Catalogue of American Amphibians and Reptiles.

Malhotra, A. and R.S. Thorpe. 1992. *Anolis oculatus.*

Anolis oculatus (Cope)
Dominican Anole

Anolis alliaceus: Cope, 1864:175.

Xiphosurus oculatus Cope, 1879:274. Type-locality, "Dominica," restricted to Roseau, [St. George Parish], Dominica by Lazell (1962: 468). Lectotype, National Museum of Natural History (USNM) 10145, (Lazell, 1972), adult male, collected by Ferdinand Ober, date of collection unknown (not examined by authors).

Anolis leachii: Boulenger, 1885:29 (part).

Anolis oculatus: Garman, 1887:30. First use of combination.

Anolis oculatus oculatus: Lazell, 1962:467.

Anolis oculatus cabritensis Lazell, 1962:469. Type-locality, "The Cabrits (=Prince Rupert Point), northwest of Portsmouth, Dominica." Holotype, Museum of Comparative Zoology, Harvard University (MCZ) 60245, adult male, collected by J. Lazell, 8 June 1959 (not examined by authors).

Anolis oculatus montanus Lazell, 1962:470. Type-locality, "Fresh Water Lake, ca. 2500 feet, [Dominica]." Holotype, Museum of Comparative Zoology, Harvard University (MCZ) 60319, adult male, collected by J. Lazell, 6 July 1959 (not examined by authors).

Anolis oculatus winstoni Lazell, 1962:472. Type-locality, "Woodford Hill, [Dominica]." Holotype, Museum of Comparative Zoology, Harvard University (MCZ) 60467, adult male, collected by J. Lazell, 29 June 1959 (not examined by authors).

Ctenonotus oculatus: Schwartz and Henderson, 1988:116.

• **Content.** No subspecies are recognized (but see Comment).

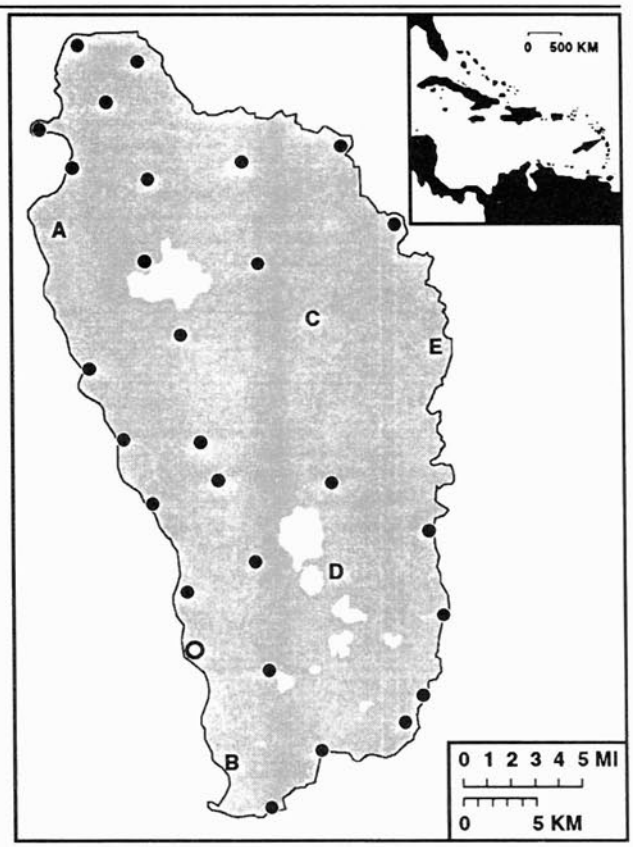
• **Definition.** *Anolis oculatus* is a highly variable species, showing coherent patterns of geographic variation in many morphological characters examined (see Comment). This species is a medium-sized anole (maximum male SVL ranges from 61-98 mm in different populations), with smooth to weakly keeled ventrals, and a double row of enlarged mid-dorsal scales. Dorsal and lateral scales are minute, and scale number is very variable; the mean number of scales around the body in 33 populations ranges between 135-204 (individuals vary between 114-220). The mean number of subdigital lamellae below the 3rd and 4th phalanges of the 4th toe on the hind foot varies between 32-39 in different populations; individual variation is in the range of 28-42. Adult males possess a caudal crest and an extensible nuchal crest, the size of which may vary locally and geographically. Supraoculars are separated by 0-3 rows of scales.

Ground color varies geographically from pale tan or ash grey to chocolate brown or deep green. The degree of patterning also varies, and can take the form of indistinct white mottling, well defined light spots and streaks, or small scattered groups of white scales. In addition, large adult males may possess one or more lateral black pigmented areas of irregular shape. In some areas of the range, scales within the white spots of large males may be enlarged to a significant degree, and are spine-like in extreme cases. Females may also have light spots and mottling, but these are usually less extensive and distinct than in males. Females exceptionally may have small black lateral spots, and possess only a rudimentary, relatively dull-colored dewlap. A middorsal stripe and a lateral streak are often present.

Females are smaller than males in any given population; the largest known female (72 mm SVL, from a population where males reach 97 mm SVL), however, is larger than most males from southern west coast populations.

The range of variation (males) for five populations (A, B, C, D, E, respectively; see map) in the following characters (n = 50) are as follows: SVL maximum (76.40, 69.90, 94.79, 82.88, 76.62); mean number of scales around body (204, 142, 135, 147, 155); mean number of lateral black patches (2, 1, 3, 1, 0); ground color (yellow-tan, pale yellow-tan, dark olive-green, dull to bright green, orange-brown).

• **Diagnosis.** *Anolis oculatus* is endemic to Dominica, and is the only *Anolis* species on the island. Morphological distinction from all other species of the *bimaculatus* group is by the presence of a subrectangular (rather than elongated) prenasal, which does not extend posteriorly to the anterior level of the nostril. Anoles of the *bimaculatus* group can be distinguished from the *roquet* group by the presence of a pair of enlarged postanal scales in males, and their relatively longer snouts.



Map. Areas of altitude > 900 m, where *Anolis oculatus* is absent, are unshaded. The large open circle indicates the restricted type-locality; solid circles mark localities at which populations were sampled by the authors. See text for details of populations A, B, C, D, and E.

• **Descriptions.** The most complete description of morphology and coloration is provided by Lazell (1972). Gorman and Atkins (1967, 1969) described the karyotype as 2N=31 in males and 2N=32 in females (23 macrochromosomes + 8 microchromosomes; males of the *bimaculatus* group all display chromosomal heteromorphism).

• **Illustrations.** Detailed line drawings in Lazell (1962) show patterns of adult males of all four described subspecies. Color plates illustrating males and females are given in Lazell (1972), and of males of three of the former subspecies in Schwartz and Henderson (1985). Karyotypes are illustrated by Gorman and Atkins (1967, 1969).

• **Distribution.** *Anolis oculatus* is restricted to Dominica in the Lesser Antilles, and is found all over the island to an altitude of ca. 900 m. Although uncommon in some habitats, the species is in general extremely abundant.

• **Fossil Record.** None.

• **Pertinent Literature.** Barbour (1930) provided some historical notes on abundance. Garman (1887) and Underwood (1959) described the existence of a high degree of intraspecific variation in coloration, but Lazell (1962, 1972) was the first to provide a coherent account of the geographic variation in morphology (with an emphasis on coloration). Lazell (1972) also provided zoogeographical notes and a phylogenetic analysis of relationships with other Lesser Antillean anoles. The latter has been the subject of much reanalysis on the basis of different data sets: Gorman and Atkins (1969), based on karyotypic evidence; Gorman and Atkins (1969) and Gorman and Kim (1976), based on protein electrophoresis; Gorman et al. (1980) and Shochat and Dessauer (1981), based on immunogenetic assays of albumins. Roughgarden and Pacala (1989) gave a phylogeny based on several of the above data sets. Schwartz and Henderson (1985) included the species in a key to *Anolis* of the Lesser Antilles. The karyotype of *A.*

Figure 1. *Anolis occulatus* males from Dominica (clockwise from upper left): Atlantic ecotype (Hampstead, St. Andrew Parish), North Caribbean ecotype (The Cabrits, St. John Parish), Montane ecotype (Syndicate Estate, St. Peter Parish), and South Caribbean ecotype (Petit Coulibri Estate, St. Mark Parish). All specimens were released at site of capture. Photographs by A. Malhotra.

Figure 2. *Anolis occulatus* females from Dominica (clockwise from upper left): Atlantic ecotype (Hampstead, St. Andrew Parish), North Caribbean ecotype (Picard, St. John Parish), Montane ecotype (Syndicate Estate, St. Peter Parish), and South Caribbean ecotype (Batali, St. Mark Parish). All specimens were released at site of capture. Photographs by A. Malhotra.

oculatus has been shown to be unique within the *bimaculatus* group in possessing an extra pair of acrocentric macrochromosomes (Gorman and Atkins, 1967, 1969). Malhotra and Thorpe (1991a) have reassessed the intra-island variation in this species, using detailed multivariate morphometric analyses. Andrews and Rand (1974) presented data on clutch weight, hatchling size, and frequency of oviposition for captive *A. oculatus* from two different populations, in a comparison with other anoline and sceloporine iguanid lizards. Basic data on reproduction in the natural habitat was provided by Somma and Brooks (1976), and on body temperatures by Brooks (1968). Ruibal and Philibosian (1970) further examined thermoregulatory strategies in different populations and illustrated the eurythermic nature of this species. Results of experimental tests are in Malhotra and Thorpe (1993). Roughgarden and Fuentes (1977) examined the relationship between average body size and insect abundance. Body size, together with that of the other Lesser Antillean anoles, is discussed by Roughgarden and Pacala (1989) and Losos (1990). Andrews (1976, 1979) provided data on growth rate, density and biomass, foraging behaviour, and diet. Bullock and Evans (1990) presented recent data on relative densities and biomass of this species in a number of different habitat types. Malhotra and Thorpe (1991b) demonstrated experimentally that ecophenotypic variation in *A. oculatus* is under strong selection pressure, and that fitness characteristics of different demes are significantly correlated with structural and climatic features of their respective habitats (see also Thorpe and Malhotra, 1992). Schwartz and Henderson (1991) provided a brief synopsis of the biology of the species, as well as a distribution map.

• **Nomenclatural History.** Cope (1864) first gave a cursory description of the species as *Anolis alliaceus* from 16 specimens in the British Museum without locality data, and later described *oculatus* from 13 specimens in the U.S. National Museum. The confusion was first sorted out by Günther (1888), who placed the two taxa together.

• **Remarks.** The behavior of this species also varies geographically; for example, activity patterns (personal observation), and thermoregulatory behaviour (Ruibal and Philibosian, 1970).

• **Etymology.** The name *oculatus* (Latin, "eyed"), refers to the light lateral spots that are a distinctive feature of this species.

• **Comment.** Four subspecies were formerly recognized. We consider the species to be monotypic after a re-examination of morphological variation involving detailed multivariate analysis (Malhotra and Thorpe, 1991a). We measured a large number of characters from three different systems (body proportions, scalation, and colour pattern) at 33 localities. The overall pattern of variation revealed is complex, containing both altitudinal and longitudinal elements. Some characters, such as scale size, show a strong altitudinal pattern, whereas others (such as the presence of black patches) show strong longitudinal elements. In addition, morphological variation was found to be correlated with aspects of environmental variation, such as differences in rainfall and vegetation type. Most significantly, different characters and character suites appear to respond to specific ecological factors (Malhotra, 1992). Although these factors may be intercorrelated to a large extent, the result is the development of incongruent patterns of variation in different character systems. Consequently, meaningful definition of boundaries between subspecies is difficult. Although striking differences in overall morphology between anoles from different parts of the island do exist, the pattern of variation is due to ecogenetic adaptation and is not adequately described by conventional subspecific designation. Therefore, in our opinion, the use of formal trinomial nomenclature is inappropriate.

Literature Cited

Andrews, R.M. 1976. Growth rate in island and mainland anoline lizards. Copeia 1976:477-482.

——. 1979. Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. Breviora (454):1-51.

——and A.S. Rand. 1974. Reproductive effort in anoline lizards. Ecology 55:1317-1327.

Barbour, T. 1930. The anoles I. The forms known to occur on the neotropical islands. Bull. Mus. Comp. Zool. 70:105-144.

Boulenger, G.A. 1885. Catologue of the lizards in the British Museum (Natural History). 2nd ed. Vol. 2. Taylor and Francis, London.

Brooks, G.R. 1968. Body temperatures of three lizards from Dominica, West Indies. Herpetologica 24:209-214.

Bullock, D.J. and P.G.H. Evans. 1990. The distribution, density and biomass of terrestrial reptiles in Dominica, West Indies. J. Zool. Lond. 222:421-443.

Cope, E.D. 1864. Contributions to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia 1864:166-181.

——. 1879. Eleventh contribution to the herpetology of tropical America. Proc. Amer. Philos. Soc. 18:261-277.

Garman, S. 1887. On West Indian reptiles. Iguanidae. Bull. Essex Inst. 19:25-50.

Gorman, G.C. and L. Atkins. 1967. The relationships of the *Anolis* of the *roquet* species group (Sauria: Iguanidae). II. Comparative chromosome cytology. Syst. Zool. 16:137-143.

—— and ——. 1969. The zoogeography of Lesser Antillean *Anolis* lizards - an analysis based upon chromosomes and lactic dehydrogenases. Bull. Mus. Comp. Zool. 138:53-80.

——, D.G. Buth, and J.S. Wyles. 1980. *Anolis* lizards of the eastern Caribbean: a case study in evolution. III. A cladistic analysis of albumin immunological data, and the definition of species groups. Syst. Zool. 29:143-158.

—— and Y. J. Kim. 1976. *Anolis* lizards of the eastern Caribbean: a case study in evolution. II. Genetic relationships and genetic variation of the *bimaculatus* group. Syst. Zool. 25:62-77.

Günther, A. 1888. Notes on reptiles and frogs from Dominica, West Indies. Ann. Mag. Nat. Hist., ser. 6, 2:362-366.

Lazell, J.D. Jr. 1962. The anoles of the Eastern Caribbean (Sauria: Iguanidae). Part V. Geographic differentiation in *Anolis oculatus* on Dominica. Bull. Mus. Comp. Zool. 127:466-475.

——. 1972. The anoles (Sauria, Iguanidae) of the Lesser Antilles. Bull. Mus. Comp. Zool. 143:1-115.

Losos, J.B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. Evolution 44:558-569.

Malhotra, A. 1992. What causes geographic variation? A case study of *Anolis oculatus*. Ph.D. thesis, Univ. Aberdeen, Scotland.

—— and R.S. Thorpe. 1991a. Microgeographic variation in *Anolis oculatus* on the island of Dominica, West Indies. J. Evol. Biol. 4:321-335.

—— and ——. 1991b. Experimental detection of rapid evolutionary response in natural lizard populations. Nature 353:347-348.

—— and ——. 1993. An experimental field study of an eurytopic anole. J. Zool. London 229:in press.

Roughgarden, J.D. and E. Fuentes. 1977. The environmental determinants of size in solitary populations of West Indian *Anolis* lizards. Oikos 29:44-51.

—— and S. Pacala. 1989. Taxon cycle among *Anolis* lizard populations: review of evidence, p. 403-432. *In* D. Otte and J.A. Endler (eds.), Speciation and its consequences. Sinauer Assoc., Inc., Sunderland, Massachusetts.

Ruibal, R. and R. Philibosian. 1970. Eurythermy and niche expansion in lizards. Copeia 1970:645-653.

Schwartz, A. and R.W. Henderson. 1985. A guide to the identification of the amphibians and reptiles of the West Indies exclusive of Hispaniola. Milwaukee Pub. Mus., Milwaukee, Wisconsin.

—— and ——. 1988. West Indian amphibians and reptiles: a checklist. Contrib. Biol. Geol. Milwaukee Pub. Mus. (74):1-264.

—— and ——. 1991. Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. Univ. Florida Press, Gainesville.

Shochat, D. and H.C. Dessauer. 1981. Comparative immunological study of albumins of *Anolis* lizards of the Caribbean islands. Comp. Biochem. Physiol. 68A:67-73.

Somma, C.A. and G.R. Brooks. 1976. Reproduction in *Anolis oculatus*, *Ameiva fuscata* and *Mabuya mabouya* from Dominica. Copeia 1976:249-256.

Thorpe, R.S. and A. Malhotra. 1992. Are *Anolis* lizards evolving? Nature 355:506.

Underwood, G. 1959. The anoles of the eastern Caribbean (Sauria, Iguanidae). Part III. Revisionary notes. Bull. Mus. Comp. Zool. 121:191-226.

Anita Malhotra and **Roger S. Thorpe**, Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB9 2TN, Scotland, United Kingdom.

Primary editor for this account, Andrew H. Price.

Published 30 November 1992 and Copyright © 1992 by the Society for the Study of Amphibians and Reptiles.