

Revision to Species of *Cyclura nubila lewisi*, the Grand Cayman Blue Iguana

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ABSTRACT.—A recent phylogenetic study of the West Indian Rock Iguana genus *Cyclura* (Malone et al., 2000) indicated that *Cyclura nubila lewisi* on Grand Cayman has diverged from nominate *Cyclura nubila* in Cuba to a degree equal to or greater than the currently accepted distinction between *Cyclura nubila* and *Cyclura cythlura* in the Bahamas. This evidence, in combination with existing and new observations of scale characters, color pattern, geographic and reproductive isolation, and phyly, leads to the conclusion that the Grand Cayman Blue Iguana, currently *Cyclura nubila lewisi*, is a population lineage evolving independently from populations on neighboring islands, and, like *Cyclura cythlura*, is sufficiently distinct and diagnosable to be considered a species, *Cyclura lewisi* Grant 1940. *Cyclura n. caymanensis* is retained as a subspecies of the Cuban Iguana, *Cyclura nubila*, since it appears to be at a much earlier stage of evolutionary divergence.

KEYWORDS.—Rock Iguana, Taxonomy, Scallation, Color, General Lineage Concept

INTRODUCTION

The strikingly blue rock iguanas native to the island of Grand Cayman were originally described as *Cyclura macleayi lewisi* (Grant, 1940). Schwartz and Carey (1977) established the currently accepted nomenclature, *Cyclura nubila lewisi* Grant. They noted that the Grand Cayman form was a strongly distinct subspecies of *Cyclura nubila* and emphasized its overall bright blue coloration. They recorded modal differences in head scalation, but identified no uniquely diagnostic scale characters.

More recently, Malone et al. (2000) used mitochondrial DNA analysis to re-examine the phylogeography of *Cyclura* and raised an unexpected question on the taxonomic rank of the Grand Cayman form. Their analysis demonstrated that *C. n. lewisi* has diverged from *C. nubila* at least as far as the Bahamian Rock Iguana, *Cyclura cythlura*. The latter is a currently recognized species with three subspecies; the distinctiveness of two of them was supported by the mtDNA analysis. Malone et al. (2000) also found that *C. nubila caymanensis*, native to Cayman Brac and Little Cayman, is more closely related to *C. nubila nubila* than *C. nubila lewisi* is to either. The mtDNA evi-

dence therefore suggests *C. nubila lewisi* should be considered a species.

An active conservation program for critically endangered *C. n. lewisi* (Burton 2000) is currently underway on Grand Cayman; it provides ready access to large numbers of all age classes for detailed examination. I present here the results of further investigation on the scalation and color pattern of *C. n. lewisi*, and integrate the results with other lines of evidence, using the general lineage concept of species (de Queiroz 1998, 1999) to reassess the taxonomic status of *C. n. lewisi*.

MATERIALS AND METHODS

I extracted and printed standard views from high resolution digital photographs of the dorsal, dorsolateral, and lateral aspect of the heads of both living and preserved animals. Using these images, I compared 31 *C. nubila nubila* from Guantanamo Bay, Cuba, 38 *C. n. caymanensis* from Little Cayman and Cayman Brac, 38 *C. n. lewisi* from Grand Cayman, and 52 *C. cythlura* from various locations in the Bahamas. Scale terminology is derived from Barbour and Noble (1916), Schwartz and Carey (1977),

and Smith (1946). I examined the following museum specimens: University of Kansas, Lawrence (KU) - *C. n. lewisi*: 245753-4; *C. n. caymanensis* 245733-245743, 245747-245751, 245755; *C. n. nubila* 245686, 245744-245746; *C. cyclura* 245707-245711, 245716-245719, 245721, 245723-4. Natural History Museum, London - *C. n. lewisi*: 1946.8.9.32 (type), 1939.2.3.69 (paratype); *C. n. caymanensis* 1939.2.3.52, 1939.2.3.65-67; *C. n. nubila* 1946.8.4.28 (type); *C. cyclura* 1987.845. I examined color patterns of *C. n. lewisi* by direct observation of 66 individuals ranging from hatchlings to adults, in the Blue Iguana Recovery Programme's captive breeding facility on Grand Cayman.

RESULTS

Scale morphology.—Systematic comparison of dorsal, dorso-lateral, and lateral head photographs of each taxon generated results consistent with those of Schwartz and Carey (1977). The set of characters used by those authors do not reliably distinguish all *Cyclura cyclura* from *C. nubila*, nor do they reliably distinguish all *C. n. lewisi* or *C. n. caymanensis* from nominate *C. nubila*. However, an almost fully diagnostic scale difference between *C. cyclura* and *C. nubila* is present. In all but two of the 52 *C. cyclura* examined, a conspicuously enlarged canthal scale is in extensive contact with the posterolateral margin of the first prefrontal. It is formed by the merging of the paired canthals and the precanthal scale. In *C. n. nubila*, *C. n. caymanensis*, and *C. n. lewisi*, these three scales are variable in shape and size but are discrete in all specimens examined (Fig. 1).

Two additional scale characters show only limited value for distinguishing *Cyclura n. lewisi*, *C. n. caymanensis*, and *C. n. nubila*. *Cyclura n. lewisi* usually has five enlarged auricular spines forming a continuous arc immediately anterior to the auricle, the dorsal most also forming the posterior terminus of the subocular scale row. Counting ventral to dorsal, the first and second are the largest, the fourth is the smallest (but still enlarged and apicular). In most *C. n. caymanensis*, the fourth enlarged auricu-

lar is absent, and the second and third tend to be separated by one or more rows of small scales, leaving a gap between the third auricular and the fifth (Fig. 1). However, in two of 38 *C. n. lewisi*, the fourth auricular is so reduced as to appear like *C. n. caymanensis*, and, in six of 38 *C. n. caymanensis*, a complete row of five auriculars is present. The character is intermediate for *C. n. nubila*, where 10 of 32 specimens show a complete auricular row.

Relative to *C. n. nubila* and *C. n. caymanensis*, many *C. n. lewisi* have an extra pair of enlarged prefrontals immediately posterior to the primary (first) prefrontals. (Note that the frontonasal scales indicated in Fig. 1 alternately may be termed prefrontal scales, *sensu* Schwartz and Carey (1977). Herein, I interpret the first prefrontal scales as those lying immediately posterior to a row of frontonasals.) These second prefrontals are always smaller than the first pair, variable in size, and are absent in the majority of *C. n. nubila* and *C. n. caymanensis*. A third row of moderately enlarged prefrontals occurs in *C. n. lewisi*, comparable to what appears as the second prefrontal row in typical *C. n. nubila* and *C. n. caymanensis*. In typical *C. n. lewisi*, the third row curves forward laterally, terminating at the precanthal. The entire row delineates the posterior margin of the prefrontal shield (Fig. 1). However, some individuals in all three taxa are incorrectly identified on the basis of auricular and prefrontal characters, and some specimens have a prefrontal scale pattern that is too disorganized to be interpreted. I conclude that no head scale characters consistently distinguish *C. n. lewisi* from *C. n. nubila* and *C. n. caymanensis*.

Color.—By far the most obvious character which distinguishes *C. n. lewisi* from *C. cyclura*, *C. n. nubila* and *C. n. caymanensis* is color (Grant 1940; Auffenberg 1976; Schwartz and Carey 1977; Coenen 1995; Knapp et al. 1999). Color can be a rather unsatisfactory character for taxonomic work in reptiles because its expression varies in life and is commonly not preserved in museum specimens (Simmons 2002). However, iguanas react strongly to color (e.g., Burghardt and Rand 1982), and this is a trait which seems subject to evolutionary

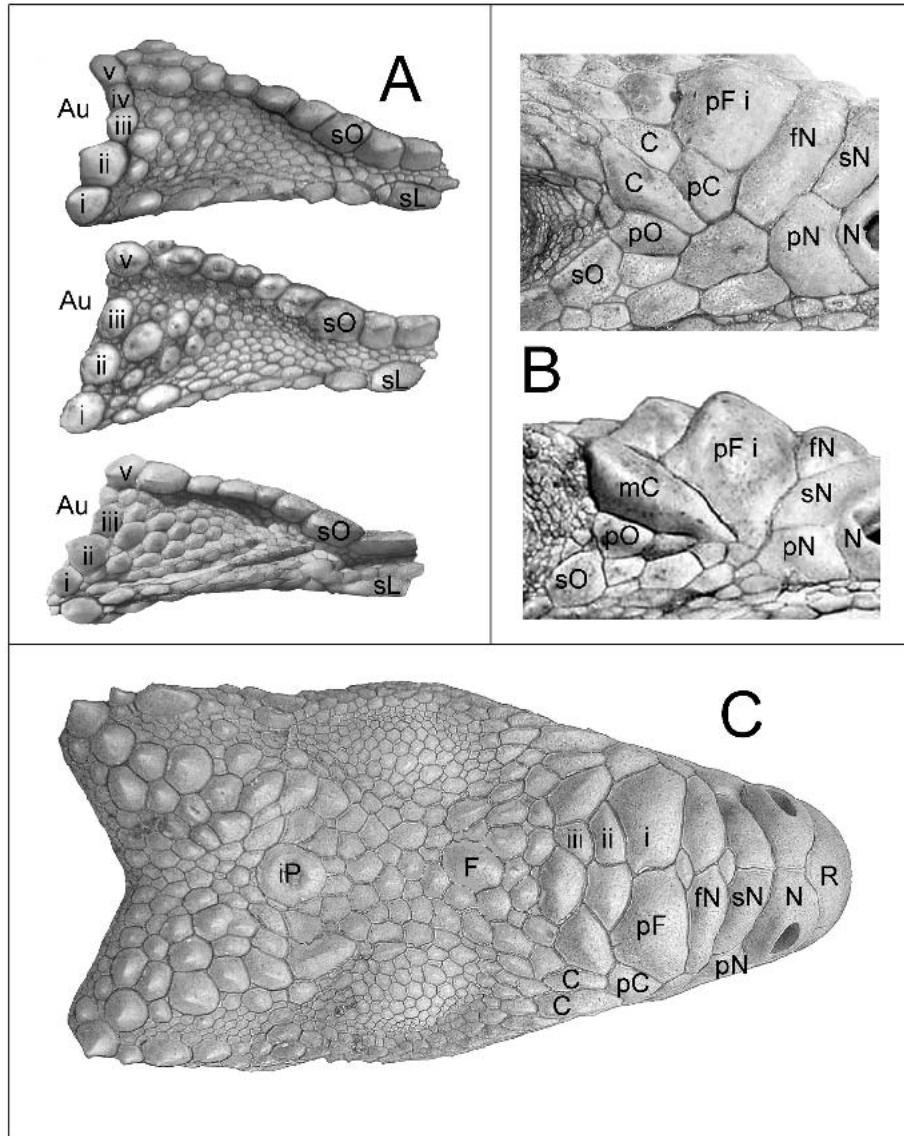


FIG. 1. A.—Scapulation in the auricular and lower temporal region of typical specimens of *Cyclura nubila lewisi* (top), *C. nubila caymanensis* (middle), and *C. cyclura cyclura* (bottom). B.—Canthal region of a typical *Cyclura nubila nubila* (top) and *C. cyclura cyclura* (bottom). C.—Dorsal head scapulation of a typical *Cyclura nubila lewisi*. Key: Au = auricular scales (numbered i-v); sO = subocular scale row; sL = supralabial scale row; R = rostral; N = nasal; sN = supranasal; pN = postnasal; fN = frontonasal; pF = prefrontal (rows i-iii); pC = precanthal; C = canthal; mC = merged canthals; F = frontal; iP = interparietal; pO = preocular.

selection. If described from healthy, warm, aroused animals without soil staining or aged skin near to shedding, color is reliably expressed.

All of the taxa under consideration here have similarly patterned hatchlings, with a grey base color, and alternating dark gray

and mottled cream chevrons angled posterolaterally from the nuchal and dorsal crest line onto the flanks. These originate from an alternating pattern of near-black and pale cream spots down the mid-dorsal line. Rows of pale cream spots precede or partially overlay the anterior margins of the

dark chevrons. The feet are patterned with ocellated spots, and the tail shows variable dark banding or streaking. As the animals mature, the juvenile pattern fades completely, except for the dark chevrons, which may persist to a highly variable degree into adulthood.

In *C. n. lewisi*, a blue base color begins to replace the hatchling base color and pattern throughout the head, thorax and abdomen within the first year and, by the time sexual maturity is attained, the entire animal is bright blue except for the feet, distal tail, and any residual chevrons, which become or remain black. In both *C. n. caymanensis* and *C. n. nubila*, the same changes occur, except in place of bright blue, the ground color becomes dull bluish gray, gray, or tan, and the crest scales become pale cream, sometimes remaining dark adjacent to dark chevrons. In *C. cyclura*, the ground color becomes dark gray to black, while the enlarged scales of the head, the nuchal and dorsal crest, and the upper limbs become orange, pink, or red, and suffused with yellow. Oculars and other small scales of the head are often blue-gray. *Cyclura n. lewisi* may appear to 'mask' the characteristic blue, becoming dark grey when cold, inactive, or seeking to remain unobserved by conspecifics. Adult color is heightened in all taxa during the breeding season.

All *C. n. lewisi* and *C. cyclura* examined in this study could be reliably distinguished from each other and from all *C. n. nubila* and *C. n. caymanensis*, on the basis of color. *Cyclura n. nubila* and *C. n. caymanensis* could not be distinguished in this way.

DISCUSSION

Determination whether *C. n. lewisi* should be considered a species requires establishing if this taxon is a lineage that is evolving independently from other related and geographically close populations of *Cyclura*. Several lines of evidence are useful in this regard.

Geographic separation.—Grand Cayman is separated from Little Cayman, where the nearest population of *C. n. caymanensis* occurs, by 108 km of open sea, and the nearest

population of *C. n. nubila*, on Cayo Largo off the southern coast of Cuba, is about 250 km from Grand Cayman. Cayman Brac is about 140 km from Cuba's Archipiélago de los Jardines de la Reina. The population of *C. cyclura* on Andros is 140 km from the nearest islands off the northern coast of Cuba. These distances are of the same order as those separating *Cyclura collei*, *C. cornuta*, and *C. nubila* on Jamaica, Hispaniola, and Cuba, respectively, which range from 90 to 190 km apart. *Cyclura n. lewisi* and *C. n. caymanensis* are thus both currently subject to similar degrees of geographic isolation as other accepted species of *Cyclura*.

Reproductive isolation.—A high degree of reproductive isolation is expected as a consequence of this geographic separation. Other than human mediation, the only modern potential for gene flow between islands separated by over 90 km is by rafting, which has been observed in the genus *Iguana* in the East Caribbean (Censky et al. 1998; Breuil 1999). Populations of *C. cyclura* were shown to be fully reproductively separated between Andros and the Exuma Cays, a distance of 90 km, with highly restricted gene flow over much shorter distances within the Exumas (Malone et al. 2003). Similarly, no discernable gene flow exists between populations of *Cyclura* on Cuba, Grand Cayman, Jamaica, Hispaniola, and the Bahamas, as evidenced by consistently distinct mtDNA haplotypes (Malone et al. 2000).

Grant (1940) reported sightings of iguanas in western Grand Cayman, which he interpreted as a possible human introduction of *C. n. caymanensis*. However, this was a sight record relying only on color, apparently during a rainy period. *Cyclura n. lewisi* would appear dark gray under these circumstances, so I do not consider this a reliable record. In the last ten years, I am aware of three *C. n. caymanensis* captured on Grand Cayman, all apparently the result of very recent human-mediated introductions in western Grand Cayman, where *C. n. lewisi* no longer occurs. If brought together, *C. n. lewisi* and *C. n. caymanensis* are capable of hybridizing and producing fertile offspring (Davis 2000). However, Malone et al. (2000) found no evidence of

characteristic *C. n. caymanensis* haplotypes in Grand Cayman samples, indicating that hybridization has not occurred in the wild.

Geographic separation of *C. n. lewisi* from *C. n. caymanensis* means the two populations have never naturally been in contact, so selective pressures for or against the evolution of intrinsic reproductive barriers between them have never existed. The fact that the two populations are capable of hybridization when artificially brought together, is therefore of limited relevance to discussion of the evolutionary divergence of these populations.

Phenetic distinctiveness and diagnosis.—Malone et al. (2000) identified distinct and consistent mtDNA haplotypes for each of *C. n. nubila*, *C. n. lewisi*, and *C. cyclura*. However, mtDNA haplotype was not fully diagnostic between *C. n. nubila* and *C. n. caymanensis*, though significant average differences were found (Malone pers. comm.). Apart from ambiguity between some individuals of *C. n. nubila* and *C. n. caymanensis*, no sampled animal was misclassified as to island of origin based on its haplotype. Although sample sizes in this study were very small, Malone et al. (2000) found the interspecific relationships of *Cyclura* as a whole could be resolved through mtDNA analysis with a high degree of support. This view is further supported by Malone et al. (2003), who sampled an additional 15 *C. cyclura* from Andros, bringing the total sample size from that population to 40, and found no variation in mtDNA haplotype. Likewise, additional *C. n. lewisi* and *C. n. caymanensis* from Cayman Brac were screened for conservation planning purposes (S. K. Davis pers. comm.) and were found to have mtDNA haplotypes identical to those reported by Malone et al. (2000). It therefore appears that *C. n. lewisi*, *C. cyclura*, and a group comprising *C. n. nubila* and *C. n. caymanensis*, can be diagnosed by distinct mtDNA haplotypes.

None of the scalation characters examined here or by Schwartz and Carey (1977) are fully diagnostic for any of the taxa under consideration. However, the enlarged canthal scale in *C. cyclura* is present in 96% of individuals examined, and absent in all Cuban and Cayman Islands specimens.

Adult color pattern is distinctive and fully diagnostic for both *C. cyclura* and *C. n. lewisi*, but not between *C. n. nubila* and *C. n. caymanensis*.

Phyly.—The analysis by Malone et al. (2000) suggested that *Cyclura nubila*, as currently defined, may be paraphyletic, with *C. n. nubila* and *C. n. caymanensis* apparently more closely related to *C. cyclura* than to *C. n. lewisi*, although this interpretation was not statistically distinguishable from monophyly. Regardless, Malone et al. (2000) inferred two independent radiations onto the Cayman Islands from ancestral forms on Cuba, an older colonization onto Grand Cayman (*C. n. lewisi*), and a more recent one onto Cayman Brac and Little Cayman (*C. n. caymanensis*). Their mtDNA evidence suggests that the *C. n. lewisi* population is probably monophyletic.

CONCLUSION

The general lineage concept of species (de Queiroz 1998, 1999) equates a species with a segment of a population level evolutionary lineage. From the analysis above, I argue that *C. n. lewisi* on Grand Cayman is a monophyletic, geographically and (extrinsically) reproductively isolated, phenetically distinct, and diagnosable population, and so appears to represent a separately evolving lineage. It seems to be at a similar stage of evolutionary separation from ancestral Cuban iguanas as the currently accepted species *C. cyclura*. I therefore propose that *C. n. lewisi* be considered a distinct species, *Cyclura lewisi* Grant 1940.

Cyclura n. caymanensis is also geographically and so presumably reproductively isolated, but can not be diagnosed from *C. n. nubila* other than by average mtDNA haplotype, which indicates that this population is at an earlier stage of evolutionary divergence. *Cyclura nubila caymanensis* Barbour and Noble 1916 is therefore retained as a subspecies of the Cuban Rock Iguana, *Cyclura nubila* Gray 1845. With the separation of *C. lewisi*, *C. nubila* becomes a monophyletic species. No species level revision is necessary for *Cyclura cyclura* Cuvier 1829.

The common name popularly used in the Cayman Islands for *Cyclura lewisi* is adopted: "Grand Cayman Blue Iguana," and in colloquial use it may be abbreviated as "Cayman Blue Iguana" or "Blue Iguana."

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LITERATURE CITED

- Auffenberg, W. 1976. Bahamas Rock Iguanas, part two. *The Bahamas Naturalist* 2:9-16.
- Barbour, T., and G. K. Noble. 1916. A revision of the lizards of the genus *Cyclura*. *Bull. Mus. Comp. Zool.* 60:139-164.
- Breuil, M. 1999. Editorial. West Indian Iguana Specialist Group Newsletter 2(1):4.
- Burghardt, G. M., and A. S. Rand. 1982. [Introduction to] Section IV. Adaptive behavior and communication. In *Iguanas of the World: Their Behavior, Ecology, and Conservation*, ed. G. M. Burghardt, and A. S. Rand, 213-214. New Jersey, Park Ridge: Noyes Publ.
- Burton, F. J. 2000. Grand Cayman Iguana. In *West Indian Iguanas: Status Survey and Action Plan*, ed. A. Alberts, 45-47. Gland, Switzerland: IUCN.
- Censky, E. J., K. Hodge, and J. Dudley. 1998. Over-water dispersal of lizards due to hurricanes. *Nature* 395:556.
- Coenen, C. 1995. Observations on the Bahamian Rock Iguana of the Exumas. *Bahamas J. Sci.* 2:8-14.
- Cuvier, G. 1829. *Le Règne Animal*. Vol. 2. Paris: Librairie Déterville.
- Davis, S. 2000. Genetic research needs. In *West Indian Iguanas: Status Survey and Action Plan*, ed. A. Alberts, 89-91. Gland, Switzerland: IUCN.
- de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. In *Endless Forms: Species and Speciation*, ed. D. J. Howard and S. H. Berlocher, 57-75. Oxford, England: Oxford University Press.
- de Queiroz, K. 1999. The general lineage concept of species and the defining properties of the species category. In *New Interdisciplinary Essays*, ed. R. A. Wilson, 49-89. Cambridge, Massachusetts: MIT Press.
- Grant, C. 1940. The herpetology of the Cayman Islands. *Bull. Inst. Jamaica Sci. Ser.* 2:1-55.
- Gray, J. E. 1831. A synopsis of the Class Reptilia. In *The Class Reptilia, Arranged by Baron C. Cuvier, with Specific Descriptions. The Animal Kingdom Arranged in Conformity with its Organization by the Baron Cuvier, with Additional Descriptions of all the Species Hitherto Named, and of Many Others*, ed. E. Griffiths and E. Pidgeon, Vol. 9, pp. 1-110 + 55 pls. London: Whittaker, Treacher and Co.
- Knapp, C., S. Buckner, A. Feldman, and L. Roth. 1999. Status update and empirical field observations of the Andros Rock Iguana, *Cyclura cychlura cychlura*. *Bahamas J. Sci.* 7(1):2-5.
- Malone, C. L., T. Wheeler, J. F. Taylor, and S. K. Davis. 2000. Phylogeography of the Caribbean Rock Iguana (*Cyclura*): implications for conservation and insights on the biogeographic history of the West Indies. *Mol. Phylogen. Evol.* 17:269-279.
- Malone, C. L., C. R. Knapp, J. F. Taylor, and S. K. Davis. 2003. Genetic consequences of Pleistocene fragmentation: Isolation, drift, and loss of diversity in Rock Iguanas (*Cyclura*). *Conservation Genetics* 4: 1-15.
- Schwartz, A. and M. Carey 1977. Systematics and evolution in the West Indian iguanid genus *Cyclura*. *Stud. Fauna Curaçao Carib. Isl.* 173:15-97.
- Simmons, J. E. 2002. Herpetological collecting and collections management. *Rev. ed. Soc. Study Amphib. Rept. Herpetol. Circ.* (31):vi + 153 pp.
- Smith, H. M. 1946. *Handbook of Lizards*. Ithaca, New York: Comstock Publ. Co.