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LATE PLEISTOCENE LIZARDS FROM BARBUDA, BRITISH WEST INDIES

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LATE PLEISTOCENE LIZARDS FROM BARBUDA, BRITISH WEST INDIES

RICHARD ETHERIDGE[1]

SYNOPSIS: In 1958, 1962, and 1963 field parties from the University of Florida collected large numbers of Quaternary vertebrate fossils from five caves near the northeast shore of the island of Barbuda, British West Indies. Fossils from the loose floors of Caves I, II and V are at least pre-Columbian in age but possibly not older than post-mid-Wisconsin. Fossils from breccia and consolidated cave earth on the walls of Caves III and IV are somewhat older but probably not older than Late Pleistocene.

Fossils of seven species of lizards are present in the caves. One species, *Leiocephalus cuneus* described as new, is extinct. A member of the West Indian section of the genus, it reached a maximum snout-vent length of 200 mm, far exceeding the largest extant species. Its occurrence on Barbuda, between *L. herminieri* on Martinique and the remaining Antillean species on Cuba, the Bahamas, and Hispaniola, indicates *Leiocephalus* was more extensively distributed in the eastern Caribbean during the late Pleistocene. Fossils of three species of *Anolis* are present in the caves. The largest reached a maximum snout-vent length of 120 mm and represents a giant ancestral population of *Anolis bimaculatus leachii* which occurs on Barbuda today. The two smaller forms of *Anolis* reached maximum snout-vent lengths of 72 and 48 mm. Their allies or descendents cannot be determined, but are probably to be found among the living species of the eastern Caribbean. One of the two smaller species may be ancestral to *Anolis forresti* which occurs on Barbuda today. Fossils of *Thecadactylus rapicaudus* and *Ameiva griswoldi* are identical in structure and size to individuals now living on Barbuda. Two fragments of a large iguanid apparently represent a large iguanine. They cannot be referred to *Cyclura* or *Iguana* and most closely resemble the Galapagoan genus *Conolophus*.

The medium sized species of *Anolis* occurs only in the younger deposits, the large iguanine occurs only in the older deposits. All other species occur in both, and the older fossils are indistinguishable from those of the same species in the younger deposits.

The affinities of most of the Barbudan lizards in the Late Pleistocene clearly lie within the islands of the eastern Caribbean. All but one of the species found as fossils occur in this region, or are related to species that occur there today. A cursory examination of lizard fossils from other West Indian islands suggests that the pattern of late Pleistocene gigantism and extinction found on Barbuda may have been of general occurrence in the West Indies.

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INTRODUCTION

Along the northeast coast of the island of Barbuda, just in from the shoreline at Two Foot Bay, is a high cliff of Miocene limestone, riddled with small caves, solution pockets, and sinkholes. The wave action of a transgressing Pleistocene sea apparently formed many of the caves near the base of the cliff, and at the same time exposed much older caves formed in the higher terrace above. In 1958 Walter Auffenberg explored a number of these caves and in the soft earth floor of two of them he found many vertebrate fossils. Among them were the bones of small mammals, birds, lizards, a snake, and a frog. Shortly after their discovery he published (1958) a description of the caves, designated I and II, and the stratigraphy of their earth floors. He identified the lizard fossils as belonging to three species that live on the island today: *Thecadactylus rapicaudus*, *Ameiva griswoldi* and *Anolis bimaculatus leachii*.

In 1962 Auffenberg visited the island again. He collected more fossils from the earth floor of Cave I and discovered two more fossil-bearing caves nearby, which he designated III and IV. According to his field notes Cave III is similar to I and II, located in the same cliff but farther to the south. It is about 30 feet above the shore and 60 to 80 feet below the top of the cliff. The fossils were contained in breccia clinging to the walls of the cave.

Cave IV is located still farther to the south and is the largest cave in the cliff. It also is about 30 feet above the shore and 60 to 80 feet below the top of the cliff. In the western part of the cave consolidated cave earth near its floor contained sea shells, sand, and vertebrate fossils. The fossil bones were in the top 12 to 16 inches of the consolidated earth. Fossils were also present in the loose earth floor of the cave. Some of these appeared to have been washed out of the consolidated earth walls, others to have been deposited much more recently.

In 1963 Clayton Ray and Robert Allen of the Florida State Museum visited the island. They collected more fossils from the four caves discovered by Auffenberg and discovered yet another cave which they designated Cave V. Ray's field notes describe Cave V as similar to Cave I and located about 200 feet south of it. The fossils in Cave V were in the loose earth floor.

According to Auffenberg (1958 and 1962 field notes) the breccia and the patches of reddish consolidated cave earth remaining on the walls of the older caves indicate that most of the deposits they formerly contained were swept out during a period of higher sea level. Then the regressing sea exposed the eroded caverns and they again became traps for animal remains. The fossils found in the loose cave earth floors of Caves I, II and V are presumably from these younger deposits, whereas the fossils contained in the consolidated cave earth on the walls of Caves III and IV are much older. The 30-foot elevation of the terrace at the foot of the cliff led Auffenberg to suggest that the terrace may be contemporaneous with the Pamlico terrace of southeastern United States, which he believed to be mid-Wisconsin. Weigel (1962) on the basis of C_{14} dates suggests that the Pamlico terrace may be pre-Wisconsin in age. Unfortunately the lack of isostatic equilibrium (Newell and Rigby, 1957) makes any correlation between southeastern United States and the Lesser Antilles highly speculative.

Auffenberg (field notes) divided the earth floor of Cave I into three strata. The upper one, which lay unconformably above the lower two, contained feathers and the unmineralized bones of bats and *Rattus*. The lower two contained mineralized bones, including those of extinct species, but no *Rattus*. For this reason Auffenberg considers that the lower two strata are at least pre-Columbian in age. We have no way of dating the older consolidated cave earths of Caves III and IV, but they are doubtfully older than Middle or Late Pleistocene.

Among the fossils collected since Auffenberg's first visit, beside many more bones of the species he reported (Auffenberg, 1958), are a badly worn brain case of a large iguanine and a number of bones of a large, extinct species of *Leiocephalus*. Neither *Iguana* nor *Leiocephalus* occurs on Barbuda today. In addition, at least three species of *Anolis* are now represented among the fossils. These are structurally similar to the two modern species on the island, but two of them grew to a greater size. These fossils, together with those of an undescribed extinct rice rat from Caves I, II and V (Ray, manuscript) indicate that in the not-too-distant past Barbuda supported a larger and more diversified vertebrate fauna than it does today.

All specimen numbers in the following sections refer to specimens catalogued in the vertebrate paleontological collections of the Florida State Museum, University of Florida.

DESCRIPTION OF THE FOSSILS

GEKKONIDAE

Thecadactylus rapicaudus

Fossils of this large gecko were first collected from the loose earth in Cave I. They have since been found in similar deposits in Caves II and V and in the older consolidated cave earths of Caves III and IV. In both structure and size the fossils are indistinguishable from the bones of living *Thecadactylus rapicaudus*. Of 68 Recent specimens from Central and South America and the Lesser Antilles now in the University of Michigan Museum of Zoology, the largest is an individual from Dominica, B. W. I., measuring 120 mm from snout to vent. The length of its dentary is exactly equal to the length of the largest fossil dentary. A plot of tooth counts in the fossils against the length of the tooth row (Fig. 1) clearly indicates an ontogenetic increase in both dentaries and maxillae. The range is from 28 to 52 teeth on the dentaries and from 30 to 48 teeth on the maxillae. Tooth counts of two modern specimens from Dominica, measuring 56 and 120 mm from snout to vent, are within the variational limits of the fossils. Recent and fossil premaxillae of all sizes have 10 teeth.

The form of the teeth distinguishes *Thecadactylus* from other large West Indian geckos. Compared to *Aristelliger* and *Tarentola* its teeth are more slender, less sharply pointed, and less strongly curved near the front of the jaw.

REFERRED SPECIMENS. Cave I: dentaries 8286 (34), 8461 (9); maxillae 8272 (4), 8273 (8), 8290 (38), 8465 (13); premaxillae 8275, 8283, 8460 (4); articulars 8276 (12), 8288 (6), 8464 (4); coronoids 8436 (3); frontals 2809 (9), 8463 (2), 8279 (3), 8291 (11); parietals 8284 (3); pterygoids 8280 (2), 8285 (8); prefrontals 8441 (2); quadrates 8287 (3), 8471; basisphenoids 8413 (2), 8462; scapulocoracoids 8419 (4); pelves 8278 (2), 8289 (15); vertebrae 8277 (10), 8281, 8282 (2). Cave II: dentaries 8293 (4); maxillae 8292. Cave III: dentaries 8296, 8393 (3); maxillae 8318, 8391 (2); premaxilla 8295; basisphenoid 8409; quadrates 8408 (4); ilium 8392; vertebrae 8294. Cave IV (breccia only): dentaries 8309 (4); frontals 8308 (2). Cave V: dentaries 8306 (6); maxillae 8303 (17); premaxillae 8298 (3); articulars 8297 (2), 8364 (3); frontals 8302 (3); parietals 8305 (5); pterygoids 8304 (3); quadrates 8300 (2); basisphenoid 8369; scapulocoracoids 8368 (4); pelvis 8301; vertebrae 8299 (10), 8307.

IGUANIDAE

Leiocephalus

A number of fossils from the Barbudan caves closely resemble skeletal elements of living West Indian species of the genus *Leio-*

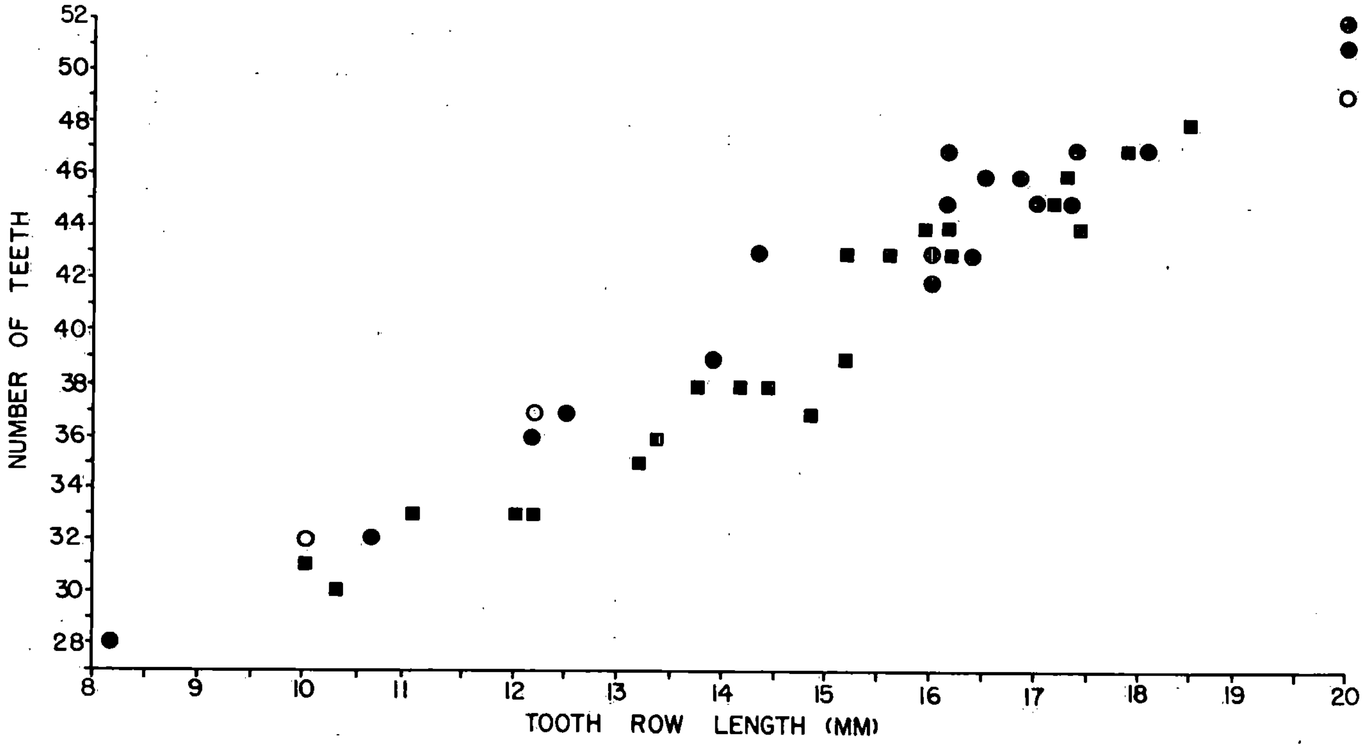

Figure 1. Ontogenetic increase in the number of teeth on the dentary (solid circles) and maxilla (solid squares) in fossils of *Thecadactylus rapicaudus* from Barbuda. Tooth counts of dentaries of Recent specimens are indicated by open circles.

cephalus. The crowns of the posterior teeth of the dentaries and maxillae distinguish them from all other West Indian lizards and from the South American species now referred to *Leiocephalus;* they are flared in an anterior-posterior direction, linguo-labially compressed to form a sharp cutting edge, and strongly tricuspid. Other distinctive characteristics of West Indian *Leiocephalus* manifest in the fossils are: (1) the former position of a large coronoid process is indicated by a shallow depression on the posterior upper labial face of the dentary, (2) the former position of overlapping nasal bones is indicated on the upper surface of the nasal process of the premaxilla, (3) the lateral borders of the adult parietal are narrowly separated where they meet the occipital border, (4) the lateral processes of the interclavicle are posterior to the anterior extremity of the median blade, (5) the autotomic caudal vertebrae have a low median neural crest and a vertical spine above the plane of fracture, and (6) pterygoid teeth are absent. These characters in combination also distinguish West Indian *Leiocephalus* from the related South American genera *Stenocercus, Tropidurus, Ctenoblepharis, Liolaemus, Urocentron, Proctotretus, Platynotus, Plica* and *Uranoscodon.*

No *Leiocephalus* occurs now on Barbuda nor on any nearby islands. The fossils appear to represent a very large extinct species which, because of its geographically intermediate position in the arc of islands between Hispaniola and Martinique where the genus does occur today, may be known as

Leiocephalus cuneus new species

TYPE. Number 8226 in the vertebrate paleontology collections of the Florida State Museum, University of Florida, Gainesville, Florida. A left dentary complete except for a small piece broken from the post-dentitional part of the labial wall.

REFERRED SPECIMENS. Cave I: dentaries 8469; premaxillae 8263, 8470; maxillae 8468, 8264-5; quadrates 8266-7; pterygoids 8268 (3); frontals 8269-70; parietal 8271; postorbital 8444; jugal 8250; pelvis 8271. Cave II: pelvis 8334. Cave III: dentary 8317; ilium 8395. Cave V: dentaries 8226 (Type), 8227-33; premaxillae 8234-5; maxillae 8236-40; articular+supraangular 8241; articular 8242; interclavicle 8249; scapulocoracoid 8251; scapula 8252; pelves 8253-4; ilia 8255-6; presacral vertebrae 8257 (14); sacral vertebrae 8258 (2), 8259 (2); nonautotomic caudal vertebrae 8261 (10); autotomic caudal vertebrae 8260 (11); limb bones 8262 (10).

TYPE LOCALITY. Cave V, Two Foot Bay on the northeast coast of Barbuda, British West Indies; Late Pleistocene. Collected by Clayton E. Ray and Robert Allen, 3 March 1963.

DIAGNOSIS. *Leiocephalus cuneus* differs from living West Indian species of *Leiocephalus* in that the transition from anterior simply pointed teeth to posterior tricuspid teeth takes place at a more forward position on the jaw. This transition begins in the upper jaws with the appearance of bicuspid teeth on the premaxilla and is completed at the level of the third tooth on the maxilla. In living species the transition begins in the upper jaws with the appearance of bicuspid teeth on the maxilla and is completed at the level of the fourth to seventh tooth of the maxilla. All premaxillary teeth are simply pointed in living species. On the dentary of *L. cuneus* the same transition is completed at the fourth or fifth tooth; in living species the transition is completed at the fifth to tenth tooth.

Leiocephalus cuneus reached a larger size than any living species. Its maximum snout-vent length is estimated to have been nearly 200 mm. The largest living forms are *L. carinatus microcyon*, which has a maximum recorded snout-vent length of 130 mm (Schwartz, 1959) and *L. herminieri* with a snout-vent length of 139 mm (Boulenger, 1885). Certain modifications peculiar to the larger fossils, such as excrescences on the upper surface of the base of the nasal process of the premaxilla, appear to be due to their large size alone.[1]

DESCRIPTION OF THE TYPE (Fig. 2). The dentary is 18.1 mm from its broken posterior border to the symphysis. Its tooth row, measured in a straight line from the anterior border of the first tooth to the projected posterior border of the missing last tooth is 15.6 mm. The height of the dentary at the position of the last tooth is 3.6 mm. There are 26 teeth or empty alveoli; missing are (front to back) teeth number 2, 5, 10, 13, 14, 16, 18, 21 and 26. The first tooth is simple, bluntly conical, and curved inward. The third and fourth tooth are similar except that the crown is slightly truncate. The crowns of the remaining teeth are tricuspid, flared in an anterior-posterior direction, linguo-labially compressed to form a cutting edge, and curved inward. The crowns become slightly wider and the cusps more prominent toward the rear of the tooth row. The cutting edge of each tricuspid tooth is slightly oblique to the main axis of the tooth row so that the anterior cusp of each tooth is overlapped by the posterior cusp of the preceding tooth.

Eight mental foramina penetrate the labial face of the dentary between the second and sixteenth teeth. The upper half of the labial

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[1] When ontogenetic trends common to all species are continued in fossils larger than the largest living form, they often produce modifications not present in the smaller living forms. This point, sometimes disregarded by paleontologists, is even more strikingly illustrated by the comparison of fossil and Recent *Anolis bimaculatus leachii* presented later.

face is smooth and convex anteriorly, becoming flattened to slightly concave and lightly scored posteriorly. The lower half of the labial face and the ventral face of the dentary are smooth and convex. A large, shallow, triangular concavity in the upper half of the posterior labial face of the dentary extends forward to the level of the anterior border of the twenty-fourth tooth, marking the former position of the anterolateral process of the coronoid. A small, oblong foramen penetrates the dentary ventrally just posterior to the symphysis. The lingual face of the dentary is produced medially as a narrow shelf just below the base of the tooth row from the symphysis to the twenty-third tooth. Beyond this the shelf has been broken away. The former position of the coronoid and splenial is indicated medially by a large indentation in the posterior border of the lingual face. Anterior to the apex of this indentation the lingual face of the dentary is shallowly concave to the level of the nineteenth tooth.

ADDITIONAL DENTARIES. Nine dentaries from Caves I, III, and V are similar to the type. Four of them lack only the postdentitional part. The lengths of their tooth rows are 16.2 mm, 15.4 mm, 14.2 mm and 11.8 mm. The three largest dentaries contained 24 teeth, the smallest

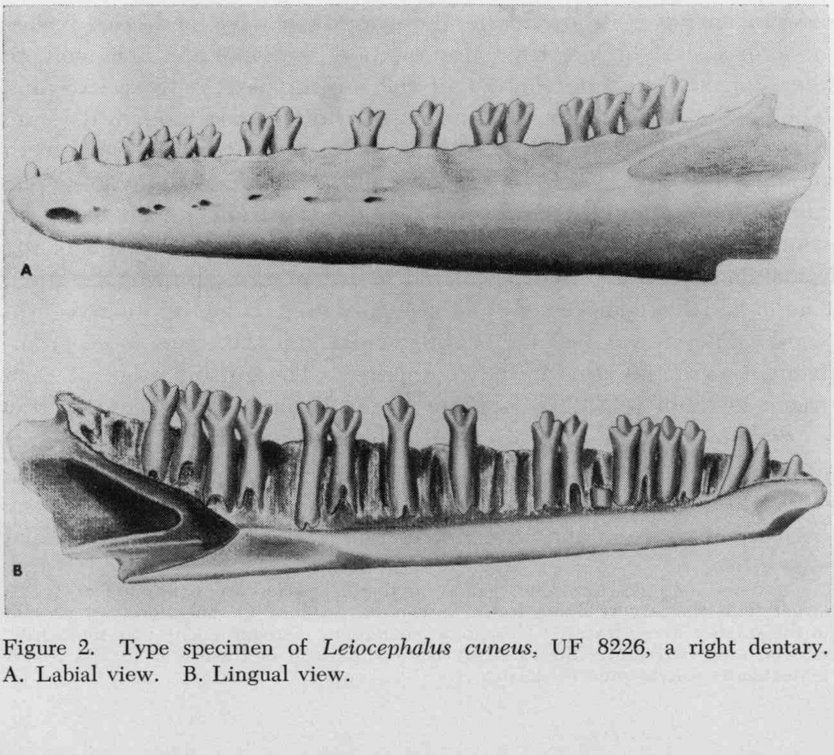

Figure 2. Type specimen of *Leiocephalus cuneus*, UF 8226, a right dentary. A. Labial view. B. Lingual view.

contained 21. The fourth tooth, lacking in the type, is present in one specimen and is of the same form as the fifth tooth of the type.

PREMAXILLAE. Two premaxillae from Caves I and V contain seven teeth or vacant alveolae, a median flanked by three on each side. The largest is 5.0 mm across the rostrum. The crown of the median tooth is simple, slightly curved, pointed, and moderately compressed to form a cutting edge. The first lateral teeth are like the median tooth except for a pair of shallow, vertical grooves on the posterior face. On the second and third lateral teeth the grooves are more distinct, the crowns slightly expanded, and there is a small secondary cusp below and median to the tip.

The former position of the overlapping nasal bones is clearly indicated by shallow concavities on both sides of the nasal process. In the largest specimen the upper surface of the nasal process anterior to the sutural scar of the nasal bones is heavily rugose. The upper surface of the rostral part is somewhat less rugose. The upper surface of the smaller fossils is smooth.

MAXILLAE. Seven maxillae from Caves I and V are referred to this species. The largest complete specimen had 21 teeth, measures 14.6 mm from the anterior border of the premaxillary process to the posterior end of the jugal process, and 6.1 mm from the alveolar border to the tip of the nasal process. The dentition of the maxilla is essentially like that of the dentary except that none of the anterior teeth has a simple point. The first three or four teeth are oblanceolate, laterally compressed, and have faint secondary cusps on either side of the median cusp. The remaining teeth are similar to the flared, strongly tricuspid teeth of the dentary.

ARTICULAR AND SUPRA-ANGULAR. A large articular+supra-angular and a small articular are from Cave V.[2] The larger specimen measures 4.7 mm from the medial border of the articular to the lateral border of the supra-angular just anterior to the condyle. The angular process extends 3.4 mm medially from the medial border of the condyle, and the broken retroarticular process is estimated to have projected posteriorly 4.0 mm beyond the posterior border of the condyle. The angular process is more or less triangular with the apex of the triangle oriented medially. It is partly set off from the retroarticular

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[2] The articular very early becomes firmly ankylosed to the prearticular in a small cup-like depression near the rear of the latter. Following Oelrich (1959) I refer to the combined articular and prearticular as the "articular". At near maximum size the "articular"—(actually only the prearticular part) fuses with the supra-angular.

process by a V-shaped indentation between the two processes. The retroarticular process was apparently more or less rectangular with raised medial and lateral borders.

QUADRATES. Four quadrates were recovered from Caves I and V. The largest measures 9.5 mm from the ventral surface of the articular condyle to the top of the cephalic condyle. The posterior crest curves forward and inward from the cephalic condyle. The upper border of the lateral process slopes downward nearly in a straight line; the lateral border curves gently downward to the ventral condyle. The medial border of the element is sigmoid, with its greatest medial extent about one third of the way down from the cephalic condyle. On the anterior face of the element a deep, broad concavity follows the curving vertical axis of the posterior crest. Near the bottom of this concavity is a small foramen.

PTERYGOIDS. Four pterygoids from Caves I and V all lack the anterior tip of the palatine process and the posterior tip of the quadrate process. The largest is estimated to have been about 18.7 mm in a straight line between the ends of these two processes. The ventral surface of the palatal shelf is slightly raised near its median border and shows no trace of teeth or vacant alveolae.

FRONTALS. Three frontals are from Caves I and V. The largest measures 12.6 mm from the parietal border to the anterior tips of the nasal processes and 3.8 mm across the orbits at the narrowest point. The sutural scars of the nasals and prefrontals indicate that these two bones were separated by the nasal process of the frontal. The upper surface of the element is moderately rugose, making the orbital borders irregular.

PARIETALS. The largest of three parietals from Caves I and V measures 11.7 mm across its frontal border and 5.0 mm between its frontal and occipital borders. In this specimen the lateral borders of the roof converge posteriorly and are only narrowly separated from one another where they meet the occipital border. This feature is simply an extension of the characteristic growth curve of the parietal roof shape in West Indian *Leiocephalus*. The upper surface of the roof is strongly rugose. A median depression in the roof is bordered laterally by low swollen areas. One of the parietals has a small rounded tuberosity in the middle of the median depression.

POSTORBITAL. A nearly complete postorbital from Cave I is estimated to have been 9.6 mm from the anterior tip of the jugal process to the posterior end of the squamosal process. The outer face of the element is moderately smooth except for a rough swelling on the frontal process.

JUGAL. A single jugal from Cave I measures 13.5 mm in a straight line from the anterior tip of the maxillary process to the posterior tip of the temporal process, and is 2.5 mm deep at the deepest part. Eight suborbital foramina form an irregular arc on its lateral face.

INTERCLAVICLE. An interclavicle from Cave V is estimated to have been about 17.7 mm long. Its lateral processes are broken near their bases, but clearly arose some distance posterior to the anterior extremity of the median blade. Both the dorsal (sternal) and ventral surfaces of the median blade have a prominent median keel.

SCAPULOCORACOID. A scapulocoracoid and an isolated scapula are from Cave V. The scapulocoracoid is 17.0 mm from the top of the scapular shaft to the ventral edge of the coracoid plate. The isolated scapula is 10.1 mm from its dorsal border to its coracoid sutural surface. A scapular, a scapulocoracoid, and a primary coracoid fenestrae are present. A small, irregular piece appears to have been broken off from the ventral margin of the coracoid plate between the distal parts of the secondary coracoid ray and plate; however, this may represent a small, natural secondary coracoid fenestra.

PELVES. Four pelves and three dissociated ilia are from Caves I, II, III and V. The diameter of the acetabulum of the largest pelvis is 6.5 mm and its ilium is 18.0 mm long. On this specimen muscle scars are indicated by well developed rugosities on the lateral face of the ischium near its anterior border, and over most of the lateral face of the ilium. No muscle scars are visible on the smaller specimens and their sacroiliac scars are not so strongly developed.

The dissociated ilia all measure 14.0 mm in length. Their acetabular ends are intact, indicating that they came from pelves in which the three components had not yet ankylosed.

PRESACRAL VERTEBRAE. Fourteen vertebrae from various regions of the vertebral column between the axis and sacrum are from Cave V. The largest, apparently from the mid-thoracic region, measures 9.0 mm from the anterior end of the centrum to the posterior tip of the condyle. The centrum is strongly compressed ventrally to form a blunt median crest, flanked by a triangular cavity on each side. The articular surface of each prezygapophysis is V-shaped, the lateral surface facing inward and upward, the medial surface facing outward and upward. The two facets form with one another an angle of about 55°. Articular surfaces of the postzygapophyses are mirror images of those of the prezygapophyses. Their vertical facets are formed by the lateral walls of a zygantrum-like excavation in the posterior base of the neural arch. The neural spine is well developed and strongly compressed with a blunt posterior border and a sharp anterior border which is continuous with a thin, high median fin-like crest projecting vertically above the neural arch.

SACRAL VERTEBRAE. Two first and two second sacral vertebrae are from Cave V. The greatest length of the centrum, including condyle, of the largest first sacral vertebra is 4.9 mm. The centrum of the largest second sacral vertebra is 4.1 mm. The articular surfaces of the prezygapophyses of the sacral vertebrae are V-shaped and the postzygapophyses have zygantrum-like excavations as in the presacral vertebrae.

NONAUTOTOMIC CAUDAL VERTEBRAE. Ten vertebrae from between the sacrum and the first autotomic caudal vertebra from Cave V vary considerably in size and proportions and doubtlessly came from different areas in this region of the tail. Living species usually have from five to seven vertebrae in this region, each one slightly different from the others. The centrum including its condyle of the largest vertebra is 6.1 mm long. The articular facets of the zygapophyses are similar to those described for the presacral vertebrae, except that the angle between the vertical and sloping facets is more acute, about 20°. The transverse processes are broad, flat, truncate, and oriented slightly backward. The neural spine is strongly compressed and wider at the top than at the base.

AUTOTOMIC CAUDAL VERTEBRAE. One intact autotomic caudal vertebra and parts of ten others are from Cave V. Measurements of the intact vertebra are: greatest length of the centrum including condyle 8.0 mm; length of the anterior segment from the anterior ventral border of the centrum to the fracture plane 2.0 mm; length of the posterior segment from the fracture plane to the ventral border of the condyle 3.4 mm. The anterior zygapophyseal articulation occurs at two pairs of surfaces, the sloping facets of the prezygapophyses proper and the vertical sides of a Y-shaped process that projects from the anterior end of the median crest of the neural arch. The fracture plane passes more or less vertically through the neural arch and centrum except where it curves around the posterior borders of the bases of the transverse process. A low median crest extends along the top of the neural arch, interrupted above the plane of fracture by the broken base of what was probably a vertical spine. The transverse processes are flat, tapered, and oriented posterolaterally.

LIMB BONES. Ten fossil limb bones from Cave V are tentatively referred to *L. cuneus* because of their large size. The largest of these is a tibia 32.0 mm long.

COMPARISONS. The general form and proportions of the dentary and maxilla are fairly uniform among living species of West Indian *Leiocephalus*. Except for the dental differences cited in the diagnosis I am unable to distinguish the fossil dentaries and maxillae from those of living species. All living forms of *Leiocephalus* also have seven premaxillary teeth. As pointed out in the diagnosis, the fossil premaxillae have bicuspid teeth laterally, whereas the premaxillae of living species have only simply pointed teeth, a difference that reflects the extreme anterior position of the simple-to-tricuspid tooth crown transition in the upper jaw of *L. cuneus*. The upper surface of the skull roofing bones tends to become rugose in large individuals of modern species, but in none do the excrescences extend forward of the nasals onto the premaxilla as in *L. cuneus*.

The configuration of the angular and retroarticular processes of the articular varies considerably among the Recent West Indian species of *Leiocephalus*. In *L. schreibersii* and *L. inaguae* the angular process is much flatter distally than in *L. cuneus* and in other living species. In *L. carinatus*, *L. punctatus*, *L. greenwayi*, and *L. loxogrammus* it curves forward and inward, whereas in *L. cuneus* and in other living species the process is triangular and oriented medially. *L. cuneus* appears to differ from all living species in that the angular and retroarticular processes are partly separated medially by a shallow, V-shaped indentation.

Pterygoid teeth are absent, as in most living species. They occur only in *L. carinatus*, *L. punctatus*, and *L. loxogrammus*.

In *L. pratensis* and *L. personatus* the dorsal surface of the frontal and parietal bones are sculptured after the pattern of the scales above them, whereas in *L. cuneus* and in all other living species these elements do not reflect the scale pattern.

Except for slight proportional differences and the much larger size of some of the fossils I am unable to distinguish the remaining elements referred to this species from those of living forms.

The approximate snout-vent lengths of the animals from which the fossils came may be calculated by multiplying their various measurements by the ratios of measurements of the same elements of living species to their snout-vent lengths. Because of ontogenetic changes and interspecific differences in these proportions, the calculations can be expected to be rather imprecise. However, assuming that the proportions in the extinct species fall within the limits of those among all the living forms, a meaningful estimate of snout-vent length may be obtained for the extinct species. These estimates, based on the largest specimens of each fossil element, indicate that *Leiocephalus cuneus* attained a maximum snout-vent length of at least 160 mm and may have reached nearly 200 mm. The maximum snout-vent length attained by any living species is 139 mm recorded for *L. herminieri* (Boulenger, 1885).

Living West Indian species of *Leiocephalus* occur on Cuba (*carinatus, cubensis, raviceps, macropus, stictogaster*), Grand Cayman (*carinatus*), the Bahamas (*carinatus, loxogrammus, punctatus, greenwayi, psammodromus, inaguae*), Navassa (*erimitus*), Hispaniola (*schreibersii, personatus, melanochloris, pratensis*) and Martinique (*herminieri*)[3]. The most distinctive species appears to be *L. herminieri,* separated by more than 700 kilometers from the nearest species on Hispaniola. Its skeletal characteristics clearly place *herminieri* with the West Indian species of the genus rather than with the South American forms, but it differs from all the island species in having distinctly keeled ventral scales; all others have smooth ventrals. The skeletal characters of *L. cuneus* do not indicate a close affinity between *L. cuneus* and any particular living form; however, its large size and its geographical proximity to *herminieri* may presage close relationship to this species.

The presence of *Leiocephalus* on Barbuda, about a third of the way from Martinique to Hispaniola, in the not-too-distant past suggests that the genus was once more widely distributed in the eastern Caribbean islands. Two other West Indian fossil herpetofaunas now

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[3] Some doubt has existed as to the range of *L. herminieri* Duméril and Bibron 1837. The species is based on three syntypes in the Museum National D'Historie Naturelle, Paris: MNHN 1826 and 6829 are labeled "La Martinique" and MNHN 2389 is labeled "Trinité" (Guibé, 1954). A single specimen, a skeleton in the British Museum (Natural History): BMNH 52.12.3.10 (123a in the osteology catalogue) is labeled "Martinique". Apparently the three Paris syntypes and the British Museum skeleton are the only specimens of *L. herminieri* ever collected. Duméril and Bibron give the type locality of *L. herminieri* as "Iles de la Trinité et de la Martinique". Boulenger (1885) gives the range as "Trinidad and Martinique". Barbour (1914) states he was unable to find the species on Martinique, and that if it actually did occur there at one time it was probably extinct. Burt and Burt (1933) give the range of *herminieri* as "probably Trinidad". Apparently Duméril and Bibron and subsequent authors believed the locality label "Trinité" on MNHN 2389 referred to the British island of Trinidad off the northeastern coast of Venezuela. However, since the other specimens are all labeled Martinique, the label "Trinité" almost certainly refers to the town of that name on the northeastern coast of Martinique.

under study also contain extinct species of *Leiocephalus,* one from western Dominican Republic and another from several localities on Jamaica, where the genus does not occur today. Both species are from Pleistocene cave deposits. In addition, Estes (1963) has reported West Indian-type *Leiocephalus* in the Thomas Farm fauna of the Florida Miocene. Unquestionably, West Indian *Leiocephalus* was much wider ranging in the past than it is today. A more thorough study of the fossils now available from other islands must precede any further speculations on the zoogeographic implications of this past distribution.

Anolis

Caves I and II contained a large number of fossil bones of *Anolis.* Auffenberg (1958) reported these as *Anolis leachii,* but mentioned that some of the smaller elements might represent *Anolis wattsi* as he was not able to distinguish the two species on any basis other than size. Since 1958 many more bones of *Anolis* have been collected from all the Barbudan caves.

Two species of *Anolis* live on Barbuda today, *A. forresti* and *A. bimaculatus leachii.* Both forms also occur on Antigua, which shares the same submarine bank with Barbuda. Other races of *Anolis bimaculatus* live on islands of the Anguilla Bank, St. Kitt's Bank, Saba, and Guadeloupe. *Anolis wattsi,* a species apparently closely related to *Anolis forresti,* occurs on islands of the Anguilla Bank, St. Kitt's Bank, and Santa Lucia. According to Williams (personal communication) his recently described *Anolis alter* (Williams, 1962) is a synonym of *Anolis forresti,* and *Anolis wattsi,* which was thought to occur sympatrically with *Anolis forresti* on Antigua and Barbuda, does not occur on those islands. No other species of *Anolis* is known to occur on Barbuda or on any other islands of the northern Lesser Antilles between the Anegada Passage and the Guadeloupe Passage.

A. bimaculatus leachii is the larger of the two Recent Barbudan species. Adult males reach a maximum snout-vent length of 90 mm, adult females 67 mm. Adult males of *A. forresti* reach a maximum snout-vent length of 50 mm, adult females 45 mm. Most of the races of *A. bimaculatus* are smaller than *A. b. leachii,* and only one race, *A. b. bimaculatus* which reaches 100 mm in snout-vent length, exceeds *leachii* in size. The maximum size of *A. wattsi* is about equal to that of *A. forresti.* Skeletons of these three species are very similar. In most cases bones of the same size from the three species are difficult to tell apart because ontogenetic changes follow parallel trends in all three. A few structural peculiarities appear in *leachii,* but not until after they have exceeded the maximum size of *forresti* and *wattsi*.

The *Anolis* fossils cover a considerable size range. The largest bones probably came from animals at least 120 mm in snout-vent length, the smallest from animals not more than 25 mm in snout-vent length. Most skeletal elements, when lined up from smallest to largest, show a continuous ontogenetic gradient; bones of equal size are structurally very similar, though they may differ structurally from larger or smaller bones of the same element. Fortunately some skeletal elements of *Anolis* assume certain characteristics only at or near maximum size. The components of the pelvis, scapulocoracoid, and basale do not become ankylosed until near maximum size, and the adult parietal bone has a characteristic shape regardless of size. From these bones the number of size classes represented among the fossils can be determined and the maximum snout-vent length of each estimated. Each size class presumably represents at least one species unless two size classes are close enough together to represent males and females of a sexually dimorphic species.

Since the components of the pelvis—ischium, ilium, and pubis—do not become ankylosed until the lizard nearly reaches maximum size, those from smaller individuals fall apart when the animal decomposes. For this reason the pelvic components of any one species will, in a collection of fossils, be dissociated except for those from nearly full grown adults. Among the Barbudan fossil *Anolis* are pelves of three distinct size classes, plus a number of dissociated ilia, pubes and ischia. (Fig. 3). Measurements taken across the greatest diameter of the acetabulum range from 1.2 to 1.6 mm in

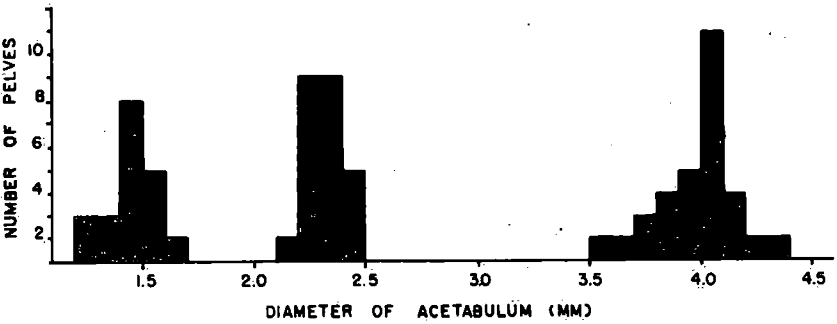

Figure 3. Three size classes of fossil pelves of *Anolis* from Barbuda. Each size class presumably represents at least one species, the smallest with a snout-vent length estimated to have been 42 to 48 mm, the medium-size species 61 to 72 mm and the largest species 91 to 112 mm.

the group of small pelves, from 2.1 to 2.4 in the medium-size pelves and from 3.5 to 4.3 in the large pelves. The snout-vent lengths of the animals from which these pelves came are calculated to have been from 42 to 48 mm for the smaller group, 61 to 72 mm for the medium-size group and 91 to 112 mm for the large group.

The scapula and coracoid also fall apart upon decomposition unless they are from an animal near maximum size. The intact fossil scapulocoracoids of *Anolis* appear to represent two size groups. Measurements taken across the greatest diameter of the glenoid fossa of the smaller fossils range from 1.0 to 1.1 mm and in the larger group from 1.6 to 2.1. The snout-vent lengths of the animals from which these scapulocoracoids came are estimated to have been from 68 to 70 mm in the smaller group and from 91 to 120 mm in the larger group.

The components of the basale—basisphenoid, otics, and occipitals,—also remain unfused until near maximum size. The fossils contain three size groups of intact basalia. Measurements taken across the base of the basioccipital between the distal extremes of the spheno-occipital tubercles are 2.5 to 2.7 mm in the small group, 3.5 to 3.7 mm in the medium-size group and 6.0 to 6.7 mm in the large group. The snout-vent lengths of the animals from which they came are estimated to have been from 45 to 48 mm in the small group, 63 to 66 mm in the medium-size group and 108 to 120 in the large group.

In most species of *Anolis* the adult parietal, regardless of the maximum size of the species, has the same characteristic shape. The roof is triangular with raised posterolateral borders. The occipital part of the element extends beyond the roofing part and has on its dorsal surface a median crest that extends back from the posterior median apex of the roof. In subadults the posterior apex of the roof reaches the posterior border of the occipital part, and in still smaller individuals the lateral roof borders converge posteriorly but fail to join one another before they reach the occipital border.

The fossils contain three size classes of adult parietals. The smallest is represented by a single specimen which measures 4.5 mm across its frontal border. The medium size class is represented by four specimens in which the width of the frontal border ranges from 6.6 to 7.2 mm, and the large group is represented by 21 parietals which range in frontal width from 8.8 to 11.8 mm. The snout-vent lengths calculated for these parietals are 45 mm for the small size group, 61 to 72 mm for the medium size group, and 89 to 113 mm for the large one.

Thus, three size groups of *Anolis* are clearly indicated by the fossil pelves, basalia, and parietals; two size groups, equivalent to the medium and large groups of the other elements, are represented by the scapulocoracoids. The snout-vent lengths estimated for these elements are in fairly close agreement with one another, considering the error inherent in such calculations. The small size group attained a maximum size of from 42 to 48 mm, the medium size group from 61 to 72 mm and the large size group from 89 to 120 mm. The maximum size of adult males is 1.34 times greater than that of adult females in living *leachii* and 1.11 in living *forresti*. The upper size limit of the group of large fossils is 1.34 times greater than its lower limit, 1.18 in the medium size group, and 1.14 in the small group. Thus, both sexes are probably included within the range of each group. For this reason it seems fairly safe to conclude that at least three species of *Anolis* are represented in the Barbudan fossils.

Sorting the other available elements of fossil *Anolis* into small, medium, and large species cannot be done so easily. All fossils from animals calculated to have measured more than 72 mm in snout-vent length may be referred to the large species. Fossils from animals between 48 and 72 mm snout-vent length might have come from either the medium or large species, and elements from animals under 48 mm snout-vent length may belong to any of the three forms. Most of the elements are present in large numbers, and they range in size from below the maximum for the small species to or near the maximum of the large species. Thus, the description of only one species, the large one, may be offered with any certainty that all the elements assigned to it came from that species only.

ANCESTRAL *Anolis bimaculatus leachii*. Certain structural peculiarities in the skeleton of adult modern *Anolis bimaculatus leachii* distinguish this race from all other anoles. The most conspicuous of these are the massive, irregular rugosities on the ventral and ventrolateral faces of the dentary. Although sculpturings of one sort or another appear on the dentaries of adult males of other West Indian species of *Anolis* (i.e. *cybotes, cristatellus, shrevei, scriptus, krugi, pulchellus,* and *evermanni*) their configurations are quite different (Etheridge, unpublished dissertation). Excrescenses similar to those on the dentary of large *A. b. leachii* also appear in *A. b. bimaculatus*, but they are not nearly so strongly developed as in *leachii* of equal size. In an adult male *A. b. bimaculatus* 100 mm in snout-vent length (near maximum size) the excrescences are only faintly indicated. Dentaries of the large fossil species bear sculpturings identical structurally to those of modern *leachii*. Other fossil elements referred to the large species are also indistinguishable from those of living *leachii* of the same size. Fossil bones from animals larger than 90 mm snout-vent length (maximum size of modern *leachii*) continue those ontogenetic trends initiated in smaller bones of living *leachii* and the smaller fossils. Thus the largest fossil elements are not only larger than those of the largest Recent *leachii,* but also differ from them in proportions and structure. Therefore, the large species of fossil Barbudan *Anolis* possibly represents a giant population directly ancestral to modern *Anolis bimaculatus leachii.*

Dentaries. (Fig. 4). Sculpturing first appears on the dentary in living *leachii* at about 80 mm snout-vent length when the dentary tooth row is 14 mm long. At this size a number of faint, shallow, more or less longitudinal grooves appear on its lower, outer face. As the dentary becomes larger the grooves deepen and the spaces between them become irregularly swollen. At maximum size (snout-vent length 90 mm, dentary tooth row 16 mm) the swellings have become quite massive and irregular. The fossil dentaries between 14 and 16 mm tooth row length show the same peculiar development.

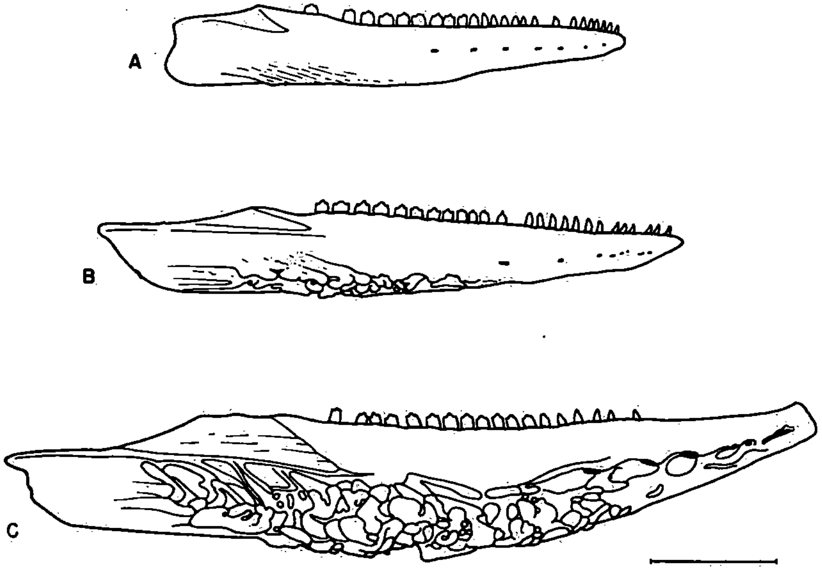

Figure 4. Labial view of the right dentary of *Anolis bimaculatus leachii.* Sculpturing first appears on the lower and outer face at about 70 mm snout-vent length (B). The sculpturing reaches grotesque, almost pathological proportions in fossil specimens near maximum size, about 115 mm snout-vent length (C).

In larger fossil dentaries the swelling continues and the pits and depressions between them deepen until, in the largest fossil dentaries (tooth row 20.4 mm, snout-vent length about 115 mm), they have reached grotesque, almost pathological proportions.

The number of teeth on the fossil dentaries increases ontogenetically (Fig. 5) but the increase is not so great nor the trend so clear-cut as in *Thecadactylus*. Because dentaries below 12.5 mm tooth row length (snout-vent length about 72 mm) may belong to either the large or the medium size species, and those below 8 mm tooth row length (snout-vent length about 48 mm) may belong to any of the three, only those larger than 12.5 mm tooth row length can be definitely referred to the ancestral *leachii*.

MAXILLA. The most conspicuous ontogenetic changes in the maxilla of *leachii* involve the development of surface irregularities and the appearance and enlargement of an acute canthus rostralis. The outer surfaces of the maxilla are smooth in very small individuals; weak sculpturings appear and become more pronounced with increasing size. Fossil maxillae equal in size to those of living *leachii* show about the same degree of rugosity. As in the dentary, the excrescenses become even more strongly developed in still larger fossil maxillae. The canthus rostralis in very small *leachii* is smoothly rounded. It becomes more angular with increasing size and eventually forms a slightly projecting ridge in adults. In the larger fossils the canthal ridge projects far above the dorsal face of the nasal process. As surface irregularities and a projecting canthal ridge develop in many species of *Anolis*, especially the larger ones, their appearance in *leachii* or the fossils is not particularly distinctive.

Fossil maxillae are nearly as abundant as dentaries, but as most have had the slender posterior process and its teeth broken away, few complete tooth counts are possible. The largest complete maxilla has a tooth row length of 17.6 mm, contains 28 teeth or empty alveoli, and probably come from an animal about 110 mm in snout-vent length.

QUADRATE. Ontogenetic changes in the quadrate of *leachii* involve a disproportionate increase in the width of the outer border of the cup-like lateral process and a disproportionate enlargement of the upper part of the medial process. These trends are continued in the larger fossils. The outer border of the lateral process becomes enormously swollen and sculptured by shallow, irregular depressions. The upper part of the medial process develops into a large, triangular projecting shelf, also covered by surface irregularities. The largest fossil quad-

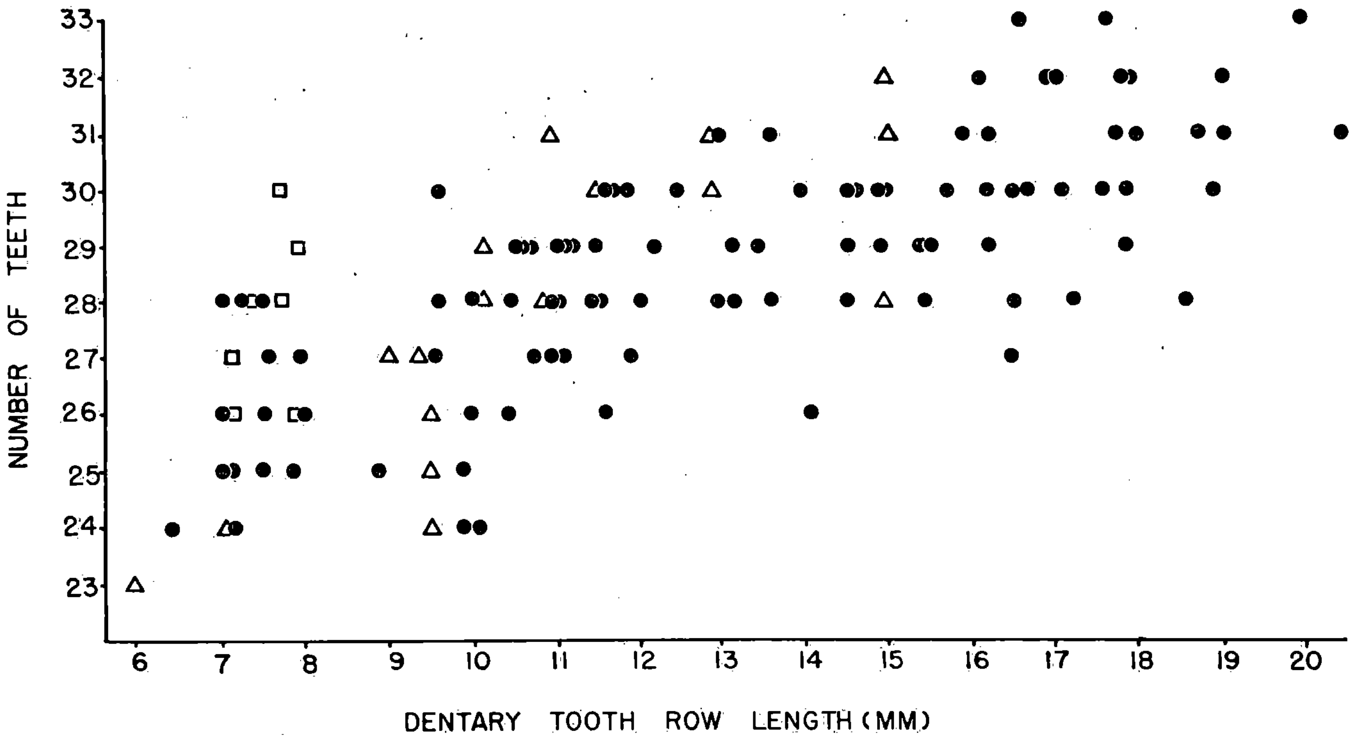

Figure 5. Tooth counts on fossil dentaries of *Anolis* from Barbuda (solid circles) compared with tooth counts of Recent *Anolis forresti* (open squares) and *Anolis bimaculatus leachii* (open triangles).

rate measures 6.3 mm from the upper surface of the supratemporal condyle to the lower surface of the articular condyle. It is estimated to have come from a lizard about 115 mm in snout-vent length.

The ontogenetic trends in the quadrate of *leachii* and the fossils also occur in other races of *bimaculatus*. The quadrate of a large specimen of *A. b. bimaculatus* 100 mm in snout-vent length (10 mm longer than the largest modern *leachii*) is very similar in structure and proportions to fossil quadrates of the same size. In other species of *Anolis*, even those that become much larger than the fossils, (*garmani, equestris, ricordii, cuvierii* for instance) no such ontogenetic changes occur.

PTERYGOIDS. Ontogenetic changes in the pterygoid involve the development of irregularities on the palatal surface, swelling of the ventral median region of the palatal portion, and the disproportionate increase in the size of the ectopterygoid process. Ventral surface sculpturing is only weakly developed in the largest *leachii* and fossil pterygoids of equal size, but becomes very prominent in the largest fossils. Near the median edge of the palatal part of the pterygoid an elongate, oval, mound-like swelling appears in small *leachii*. From one to three simply pointed teeth project from near the anterior end of this mound. With increasing size the mound becomes more and more prominent and ornamented with a series of close-set, irregularly oblique folds.

Similar changes occur in the pterygoid of other races of *bimaculatus* and in other species of *Anolis*. The largest fossil pterygoid is estimated to have come from an animal about 118 mm in snout-vent length. Pterygoid teeth are lacking in *wattsi* and *forresti*. They are present on all the fossil pterygoids, even those small enough to have come from the small or medium size species. Thus either all the fossil pterygoids must be referred to the large species, or the smaller species do not represent fossil *wattsi* or *forresti*.

OTHER ELEMENTS. Less striking ontogenetic changes occur in other skeletal elements, none of which can be used as diagnostic for *leachii*. The frontal develops excrescences on its upper surface, and the width between its orbits becomes relatively greater. The largest fossil frontals are considerably more sculptured than those of the largest Recent *leachii*. The ratio of parietal border width to narrowest interorbital width is 2.7 in Recent *leachii* 85 mm in snout-vent length and 3.6 in the largest fossil, which is estimated to have come from an animal about 118 mm in snout-vent length.

Surface irregularities appear on the nasal process of the larger fossil premaxillae. They are not present in even the largest Recent *leachii*. The largest fossil premaxilla measures 6.0 mm across the rostral part and is estimated to have come from an animal about 120 mm in snout-vent length. All fossil premaxillae have 11 teeth or empty alveoli, the same number found in modern *leachii*.

Other fossil elements referred to the large species because of their size include palatines, jugals, prefrontals, postorbitals, ectopterygoids, squamosals, palatines, coronoids, vertebrae, interclavicles, and limb bones. All are similar to those of modern *leachii*, though some are larger, but nothing about them is distinctive enough to identify them positively as *leachii*. Snout-vent lengths calculated for the largest of these elements range from 105 mm to 120 mm.

Nothing indicates that the fossils with calculated snout-vent lengths greater than 72 mm represent more than one species. Some of the fossils elements, especially the dentaries, maxillae, and quadrates, are most distinctive and present in great numbers, yet only one structural type of each is recognizable. The presence of subspecifically diagnostic skeletal characters is uncommon in lizards. In this respect *Anolis bimaculatus leachii* is unusual. Most of the large fossil elements might belong to almost any species of *Anolis*, but the unusual quadrate of *bimaculatus* is peculiar to that species, and the massive, excrescenses on the dentary are peculiar to the subspecies *leachii*. For this reason there seems little doubt that the large Barbudan fossil *Anolis* is directly ancestral to the modern Barbudan population of *Anolis bimaculatus leachii*.

THE TWO SMALLER SPECIES OF FOSSIL *Anolis*. The identification of the large species of fossil *Anolis* as ancestral *Anolis bimaculatus leachii* can be made with a fair degree of confidence because of the unique sculpturing on the dentary. Unfortunately, not much can be said about the two smaller species. Their existence is predicated only on fossil pelves, scapulocoracoids, basalia, and parietals. Presumably other elements from these two species are present among the fossils, but they are indistinguishable from those of small *leachii*.

On zoogeographic grounds it seems most likely that the relatives or descendents of the smaller fossil species should be found among those now present on Barbuda or nearby islands. Although the smaller fossils, except as noted above, are indistinguishable from the bones of young *leachii* and from many other anoles of the eastern Caribbean, most of the species in the genus may be eliminated as near relatives on purely structural grounds.

All the anoles of Mexico and Central and South America are eliminated by their caudal vertebrae. Two types of caudal vertebrae occur in mainland Middle and South American anoles: (1) autotomy planes of fracture and long, anterolaterally oriented transverse processes present, and (2) autotomy planes of fracture and transverse processes absent. All the fossil *Anolis* caudal vertebrae (more than 200) lack transverse processes but have planes of fracture, a condition found only among certain West Indian *Anolis*, and in *A. carolinensis* of North America and *A. agassizi* of Malpelo island in the Pacific southwest of Panama. The character also eliminates many West Indian species. All the anoles of Jamaica and the Swan Islands and about half the species of Cuba and the Bahamas have caudal vertebrae with fracture planes and transverse processes.

Four species from the southern Lesser Antilles, Trinidad, and the Dutch West Indies, *trinitatis*, *roquet*, *richardi*, and *bonairensis*, are eliminated by the shape of their adult parietal. In these forms the lateral borders of the parietal are separated where they meet the occipital border and there is no median occipital crest. (This same shape is also found in *A. agassizi* and in the mainland anoles that lack fracture planes and caudal transverse processes). In this regard these four species differ from all other West Indian *Anolis*, including the three fossil species of Barbuda.

The remaining anoles of Cuba and Caymans and about half the species of Hispaniola are eliminated by their interclavicle, which is nearly T-shaped, its lateral processes in contact throughout their length with the clavicles. The fossil interclavicles are distinctly arrow-shaped, and the point of divergence of their lateral processes from the clavicles is marked by a posterior bend near their base. The remaining Hispaniolan species and all the West Indian anoles east and south of Hispaniola have the type of interclavicle found in the Barbudan fossils.

Of the Hispaniolan species remaining two more can be eliminated. *Anolis cybotes* and *A. shrevei* adult males have a peculiar type of dentary sculpturing not found in the Barbudan fossils, large or small. In the Puerto Rican species *A. krugii*, *A. poncensis*, *A. pulchellus*, and *A. gundlachi* the parietal foramen penetrates the parietal bone some distance posterior to the frontoparietal suture. In the three fossil species the former frontoparietal position of the foramen is indicated by a U-shaped notch in the frontal border of the parietal.

Although most *Anolis* species can be eliminated as possible relatives or descendents of the two smaller fossil species, the genus is so large that a number of species still cannot be distinguished from them. These remaining species are, however, geographically restricted to Hispaniola and the eastern Caribbean north of the Martinique passage. There seems little profit in trying to carry the identification of the smaller fossil species further than this. The size differential between ancestral and modern *leachii* on the island warns that size differences should not be used as a basis for identifying the fossils. Furthermore, the presence of an extinct species of *Leiocephalus* on Barbuda shows that the two smaller fossil *Anolis* species need not necessarily be referred to some still extant species or only to those anoles now living on Barbuda and nearby islands. Also the presence of ancestral *leachii* does not preclude the possibility that one or both of the smaller forms may be referable to other "subspecies" of *bimaculatus*. No osteological evidence forbids this and, as the races are all allopatric, we have no way of knowing whether or not they are, or ever were, reproductively isolated. Certainly the differences in color, scalation, and size between the races of *bimaculatus* are as great or greater than those that distinguish many sympatric species of *Anolis*, such as *A. trinitatis* and *A. roquet*.

If one or the other of the two smaller fossil species does represent an ancestral population of *Anolis forresti*, then either the species has remained approximately the same size (if the smaller) or decreased in size by about 35% (if the larger). Recent *leachii* are about 25% smaller than their ancestors.

SPECIMENS REFERRED TO ANOLIS. Cave I: premaxillae 8382, 8424 (35), 8477 (30); maxillae 2759 (62), 8434 (72), 8435 (86), 8472 (21), 8488 (33); jugals 8384 (14), 8445 (81), 8485 (33); postorbitals 8443 (100), 8462 (21); squamosals 8439 (25); quadrates 8438 (51), 8484 (19); prefrontals 8440 (11); frontals 8371 (46), 8430 (60), 8479 (46); parietals 8433 (2), 8379 (5), 8381 (2), 8432 (18), 8475 (10), 8476; basale 8372, 8415 (7), 8416 (2), 8417 (3); 8478 (7); basisphenoids 8414 (22), 8473 (2); palatines 8459 (5); pterygoids 8425 (23), 2757 (4), 8472 (6); ectopterygoids 8442 (9); dentaries 2756 (31), 2758 (136), 8455 (58), 8456 (93), 8480 (40), 8481 (37), 8482 (17), 8483 (18); coronoids 8437 (15); articulars 8373 (29), 8431 (49), 8474 (3); scapulocoracoids 8422 (2), 8383, 8420 (15), 8421 (7); coracoids 8423 (3); interclavicles 8458 (4); pelves 8374 (8), 8375 (11), 8376 (2), 8426 (14), 8427 (11), 8428 (29); ilia 8377 (3), 8429 (10); ischia 8429; vertebrae 8447-52 (750). Cave II: premaxillae 8329; maxillae 8330 (8); frontals 8378 (2); parietals 8380 (2); basale 2810 (2); dentaries 8331 (7), 8332 (18); articulars 8328 (2). Cave III: premaxillae 8320 (2); maxillae 8397 (5); quadrates 8399 (2); frontals 8323, 8398 (3); parietal 8322; dentaries 8321 (4), 8333 (5), 8396 (5); coronoid 8326; articulars 8316 (3), 8403; pelves 8324 (2), 8400; ilia 8324 (2), 8401 (2); coracoid 8402. Cave IV (breccia): maxillae 8349 (5); prefrontal 8351; dentaries 8348, 8347 (11); articulars 8350 (3); scapulocoracoid 8352. Cave V: maxillae 8355 (11); quadrate 8358; prefrontal 8359; frontal 8356 (3); parietal 8360; pterygoid 8361; dentaries 8357 (18); articular 8411; pelves 8362 (2), 8363, 8411.

Genus and species indeterminate

A fragmentary braincase (8784) and a body vertebra from Cave III resemble those of the large iguanine genera *Amblyrhynchus, Conolophus, Ctenosaura, Cyclura,* and *Iguana,* but cannot be referred with certainty to any one of them. Both fossils are estimated to have come from animals about 400 mm snout-vent length. The components of the braincase are firmly ankylosed and the sutures between them are obscure, indicating that the specimen is from an adult.

Generic differences in the shape of the basisphenoid among the large iguanines have been pointed out by Boulenger (1890). The element is much wider than long and slightly to moderately constricted behind the pterygoid processes in *Iguana* and *Cyclura,* about as wide as long and strongly constricted in *Amblyrhynchus* and *Conolophus,* and much longer than wide and strongly constricted in *Ctenosaura.* The ratio of the basisphenoid length, measured from its posterior border to the apex of the indentation between a pterygoid process and the parasphenoid process, divided by its narrowest width posterior to the pterygoid processes show the following variation in Recent forms: *Iguana* (*iguana, delicatissima*) .40-.65, *Cyclura* (*cornuta, figginsi, ricordi, maclaeyi*) .64-.72, *Amblyrhynchus* (*cristatus*) .79-.91, *Conolophus* (*pallidus*) .86-1.10, *Ctenosaura* (*hemilopha, pectinata, similis*) 1.45-1.96. This ratio in the fossil is 1.00. In this, and in most other features the fossil closely resembles the Galapagoan genus *Conolophus.* They differ in that in *Conolophus* the anteroventral border of the occipital condyle forms a distinctly projecting lip.

The body vertebra has a high, robust neural spine and well developed zygosphenes and zygantra, and in all other respects is similar to those of other large iguanines.

On zoogeographic grounds one might reasonably expect either *Cyclura* or *Iguana* to have occurred on Barbuda. *Iguana iguana* is found on many islands between the Virgin Islands and the South American mainland, and *I. delicatissima* occurs in the Leeward Islands and Guadeloupe (Dunn, 1934). *Cyclura* now finds its eastern limit on Anegada Island (*C. pinguis*) and recently extinct species are known from St. Thomas (*C. mattea*) and Puerto Rico (*C. portoricensis*). But the Barbudan fossil falls far outside the known limits of variation of both *Cyclura* and *Iguana.*

TEIIDAE

Ameiva griswoldi

To the single dentary Auffenberg (1958) originally reported from Cave II the following elements have been added: three maxillae

(8446, 8467) and one dentary (8466) from Cave I, one maxilla (8394) from Cave III and two maxillae (8412) from Cave V. All are indistinguishable from those of modern *Ameiva griswoldi* both in size and structure.

COMPARISON OF THE CAVE FAUNAS

The fossils from Caves I, II, and V were recovered from soft cave-earth floors, those from Caves III and IV from more consolidated cave earths clinging to the walls. Also recovered from the floor surface of Cave IV were a number of very recent bones mixed with fossils that had washed out of the consolidated cave earth on the cave walls. These recent bones have not been included in this study. As mentioned in the introduction, the fossils from the consolidated earths are probably much older than those of the soft earth floors. The younger fossils are very probably pre-Columbian in age and possibly no older than mid-Wisconsin; the older fossils are probably not older than Late Pleistocene.

Samples from the five caves are unequal in size, partly because the amounts of fossil-bearing material found varied in each cave, and partly because different amounts of time were spent in sorting the fossils from this material. The low number of fossils from Caves III and IV also reflects the difficulty of recovering them from the consolidated cave earths. Nevertheless, every care was taken to obtain unbiased samples from each cave. All bony fragments, however small or seemingly unidentifiable, were removed. Thus although the absolute numbers of fossils of each species from different caves are not comparable, the relative abundance of fossils of each species within each cave should be comparable.

Table 1 lists the minimum number of individuals found of *Thecadactylus rapicaudus*, *Leiocephalus cuneus*, *Anolis* spp., the large iquanine, and *Ameiva griswoldi*. In this table the three species of *Anolis* are lumped together. The minimum number of individuals is equal to the most abundant element of each species in the sample; left and right bones of paired elements are counted separately. For example, the most abundant element of *Thecadactylus rapicaudus* in Cave I is the right dentary, of which there are 36. Thus, at least 36 individuals of this species must be represented in the sample. The per cent occurrence of each species, also listed in table 1, is calculated from this figure. Thus of the 262 lizards represented in the sample from Cave I, 36 individuals, or 13.7 per cent, are *Thecadactylus rapicaudus*. As only certain elements of *Anolis* may be referred to one of the three species with any certainty, their per cent occur-

TABLE 1. Relative abundance of lizards in Barbudan Caves

Species	Cave I		Cave II		Cave III		Cave IV		Cave V	
	N	%	N	%	N	%	N	%	N	%
Thecadactylus rapicaudus	36	13.7	2	11.1	3	16.6	3	27.3	9	27.3
Leiocephalus cuneus	3	1.1	1	5.6	1	5.6	0	0	7	21.1
Anolis spp.	224	85.5	14	77.7	12	66.7	8	72.7	11	33.4
iguanine Genus ? sp. ?	0	0	0	0	1	5.6	0	0	0	0
Ameiva griswoldi	2	0.7	1	5.6	1	5.6	0	0	4	12.2

N = minimum number of individuals; % = per cent of total number of individuals in each cave.

Note: Three species of *Anolis* are present in Cave I, two species in Caves II, III and V and one species in Cave IV. For an estimate of the relative abundance of these species in each cave see table 2.

TABLE 2. Relative abundance of three species of *Anolis* in Barbudan Caves

Species	Cave I		Cave II		Cave III		Cave IV		Cave V	
	N	%	N	%	N	%	N	%	N	%
Large species (ancestral *A. bimaculatus leachii*)	16	34.2	2	38.9	2	44.3	1	66.7	2	13.3
medium-size species	12	25.6	0	0	0	0	0	0	0	0
small-size species	12	25.6	2	38.9	1	22.3	0	0	3	20.1

N = minimum number of individuals based on pelves, scapulocoracoids, basale and parietals.
% = per cent of total number of individuals of all lizard species.

rence has been calculated indirectly. First, the relative abundance of the genus was calculated as for each of the other lizard species (table 1). The relative abundance of each species of *Anolis* was then calculated by comparing the minimum number of individuals based on pelves, scapulocoracoids, basale and parietals. These figures are listed in table 2.

The caves differ somewhat from one another in the species of lizards they contain and in the relative abundance of those species. Present in both the older deposits of Caves III and IV and the younger deposits of Caves I, II and V are the large species of *Anolis, Thecadactylus, Leiocephalus* and *Ameiva*. In structure and in size the older fossils are indistinguishable from the younger ones. The absence of the large iguanine in all of the caves except III may be due to its extinction before the accumulation of younger fossils began. The absence of the medium-sized species of *Anolis* in Caves III and IV may signify its arrival on the island after these caves had been filled.

The order of abundance of lizard genera is the same in all the caves. Fossils of *Anolis* are most abundant, followed in order by *Thecadactylus, Leiocephalus, Ameiva,* and the large iguanine. However, the relative abundance of species differs; in this regard Cave V is the most distinctive. I suspect that these differences are due primarily to the circumstances surrounding the accumulation of fossils in each cave, for example, the dietary selectivity of predatory birds. At any rate, it is clear that the lizard faunas of the younger deposits are more similar to those of the older caves than they are to the present lizard fauna of Barbuda.

DISCUSSION AND SUMMARY

Five species of lizards now live on Barbuda: *Sphaerodactylus elegantulus, Thecadactylus rapicaudus, Anolis bimaculatus leachii, Anolis forresti* and *Ameiva griswoldi*. The absence of remains of *Sphaerodactylus,* the only genus not identified among the cave fossils, cannot be taken as clear evidence that these geckos were not part of the island's pre-Columbian lizard fauna. Probably, as in other West Indian cave deposits, owl pellets were a major source of these lizard remains, and the owls could well have overlooked or disdained the little geckos because of their small size.

Of the seven species of fossil lizards found in the Barbudan caves *Ameiva griswoldi* and *Thecadactylus rapicaudus* are indistinguishable from those on the island today. Bones of a large species of *Anolis* appear to represent a very large ancestral population of *Anolis bimac-*

ulatus leachii. Fossils of two smaller species of *Anolis* cannot be assigned definitely to any modern species; however, it is possible to eliminate as their allies or descendents all the anoles of the extreme southern Lesser Antilles, the American mainland, Jamaica, Cuba, the Bahamas, and the Cayman Islands. The caves contain remains of one extinct species of lizard, *Leiocephalus cuneus.* All but one species of the West Indian section of *Leiocephalus* now occur on Cuba, Hispaniola, the Cayman Islands, and the Bahamas. A disjunct form occurs (or did in post-Columbian times) on Martinique. The extinct Barbudan species therefore occupied a geographically intermediate position between the Martinique species and those of the western and central Caribbean. A fragmentary braincase and vertebra apparently represent a large iguanine, which most closely resembles the Galapagoan genus *Conolophus.*

Except for the large unidentified iguanine, the species found as fossils on Barbuda still occur in the eastern Caribbean or are allied to species that occur there today. The island lizard fauna most closely resembling that of Barbuda today is the Antigua fauna. The two islands occupy the same submarine bank, the waters separating them are rather shallow, and Underwood (1962: 139) believes they were probably joined within the last 10,000 years. Of the modern native[4] lizard faunas of the two islands, four species are endemic. *Thecadactylus rapicaudus* occurs on other West Indies islands, as does *Iguana delicatissima,* which still survives on Antigua but is unknown on Barbuda. It seems reasonable to expect that *Leiocephalus cuneus* and the two smaller species of *Anolis* might once have occurred on Antigua also.

A number of Late Pleistocene herpetofaunas have been discovered in caves on other West Indian islands. These have not yet been studied but I have examined cursorily the fossil lizards of New Providence, Jamaica, Hispaniola, and Anguilla. The Jamaican caves contain another extinct species of *Leiocephalus* (the genus does not occur on the island today), giant extinct species of *Aristelliger, Celestus,* and *Anolis,* and most of the species still living on the island today. At least one giant extinct species of *Leiocephalus* is also present in the Hispaniolan cave faunas. Thus, the Late Pleistocene gigantism and extinction found on Barbuda were not restricted to that island. This pattern, which may be of general occurrence in the West Indies, is strikingly different from that found in the fossil lizards of the North American continent. The many Pleistocene lizard faunas known from

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[4] An African gecko, *Hemidactylus mabouya,* has been introduced on Antigua but not on Barbuda.

Florida, Texas, Kansas, and California (Auffenberg, 1955, 1956; Brattstrom, 1953, 1954, 1955, 1958; Etheridge, 1958, 1960, 1961; Holman, 1958, 1959, 1962, 1963) are all essentially modern in composition. Not one of them contains extinct species of lizards and only among the Florida fossils of one living Anole (Auffenberg, 1956: 163) do elements exceed those of its modern descendants in size. As we learn more of the Pleistocene herpetofaunas of other West Indian islands perhaps the reasons for these differences will become clear.

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