined loreal rows and do not have enlarged median dorsal postsacral scales or enlarged middorsal scales in the caudal verticils.

REMARKS. — As far as known, C. r. nuchalis is restricted to two cays (Fish Cay, North Cay) in the Bight of Acklin's in the southeastern Bahamas; the species has also been taken on Fortune Island, which forms the western margin of the Crooked-Acklin's Bank. The animals are common on the two isolated cays in the Bight and apparently much less so on Fortune Island. USNM 61312 is recorded as questionably from Cat Island in the Bahamas, and George R. Zug has suggested that this individual may be the source of the record (Cope, 1887) of Cyclura nubila from Cat Island — an island whence no further Cyclura have been reported. The

specimen is C. r. nuchalis, and we can only assume that the locality data are incorrect.

SPECIMENS EXAMINED. – Bahama Islands, Crooked-Acklin's Bank, Fish Cay (ASFS V8722, ASFS V8942–45, ASFS V8947–48, MCZ 31493–94); North Cay (MCZ 31865–69, MCZ 125170–73); Fortune Island (USNM 84250); "Cat Island" (USNM 61312).

Cyclura rileyi cristata Schmidt

DEFINITION. – A subspecies of C. rileyi with modally 6 rows of scales between the prefrontal shields and the frontal scale, modally 9 and 10 scales between the anterior canthals, 6 to 9 ($\bar{x} = 7.4$; modally 7) scales bordering the frontal, vertical loreal rows poorly defined and not countable, modally 6 lorilabial rows, modally 7 supralabials to eye center, modally 9 superciliaries, modally 7 sublabials to eye center, modally 3 rows of scales between infralabials and sublabials; postsacral crest scales well defined (18 to 27), total dorsal crest scales 104 to 123, caudal verticils well defined with 40 to 48 scales around tail and modally 5 scales in fifth caudal verticil, modally 2 scale rows between prefrontals; adults dorsally dark gray with brown to orange-brown vermiculations; dorsal crest scales orange, throat pale gray and orange, sides of jaws, eyeskin, and snout orange, forelimbs orange with gray marbling.

DISTRIBUTION. - White Cay, Exuma Cays, Bahama Islands.

VARIATION. – The largest male (ASFS V10782) has a snout-vent length of 280, the largest female (ASFS V10783) 254. The longest head in males measures 54.3, in females 45.3; the maximum head breadth in males is 28.6, in females 24.9. Head length and breadth data are from the maximally sized male and female noted above. The smallest juvenile (ASFS V10791) has a snout-vent length of 114.

In life, the males were gray dorsally with brown to orange-brown vermiculations; the dorsal crest is orange, and there is some orange marbling on the chin; the throat is pale gray with an orange suffusion, and the sides of the jaw, the eyeskin, and the snout are orange; the forelimbs have orange and gray marblings. Females

and small males resemble the adult males in both color and pattern, except that they have less orange on the sides of the head and the throat. Juveniles are longitudinally patterned like juvenile $C. \ r. \ rileyi$ and $C. \ r. \ nuchalis$ and have no evidence of diagonal markings. Although the similarities in pattern between the juveniles of the three subspecies of $C. \ rileyi$ are obvious, juvenile cristata lack a dark area in the very vague middorsal pale band.

COMPARISONS. - C. r. cristata is the most brightly colored of the three subspecies of C. rilevi. The bright orange dorsal crest scales and the orange facial and anteroventral suffusions and colors are considerably more apparent and distinctive than the somewhat more drab colors and patterns of rileyi and nuchalis. The median dorsal postsacral crest scales are well developed in cristata, whereas they are inconspicuous and not greatly enlarged in rilevi or nuchalis. The same is true of middorsal verticil scales, which are obvious and countable in cristata and are inconspicuous in the two other subspecies. C. r. cristata has a mode of 6 scale rows between the prefrontal shields and the frontal scale (5 in rileyi, 4 in nuchalis), has a mode of 9 scales between the anterior canthals (7 in both rileyi and nuchalis), has poorly defined loreal rows (well defined in rileyi and nuchalis), has 6 rows of lorilabials (5 in rileyi and nuchalis), has 7 supralabials to eye center (6 in rilevi and nuchalis), has 9 superciliaries (10 in rileyi, 8 in nuchalis), has 7 sublabials to eye center (6 in rileyi and nuchalis), has 3 rows of scales between the infra- and sublabials (2 rows in rileyi and nuchalis), and modally has 2 rows of scales between the prefrontals (1 in rileyi and nuchalis).

REMARKS. — The differences between cristata on one hand and rileyi and nuchalis on the other are such that one might interpret cristata as a species distinct from rileyi and nuchalis. In addition, as we have already pointed out, one might with some propriety associate cristata with C. cychlura, its geographically closest congener. In some ways, cristata seems to bridge the gap between C. cychlura and C. rileyi; the distinct postsacral median crest scales, the low dorsal crest scales, and the bright orange in the pattern all tend

towards C. c. cychlura or even C. c. figginsi, rather than towards C. rileyi. Militating against a close relationship with (or derivation from) C. cychlura is the fact that the juvenile pattern of cristata is that of C. rileyi (longitudinally zonate) rather than that of C. cychlura (diagonally barred dark and light). We have here followed a conservative course and have placed more emphasis on juvenile pattern than on some structural features which might be of more importance. Although variable in C. cychlura, the absence of azygous scales in the prefrontal suture in all taxa we associate with C. rileyi would also seem to ally cristata with that species rather than with C. cychlura.

C. r. cristata seems to be moderately abundant on White Cay; the island itself is small (about 0.25 km²) and thus the population probably is never huge. The small size of many of the islands and islets where members of Cyclura occur (especially in the Bahamas and the Turks and Caicos islands) should always be considered in assessing the status of populations inhabiting them. The biological resources of such small islands unquestionably restrict the population density of any animal, and they may affect the population size of large animals as Cyclura more severely than smaller ones.

SPECIMENS EXAMINED. - Bahama Islands, White Cay (ASFS V10782-91).

ARTIFICIAL KEY TO THE LIVING TAXA OF Cyclura

	Upper surface of head with 3 or 5 scales (frontal + 1 or 2 pairs of prefrontals) enlarged and horn-like
1′	Upper surface of head without enlarged horn-like scales .
2	Rostral scale usually in contact with nasals C. cornuta stejneger
2′	Rostral rarely in contact with nasals
3	Fourth toe subdigital scales 30-37; dorsal scales in naris-eye
	distance 13–26
3′	Fourth toe subdigital scales 38-41; dorsal scales in naris-eye
	distance 30-44 C. cornuta onchiobsi

4	Rostral scale separated from nasal scales by 1 row to very many tiny scales
4′	Rostral scale in contact with nasal scales 6
5	Dorsolateral scales large, 6-8 in naris-eye distance; rostral scale separated from nasal scales by 2 rows of scales C. pinguis
5′	Dorsolateral scales small, 20-24 in naris-eye distance; rostral scale separated from nasal scales by 1 row (or many tiny granules) of scales
6	Two pairs of very greatly enlarged prefrontals, usually with azygous scales between them
6′	Prefrontal scales only slightly or not enlarged; azygous scales absent
7	4 to 11 scales between anteriormost canthals; first prefrontal rarely in contact with precanthal; total dorsal crest scales 52 to 85
7′	3 to 7 scales between anteriormost canthals; first prefrontal almost always in contact with precanthal; total dorsal crest scales 67–118
8	Dorsum in adults blue to blue-green, often intensely so on head
8′	Dorsum never brightly colored
9	Usually 3 azygous scales in prefrontal suture; usually 6 scales between anteriormost canthals; usually 5 vertical loreal rows; usually 10 superciliaries; usually 3 postmentals <i>C. nubila nubila</i>
9′	Usually 2 azygous scales in prefrontal suture; usually 10 scales between anteriormost canthals; usually 8 vertical loreal rows; usually 12 or 13 superciliaries; usually 2 postmentals
10	Usually no azygous scales in prefrontal suture; usually 4 lori- labial rows; body and dorsal crest scales orange or orange- blotched

10'	Usually 1 azygous scale in prefrontal suture; usually 3 lorilabial rows; body and dorsal crest scales not orange or without orange blotching
11	Usually 4 scale rows between prefrontal shields and frontal scale; usually 7 vertical loreal rows; usually 2 postmentals; dorsum black, mottled cream; head at times with pink and orange
11'	Usually 3 scale rows between prefrontal shields and frontal scale; usually 6 vertical loreal rows; usually 1 postmental; dorsum dull gray-brown to bluish with white dorsal crest scales
	Caudal verticil scales greatly enlarged and spinose 13 Caudal verticil scales not greatly enlarged and spinose 15
13	Dorsum and sides with dark gray to black diagonal bars; a regular series of sublabial scales; total dorsal crest scales 51-78
13′	Dorsum and sides drab and without dark diagonal markings; no regular series of sublabial scales; total dorsal crest scales 61–101
	Usually 2 postmentals and 1 scale between the nasal scales
15	Postsacral dorsal crest scales well developed, 18–27; adults dark gray with orange to orange-brown vermiculations
15 ′	Postsacral dorsal crest scales poorly differentiated from adjacent scales; adults dark orange with pale blue vermiculations or blackish to bluish gray marbled with orange-brown or blackish
16	Usually 9 or 10 scales bordering interparietal: usually 10 super-

DISCUSSION

BARBOUR & NOBLE (1916) made no attempt to synthesize an evolutionary sequence within the genus Cyclura; although their comparisons of taxa are at times pertinent, they did not use trinomials. even where they were convinced that two taxa were indeed quite closely related. Such actions doubtless were in part due to the insularity of the taxa and in part to the extreme paucity of material available to them. Cochran (1934: 29) suggested that C. c. bartschi was intermediate between the nominate subspecies and C. nuchalis, but she did not justify her comments in detail and made no nomenclatorial adjustments. At least STEINEGER (1904: 670-671) noted the similarities between Isla Mona Cyclura and C. cornuta, and SCHMIDT (1928: 103) showed a dorsal view of the head of C. steinegeri and suggested its alliance with Hispaniolan C. cornuta and Navassan C. nigerrima. Gradually, some trinomina have come into use for various populations of ground iguanas, but these combinations have remained few (GRANT, 1941: 29-37; BARBOUR, 1937: 132; THOMAS, 1966: 80) and have rarely been justified by any concrete morphological evidence from examination of suites of specimens. Although we have studied far more material than any previous workers, our own arrangements are still to some extent inductive. Too many pieces of the Cyclura puzzle are missing. The fact that two taxa (mattea, portoricensis) are known only from skeletal remains and that in the Bahamas Cyclura is known from fossils from New Providence (where it does not now exist) and questionably from Barbuda (ETHERIDGE, 1966: 353-54 and 1964: 68) in the Lesser Antilles whence the genus is presently unknown, suggests that Cyclura was once much more widly distributed than it is

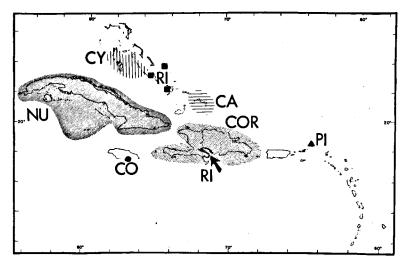


Fig. 19. Map of the Antilles, showing the distributions of the species of Cyclura; detailed maps of distributions of some species are gives elsewhere in the present paper (Figs. 8, 9, 11, 13). Symbols used in this figure are: NU = C. nubila (dense diagonal lines); CY = C. cychlura (vertical lines); RI = C. rileyi (solid squares); CA = C. carinata (horizontal lines); COR = C. cornuta (dense stippling); CO = C. collei (solid circle); PI = C. pinguis (solid triangle); RI = C. ricordi (area enclosed by solid line in southern Hispaniola.

now. We have examined also fossil material from Great Exuma in the Bahama Islands.

The scattered nature of locality records of ground iguanas from many apparently suitable islands and islets in the Bahamas has been attributed to human activities, but this may be a gross oversimplification of a much more complex problem. The absence, for instance, of C. carinata from South Caicos Island and its abundance on Long Cay, separated from South Caicos by a channel less than half a kilometer wide, might be cited as the aftermath of human settlement of South Caicos and lack of a permanent settlement on Long Cay. But, on the other hand, South Caicos is a relatively large island $(8.0 \times 4.0 \text{ km})$, Long Cay much smaller $(4.0 \times 0.8 \text{ km})$, and the human population of South Caicos is fairly localized with apparently both ample space and ample resources still remaining to support at least a minimal Cyclura population; South Caicos is in

no way a densely populated island, yet it lacks ground iguanas. We cite this one example, which could be further multiplied, to emphasize our point that human intervention need not be – perhaps is primarily not – the major reason for the peculiarly sporadic nature of extent *Cyclura* populations in the Antilles, most especially the Bahamas and the Virgin Islands.

Although we may never know the primal total geographic distribution of *Cyclura* in the West Indian region, it still is mandatory to use what information we can retrieve in order to construct some sort of hypothetical phylogenetic relationship within the genus. If we accept the eight species herein defined (and we are well aware that there are many who will disagree with our taxonomic treatment, or at least regard it with some scepticism), then the following seems a reasonable arrangement and evolutionary schema for *Cyclura*.

As early as Barbour & Noble (1916: 140) the suggested origin of Cyclura has been from the mainland (and in part non-Antillean insular) genus Ctenosaura. The two genera differ externally primarily in that Ctenosaura lacks combs (= longitudinal short series of fused ventrolateral digital scales) on the hindfeet, a character that occurs in all Cyclura. A second morphological Ctenosaura character is the presence of enlarged scales setting off the caudal verticils. But Ctenosaura shares this character with two species (ricordi, carinata) of Cyclura. It seems likely that C. carinata and C. ricordi represent one line of ground iguanas in the West Indies. If we postulate an Antillean invasion of a pro-Ctenosaura stock via Hispaniola, and this route for Antillean invasion has been suggested for a variety of groups by DARLINGTON (1957: 510 et seq.), then the presence of ricordi on Hispaniola and carinata on the Turks-Caicos-Mayaguana complex of islands south of the Crooked Island Passage lends credence to the basic nature of this pair of species. Two factors should be recalled: (1) those islands which are occupied by C. carinata are in effect "satellites" of Hispaniola, where C. ricordi occurs, and (2) those islands south of the Crooked Island Passage are old volcanic islands whose geological history as been quite distinct from that of the rest of the Bahamas north of the Passage (see Schwartz, 1968, for details of the herpetofauna and its interpretation). Thus, entry of a pro-Ctenosaura stock via Hispaniola and divergence there into comb-bearing lizards with one species limited to the island of entry and the other to old islands associated peripherally with Hispaniola are consonant with our contention that C. ricordi and C. carinata are basal Cyclura, most closely related to Ctenosaura.

A second evolutionary line within the genus is that including nubila, cychlura, cornuta, collei, and rileyi. Of these, nubila (Cuba, Cayman Islands) seems ancestral to cychlura (Bahamas); the two species have several features in common (presence of azygous scales, enlarged prefrontals) but differ in other details (reduced size of dorsal crest scales in cychlura). Since the Bahamas have been inundated at various times in the past and have only relatively recently been emergent to about their present configuration, it seems reasonable to assume that Cuban nubila invaded the Bahamas and there gave rise to cychlura. The invasion of C. nubila onto the Cavman Islands would seem to have been more recent than the invasion of the Bahamas, since the Caymanian subspecies (caymanensis, lewisi) differ from nominate nubila in less striking ways (with the exception of the blue colors in lewisi) than does Bahamian cychlura. To these comments it should also be added that the outer islands of both the Great and Little Bahama banks apparently are in part volcanic; Schwartz (1968: 265-267) suggested that perhaps some Cyclura persisted on these higher and older outer-arc islands and later invaded other emerged Bahama Islands as they became suitable for inhabitation. If this hypothesis is tenable, then C. cychlura may have reached the Bahamas before or during periods of more or less complete inundation and have persisted (and differentiated) on some of the outer-arc volcanic islands; if this is the case, then the origin of cychlura from nubila may well have preceded the invasion of the Caymans by nubila by many millenia. This would help account for the species-level division between Cuban nubila and Bahamian cychlura, but only subspecies-level differentiation of nubila on the Cayman Islands.

We relate C. cornuta (Hispaniola, Mona, Navassa) to the foregoing species-pair on the basis of its large size and the specialization of the frontal and one or two pairs of prefrontals, scales already large and conspicuous in nubila and cychlura but not hornlike. There are other similarities (high dorsal crest scales as in nubila), but C. cornuta sets apart from nubila-cychlura in several ways, including the horn-like development of some of the head scales, the double or triple rows of femoral pores, and the virtually patternless juveniles (although remnants of the typical boldly diagonal dorsal pattern of cyclura and nubila may be seen in C. c. steinegeri). It seems likely that C. cornuta represents an Hispaniolan endemic, early derived from a pro-nubila stock on Cuba, that invaded Isla Mona on one hand and Navassa Island on the other. The Navassa Island subspecies (onchiopsis) is unique in the very high number of dorsolateral scales, in contrast to much lower counts in cornuta and steinegeri. On this basis it might be permissible to consider ochiopsis as a species distinct from C. cornuta, but since both taxa are "horned," we choose to de-emphasize this difference. It would seem likely that C. cornuta was an earlier adventive on Navassa (where it has differentiated in at least one character to a greater degree) than on Isla Mona (where its degree of differentiation has been of a lesser nature).

The fourth member of the complex is *C. collei* on Jamaica. This species likewise has enlarged snout scales which would seem to ally it with the balance of the complex. But it differs in many details from its relatives; the variability and at times absence of femoral pores is a distinctive feature within the genus. The profile is peculiarly flattened in contrast to profiles of other members of the complex, where the profile is more convex. Since skulls of *collei* are not available, we can only assume that this flattening of the head is correlated with interior osteological differences or interrelationships. Because of its peculiar combination of characteristics, it seems probable that *C. collei*, like *C. cornuta* on Hispaniola, has had a long independent history on Jamaica.

Cyclura rileyi remains for discussion. We consider rileyi as the fifth member of the nubila-cychlura complex, since it has the

requisite traits (enlarged prefrontals, enlarged body crest scales) to be so included. But two factors are puzzling. First, in the subspecies rileyi and nuchalis, the postsacral crest scales are very poorly developed and uncountable. Secondly, in cristata, these scales are well shown and in fact the entire dorsal crest series resembles in height that of geographically adjacent C. cychlura. We have elected to consider cristata as a subspecies of rilevi, and rilevi as a separate species, primarily on the basis of the juvenile coloration and pattern (see text). It may well be that C. r. cristata should be regarded either as a distinct species, or that it should be combined nomenclatorially with C. cychlura. Neither course recommends itself; the first beclouds the issue of affinities, the second violates our concepts of cychlura both in juvenile pattern and in head scutellation. It seems preferable, on the basis of these very characters, to consider rilevi (including cristata) as a derivative of the nubilacychlura line that has diverged on San Salvador and on the Crooked-Acklin's Bank islands and has invaded the Great Bank in one small area (White Cay), where its closest geographic neighbors are C. cychlura (thus C. rileyi is the historical southern cognate of northern C. cychlura, although of much greater age). Such an hypothetical history seems valid except for one point: the subspecies cristata (i.e., that population of rileyi which we postulate to have been derived from extra-Great Bank rilevi on islands south of the Crooked Island Passage) retains a "primitive" feature in having well developed postsacral crest scales, a character that is obsolescent in presumably ancestral rileyi and nuchalis. It seems reasonable to assume that well developed crest scales is a primitive feature in Cyclura, and if so, then it should likewise be so interpreted in C. rilevi. In effect, then, we admit to reversing our philosophy when it is a question of cristata and its affinities, but no other rationale suggests itself.

Cyclura pinguis, now isolated on Anegada Island, the outermost of the Virgin Islands, is so different in a large number of features, not the least of which is the relatively high body scales and the peculiar color pattern, that we cannot relate it with certainty to any other species. One feature, the presence of somewhat enlarged

prefrontals (most apparent in subadults), suggests a relationship with nubila-cychlura, but a very remote one. If material, other than fossil, of mattea and portoricensis were available, or if adequate fossil and/or skeletal material of these three taxa were at hand, we might better be able to place these three taxa in some rational scheme. What seems most likely is that binguis is a relict population of a once widely distributed distinctive species (related to nubila-cychlura) which occurred throughout the Virgin Islands and Puerto Rico. What the affinities of this hypothetical species were with other Cyclura remain in some doubt. The large size of the dorsolateral body scales militates against either ricordi-carinata or nubila-cychlura-cornuta-collei-rileyi as immediate ancestors or very close relatives. We would perhaps suggest that C. pinguis represents a highly divergent and old stock from the nubila-cychlura line. This suggestion ignores the distinctive dorsolateral scutellation, the peculiar coloration and pattern, and rather puts (weak) emphasis on the head scutellation.

All species except two are allopatric; Hispaniola is the only island where two Cyclura (ricordi and cornuta) are not only sympatric but also in places broadly syntopic. In the Valle de Neiba both species are about equally abundant. Elsewhere, they are known to be sympatric only on the Península de Barahona, but C. cornuta is widespread in xeric habitats on Hispaniola and also occurs on several satellite islands. Of this pair, one (ricordi) we consider primitive, whereas the other (cornuta) we consider a species derived from nubila, and thus more advanced and specialized. If this postulate is correct, then ricordi would seem to have been longer in residence and should likewise have a broader distribution than it now does (the fact that there are no specimens of ricordi from the Haitian Cul-de-Sac does not necessarily mean that the species is absent from that valley which is a continuation of the Dominican Valle de Neiba). Nevertheless, ricordi is known from only two general areas (Valle de Neiba; Península de Barahona), in one of which it seems to be far outnumbered by C. cornuta. This situation (limited and local distribution of ricordi; widespread distribution of cornuta, both species occupying similar habitats) is precisely what one might

N = number of individuals examined. A "-" indicates that the count is not applicable to a particular species. Vertical column headings (= 6, 7, 8, etc.) refer to character numbers as given in the introduction to the present paper. $M_0 = \text{mode}$; $K_0 = \text{mode}$ and $K_0 = 0$, $K_0 =$				SCA	LE COUN	SCALE COUNTS ON EIGHT SPECIES OF Cyclura	IT SPECIE	S OF $C_{\mathcal{N}}$	clura				
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expect of a more advanced and more specialized species (cornuta) interacting with an already established but more primitive species (ricordi). The more primitive species might gradually be pushed back, out of, and away from those habitats which it once occupied by the more advanced invader. Such a relationship might be even more pronounced if both the resident and invader species were vying for the same habitat and its resources. Another explanation of the peculiarly limited distribution of C. ricordi is that it was orignally a south island (sensu WILLIAMS, 1961) species, restricted to coastal situations along the northern shore of that paleoisland (i.e., along the southern edge of the modern Valle de Neiba) and the xeric Península de Barahona, whereas C. cornuta was more tolerant of less xeric situations (there is evidence that this is the case even today) and was able to spread widely over both the north and south islands and thus reach xeric regions which, because of intervening unfavorable (= more mesic) habitats, were unreachable by less tolerant and ecologically more rigidly restricted C. ricordi.

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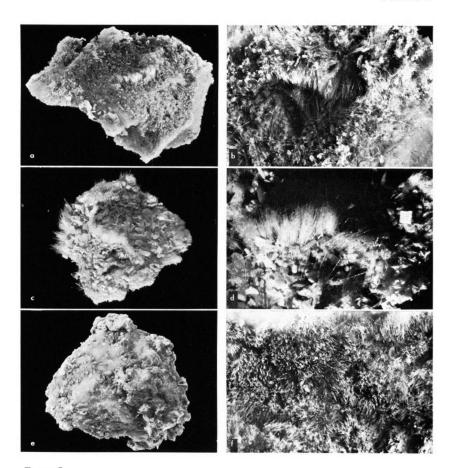


PLATE I

a. Acanthotetilla hemisphaerica, holotype (× 0.8), b. detail of the surface of the same (× 6), c. Acanthotetilla enigmatica, holotype (× 3.5), d. detail of the surface of the same (× 6), e. Acanthotetilla gorgonosclera n. sp., holotype (× 0.7), f. detail of the surface of the same (× 6).

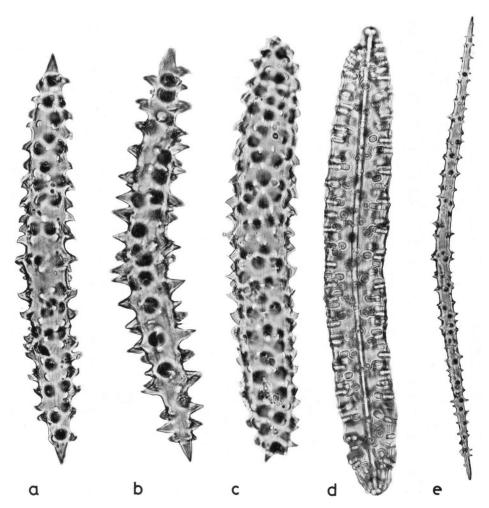


PLATE II

Megacanthoxea of Acanthotetilla species: a. A. gorgonosclera n. sp. (× 450), b. A. enigmatica (× 500), c. A. hemisphaerica (× 300), d. growth stage of the same (× 350), e. A. seychellensis (× 500).

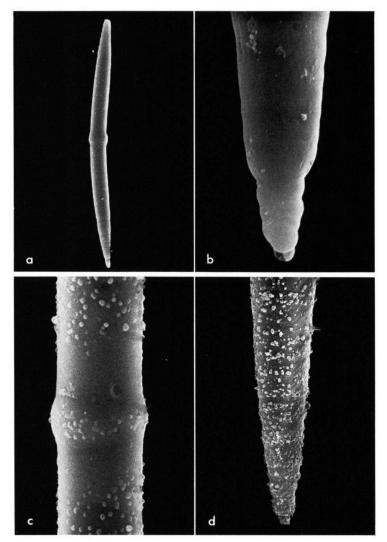


PLATE III Development of the megacanthoxea of Acanthotetilla gorgonosclera n. sp.: a. smooth initial stage (\times 325), b. detail of the same (\times 2000), c-d. details of granulated stage (\times 1100–1250).

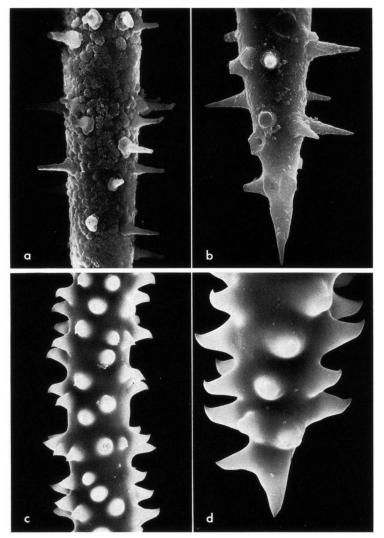


PLATE IV

Development of the megacanthoxea of Acanthotetilla gorgonosclera n. sp. (contin.):
a. detail of granulated-spiky stage (× 1000), b. detail of smooth spiky stage (× 900),
c-d. details of fully developed ("thorny") stage (× 650–800).