

## MORPHOLOGICAL VARIATION AND SYSTEMATICS OF THE GREEN ANOLE, *ANOLIS CAROLINENSIS* (REPTILIA: IGUANIDAE)

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### Abstract

This paper reports on the morphological variation of the green anole, *Anolis carolinensis*. Scutellation features, head shapes, 4th hind toe widths and lamellar counts, and color patterns were observed and recorded which result in the description of a subspecies from Florida. In addition, the problematical systematic history of this species is reviewed and a neotype is designated in lieu of the absence of a holotype. Finally, the study of numerous preserved specimens provide additional county records for several of the Gulf Coastal states.

### Introduction

The green anole or chameleon of southeastern and south-central United States is a well known reptile to most herpetologists and pet fanciers. This is due to its abundant occurrence within its wide range as well as its captive adaptability. It has been studied both in field and laboratory for over 200 years, resulting in publication of a voluminous amount of literature (Vance, in press). Few reptiles of the United States have been as intensely studied as *Anolis carolinensis*.

The currently understood descriptive information of *A. carolinensis* may be summarized in the following sentences. In adults the head is long, wedge shaped, flattened ventrally and dorsally and is covered by small heavily keeled scales. In juveniles the head is not as long nor is it as wedge shaped nor dorsally flattened. Females tend to show an intermediate variation between adult males and juveniles. The head has marked indications of a frontal and canthal ridge and has somewhat enlarged supraocular scales. The interparietal scale (occipital scale of early authors) is nearly the size of the ovular ear opening. Scales on the tip of the snout follow the basic pattern of the species complex as defined by Ruibal and Williams (1961) among others. The mental scale is divided. The dorsals are granular with blunt keels which may be seen only with aid of a lens.

Ventrals are also granular and are usually slightly more keeled and larger than dorsals, but an exception has been noted by Duellman and

Schwartz (1958) (see Taxonomic Variability). Except for the first toe of the forefoot, digits are expanded while the underside contains transverse rows of lamellae that have microscopic hooklets used for climbing. Femoral pores are absent. Males have two enlarged postanal scales and a highly functional dewlap, whereas females and juveniles do not exhibit as functional a dewlap; however, one may be coaxed into expanding it by picking up the animal by the base of the tail and holding it head downward. When the dewlap is expanded, scales are separated by colored skin. Some scales on the calf of the hind leg tend to be enlarged and keeled. Tail scales sometimes have inconspicuous rings of larger scales, but these rings represent external evidence of breakage planes. The tail is round in cross section and the scales are keeled, but may vary in size. When the anole is not excited, a nuchal crest is absent. A caudal crest is never present.

### Material and Methods

In order to gain an understanding of *A. carolinensis* a total of 21 morphological characters were recorded of which 12 were found to be of diagnostic use which are based on 897 specimens studied (Figs. 1 & 3). The number of canthal scales counted include those which come into contact with the loreals; the number of scales counted on the frontal ridge include the supraorbital semicircles and extend to the postrostral; the number of scales counted between the canthal and frontal ridge extend posteriorly on the nasal scale to the anterior aspect of the orbit; the number of scales counted between the frontal ridges extend from the junction of the anterior frontal ridge scales to the midpart between the supraorbital semicircles; the number of scales counted around the nostril are the granules surrounding it; the number of loreal scales counted include all of the loreals and the number of rows counted are those of the highest number between the canthal ridge and upper labials; the supraocular scales are those immediately superior to the orbits; the temporal scales between the eye and ear opening are usually represented by an area of dark coloration; the number of the postanal scales are a typical male characteristic and are located posteriorly of the vent; the interparietal and ear openings are measured according to their longest length and compared; the number of digital lamellae of the 4th toe of the hind foot are those which begin at the junction of the foot and toe and extend to the toenail; the amount of digital expansion of the 4th toe of the hind foot is the amount in relation to the length of that toe; the axillary spot is a dark blotch usually surrounded by one row of light scales above the foreleg and is commonly seen on many preserved specimens; the snout shape is based on the angle of the anterior portion as compared with the posterior of the head; the head length is measured in millimeters from the tip of the snout to the posterior suture of the interparietal; the head width is measured across the center of the eyes; and the body length is the distance from the tip of the snout to the vent.

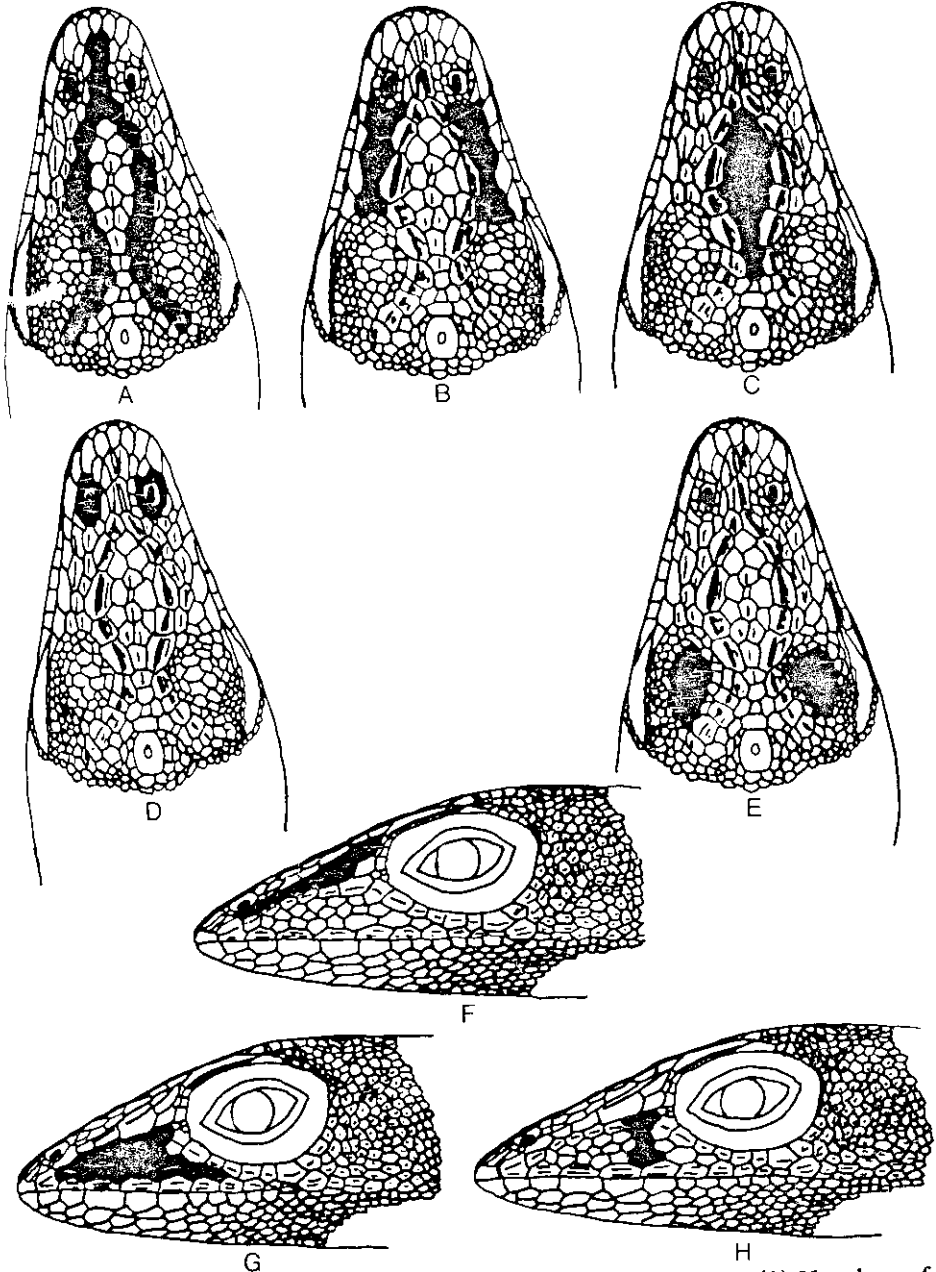


Fig. 1. Illustrations of diagnostic characters of *A. carolinensis*. (A) Number of scales on frontal ridges, (B) number of scales between frontal and canthal ridges, (C) number of scales between frontal ridges, (D) number of granules surrounding nostril, (E) posterior grading of supraoculars, (F) number of canthal scales, (G) number of loreal scales, and (H) the number of loreal scale rows. (Redrawn from Cope, 1900).

MUSEUM ACRONYMS

AMNH	American Museum of Natural History
CR	Charleston Museum
DMNH	Dallas Museum of Natural History
FMNH	Field Museum of Natural History
FSM	Florida State Museum
LACMNH	Los Angeles County Museum of Natural History
MPM	Milwaukee Public Museum
NC	Navarro College
TMM	Texas Memorial Museum
UAM	University of Arkansas Museum
UCMZ	University of California Museum of Zoology

*Anolis carolinensis* Voigt

*Lacerta Plica*, Castiglioni, 1770 [Inference by Dundee and Ewan, 1979; misidentified as *Plica plica* Linnaeus].

*Iguana strumosa?*, Brongniart, 1805, p. 33 [*nomen dubium*].

*Anolis bullaris*, Harlan, 1827, p. 16 [Part].

*Anolius carolinensis*, Voigt, 1832, p. 71. [Type specimen undesignated and presumed to be lost (see Nomenclatural History) or non existent (Brown, 1950). CR862 is designated as a neotype. Type Locality: Not present in original publication, but Stejneger and Barbour (1917, et seq.) assigned the locale as "Carolina"; however, Schmidt (1953) further restricted the type locality to "Charleston, South Carolina" (see Nomenclatural History). The current designated neotype was collected in Charleston County, South Carolina, on September 29, 1929, by an unknown collector.]

*Anolis strumosa*, Harlan, 1835, p. 143.

- Anolis Carolinensis*, Dumeril and Bibron, 1837, p. 120 [Part].
- Anolis podargicus*, Richardson, 1837, p. 200 [Part].
- Anolis bimaculatus*, Richardson, 1837, p. 200 [Part].
- Anolis Carolinensis*, Holbrook, 1842, p. 67.
- Dactyloa carolinensis*, Fitzinger, 1843, p. 68 [Part].
- Dactyloa biporcata*, Fitzinger, 1843, p. 68 [Part].
- Anolis principalis*, Gray, 1845, p. 202.
- Anolis carolinensis*, Baird, 1859, p. 12.
- Lacerta bullaris*, Troschel, 1868, p. 51 [allocated to *A. carolinensis* by Smith and Smith, 1976, p. L-B-94 (*nomen dubium*)].
- A. [nolis] principalis*, O'Shaughnessy, 1875, p. 276 [Part].
- [*Anolis*] *Lacerta principalis*, Garman, 1884, p. 19.
- Anolis carolina*, Wood, 1898, p. 81.
- A. [nolis] carolinensis*, Gadow, 1905, p. 212 [Part.]
- Uta ornata?* Grinnell and Camp, 1917, p. 157 [Part?].
- Anolis carolinensis carolinensis*, Cook, 1942, p. 8.
- Anolis carolinensis [carolinensis]*, Oliver, 1948, p. 13.
- Anolis c. [arolinensis] carolinensis*, Oliver, 1950, p. 56.
- Anolis [carolinensis]*, Goin, 1958, p. 62.
- Anolis* sp., Hamilton and Pollack, 1958, p. 25 [sensu stricto].
- A. [nolis] c. [arolinensis] carolinensis*, Buden and Schwartz, 1968, p. 295.
- Anolis caroliniensis*, Simon, 1973, p. 48 [lapsus calami].
- [*Anolis*] *carolinensis*, Williams, 1976, p. 13.
- A. [nolis] carolinensis carolinensis*, Vance, 1976, p. 113.

Content:

Polytypic, two subspecies are presented herein (see Taxonomic Remarks)

Diagnosis:

*Anolis carolinensis* is a member of Etheridge's (1960) alpha group of *Anolis* and is a member of the *carolinensis* species group as defined by Ruibal and Williams (1961).

This species differs from all other species of the *carolinensis* group by the presence of 9/9 - 16/15 scales on the frontal ridges inclusive of the supraorbitals; frontal ridges usually 3 scales wide at the widest area between the frontal ridges; 5/5 - 7/7 scales present between frontal and canthal ridges; the number of scales between the frontal ridges vary from 3-21 up to the narrowest area between the supraorbitals; 6/6 - 9/9 of scales surrounding the nostrils; 15/16 - 43/45 loreal scales; first sublabial only in contact with first infralabial; adpressed hind legs fail to reach ear opening; ear opening oval; head shape blunt to sharply pointed east of the Mississippi River and somewhat longer west of the Mississippi River (Figs. 4, 5); frontal ridges not as evident from the lateral aspect; 4th hind toe is dilated one quarter to one half the distance of the toe; 33/32 - 50/50 lamellae present from the junction of the toe and foot to the toe nail. The illustration presented in Cope's (1900) monograph is taken from an individual of an unknown locality, but the geographic variation of the specimens studied indicates that the figured animal was native to the Carolinas or northern Georgia or Alabama.

Distribution:

The general range of *A. carolinensis* has been generally interpreted as from either southeastern Virginia, or northern North Carolina, depending on the authority, southward through Florida and the Keys, westward into the southernmost portion of Texas and through eastern central Texas, and northward into southeastern Oklahoma, the southern half of Arkansas, and southern and southeastern Tennessee (Fig. 2). It has been variously described as inhabiting the Austroriparian, Texan, and eastern Tamaulipan biotic provinces (Conant, 1975; Vance, in press). A complete listing of distributional literature is provided in another report (Vance, in press).

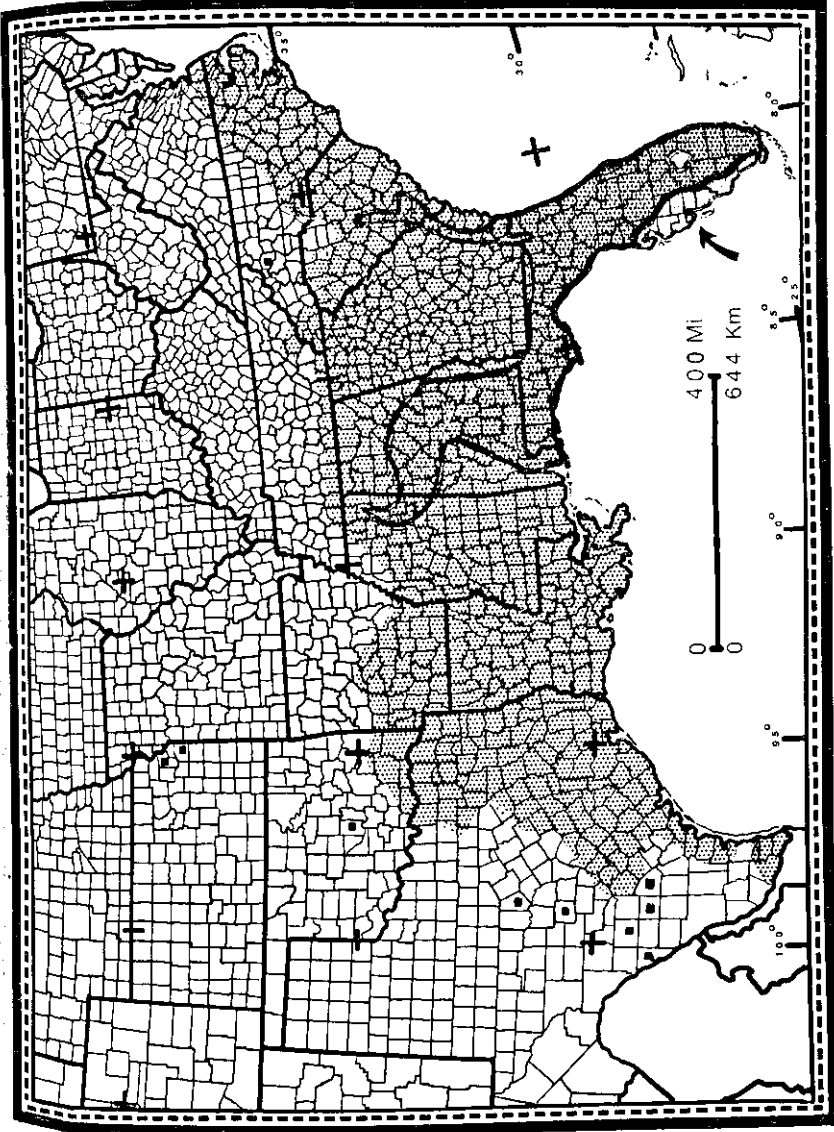


Fig. 2. Generalized and expected distribution of *Anolis carolinensis* in the United States based on literary and observed accounts. The arrow is pointing to the range of *A. c. seminolus* subsp. nov., heavy stippling represents intergradation areas of *A. c. carolinensis* X *A. c. seminolus*. Squares represent records outside of the general range. Crosses indicate areas of latitude and longitude.

### Nomenclatural History:

*Anolis carolinensis* has had a perplexing and often questionable taxonomic history which has caused several problems regarding the correct scientific name, type locality and holotype. Of all the early works on this subject, the first acceptable (to some authors) descriptive account of what could be this taxon was provided by Voigt (1832). In addition, it has been referred to as *A. bullaris*, *A. principalis* and *A. carolinensis*. Unfortunately, this is due to one author basing the usage and authority on another's usage. All in some way have been based on Linnaeus. In spite of this, other early authors attributed the source to Linnaeus, Cuvier, or even Dumeril and Bibron. Some authors have tended to misspell Voigt's name as "Voight."

This species has been well known even from colonial times. The green lizard of Lawson (1709) may have been one of the first accounts of *Anolis carolinensis*. Brickell (1737) provided another account of the species and supplied the first illustration of this animal, but it was poor in quality. Bartram (1791) briefly noticed the lizard while he traversed the southeastern United States.

The actual problem regarding the classification of this taxon began with the publication of Mark Catesby's book "*Natural History of Carolina, Florida and the Bahama Islands...*" which was prepared during the period 1731-1747. He described the size, habits, and color of a lizard of the anoline type and named it *Lacertus viridis carolinensis* or the green lizard and artistically posed it on a shrub. An accompanying engraving depicting a lizard on a shrub was typical of Catesby's illustrations and lacked sufficient detail to be identified as *A. carolinensis*. He also presented another description of an anole, along with an engraving, as *Lacertus viridis jamaicensis*. Lynn and Grant (1940) thought this was *Anolis grahmi iodurus*; however, Frick and Stearns (1961) referred it to *A. g. grahmi*. Thus, Mark Catesby's work ended the period of pre-Linnaean literature on this subject.

Problems regarding this species scientific name became more acute when Linnaeus (1754, 1758, 1766) published his series of monographs on organism classification. In 1754 he named *Lacerta principalis* and provided a very brief description of it. He said the habitat was "India"; however, in his taxonomically important 10th edition (1766), he stated the habitat of *L. principalis* as "America Meridionali." In the English translation his description is; "Tail subcarinate, crest on the throat very entire; back smooth. Inhabits South America; of an uncertain tribe. Skin very thin; tail jointed, each joint consisting of 5 rings of very thin scales; the last joint but one of the toes broader." He also provided a description of another closely related lizard, "*Lacerta Bullaris*", "Tail round, long; chin pouched. Inhabits Jamaica;



small green gular pouch globular, and retractile, which the animal when terrified is able to inflate." This latter description is important because other authors used this name for mainland *A. carolinensis*. Could this be the *A. jamaicensis* of Catesby? Sherborn (1929) thought *Lacerta principalis* was the earliest name.

The proper application of *A. principalis* or *A. bullaris* have not been determined (Barbour, 1930). These names were used by Gray (1845) and were considered separately, but he assigned *A. chlorocyanus* of Dumeril and Bibron (1837) to synonymy of *A. bullaris*. It is possible that *Lacerta bullaris* may be *Lacerta viridis jamaicensis*, but this is only conjecture. Barbour (1930) placed specimens listed by Gray (1845) in the species *A. chlorocyanus*.

Daudin (1802) is credited with naming the genus *Anolis* and designating *Anolis bullaris* Latreille as the type species. He questionably regarded *carolinensis* as "L'*Anolis* roquet" from Catesby's work, and he questionably considered *L. principalis* Linnaeus as "L'*Anolis* bimacule" which was based on the Jamaican studies of Sloan (1725) (see Ahredfeldt, 1954). Conceivably, *L. bullaris* Linnaeus belongs to a Jamaican form of *Anolis* (Barbour, 1930). Merrem (1820) thought Catesby's green lizard was *A. bullaris* and *L. principalis* Linnaeus as a then currently recognized species, but his references were confused. Thunberg (1823) provided a highly questionable citation of *Lacerta principalis* which was simply in a list of species (Vanzolini, 1977). Wagner (1830) considered Catesby's *L. v. carolinensis* to be *L. principalis* of Linnaeus. He also lumped these two names under the genus *Dactyloa*. Once again, their true designation is not known. The *Anolis Bullaris* mentioned by Kirby (1832) is not thought to be *A. carolinensis* because of the "reddish" color description. Brief summaries of Daudin (1802), Merrem (1820), and Wagler (1830) are presented by several authorities; however, Harper (1940) and Vanzolini (1977) provided the best herpetological accounts. Frick and Stearns (1961) and Adler (1979), among others, give brief summaries of Mark Catesby's work.

Voigt (1832) is currently credited with formally naming *Anolis carolinensis* and is recognized as the authority by most recent authors. Voigt based this name on Catesby's assignment and also recognized *A. bullaris*. In neither case did he provide type material, and descriptions of both were very brief and inadequate. This was, in part, a translation of Cuvier's "Regne Animal..." (Smith and Smith, 1973) which Vanzolini (1977) briefly discussed. Sherborn (1922) considered Voigt's description the earliest usage of the name and *Lacerta principalis* as the earliest name (Sherborn, 1929).

Dumeril and Bibron (1837) were unconvincing in their argument

that *L. principalis* Linnaeus and *A. carolinensis* were the same species. A woodcut illustration of the dorsal aspects of the head of "*A. principalis*" was presented by Dumeril et al. (1870, Atlas), but its features agree with those of *A. porcatius* of Cuba and elsewhere (Vance, 1987). Rhoads (1895) did not accept Dumeril and Bibron's reasons and discarded the Linnaean name. Rhoads also stated that Cuvier did not apply a binomial to this species, leaving Voigt's (1832) name next in line for possible recognition, but Rhoads did recognize Dumeril and Bibron as authorities on *A. carolinensis*.

Stejneger (1904) considered *A. bullaris* as the type species of the genus, but admitted that the species could not be readily placed. He also stated that *A. bullaris* Linnaeus rest on Catesby's illustration and that *A. bullaris* Daudin is also based on Linnaeus.

Dumeril and Bibron (1837) divided *A. bullaris* Daudin into *A. chlorocyanus* and *A. carolinensis*. According to Brown (1908), *A. carolinensis* Dumeril and Bibron rests on Catesby's work and is acceptable only on an "act of faith," but Dumeril et al. (1870-1909) apparently based their report on Linnaeus.

The work of Richardson (1837) proved to be one of utter confusion. He seemed entirely unsure of how this species should be assigned (see annotations).

Much of the above paragraphs have been summarized by Smith et al. (1963). Frick and Stearns (1961) stated, "None of this early group of Catesby's lizards provided the bases for Linnaean names, though his two final efforts, which has pronounced markings, did."

It is in this respect that one author has based usage and authority of this taxon on another author's usage, and these had in some way been based on the work of Linnaeus. Whether or not Linnaeus based his two anoles on Catesby's (1731-1747) book is conjectural. Thus, *A. bullaris*, *A. principalis*, and *A. carolinensis* were used interchangeably as names for a single taxon from the late 1700's through the early 1900's.

Although the type species, as previously stated, has been considered *A. bullaris*, an accurate allocation has never been furnished. Stejneger and Barbour (1917, et seq.) used the combination of "*Anolis bullaris = carolinensis*" as the type species, and this was subsequently followed by Burt and Burt (1933), Cochran (1941), Smith and Taylor (1950), Schmidt (1953), and Stuart (1963). Smith et al. (1963) petitioned the International Commission of Zoological Nomenclature to designate the type species as *Anolis carolinensis* because the *bullaris = carolinensis* posed a conflict. Peters and Donoso-Barros (1970) thought *A. carolinensis* as the type species, thus

rejecting Smith et al.'s (1963) proposal, but Williams (1976) suggested *A. carolinensis* as the type species. Stimson and Underwood (1983) accepted Stejneger's (1904) designation of *Lacerta bullaris* Linnaeus (1758) as the type species of *Anolis* genus, and agreed that *L. bullaris* is a *nomen oblitum* and is based on *L. viridis jamaicensis* of Catesby. They also considered *L. v. jamaicensis* to be the same as *A. garmani* and a junior synonym of *L. bullaris* Linnaeus (1758). Stimson and Underwood (1983) did not accept *A. carolinensis* as one of the species presented in the work of Daudin (1802). Savage (1983) supported the proposal of Smith et al. (1963) to fix the type species of *Anolis*, and he counters the proposals of Sabrocky (1983) and Stimson and Underwood (1983). In a reply, Stimson and Underwood (1983) reject Savage's comment. Sabrocky (1983) rejects the proposal of Smith et al. (1963). Finally, the International Commission of Zoological Nomenclature ruled that *Anolis carolinensis* Voigt is to be designated as the type species of *Anolis* Daudin (Bull. Intl. Comm. Zool. Nomencl., 1986, p. 125). The names *Anolis principalis*, *Anolis bullaris*, *Iguana strumosa*, and *Anolis strumosa* should be considered as *nomina dubia*.

The questionable authority of *A. carolinensis* and the questionable type species for *Anolis* genus poses another problem. Stejneger and Barbour (1917, et seq.) stated their *A. carolinensis* type locality to be "Carolina." This may have been due, in part, to Catesby's original work which centered, to some degree, in the Carolinas. Voigt (1832) clearly did not provide a locale; however, this was repeated in all of the checklists that Stejneger and Barbour prepared. Smith (1946) and Brown (1950) followed the type locality provided by Stejneger and Barbour, but Schmidt (1953) restricted, for unknown reasons, the type locality to "Charleston, South Carolina." Thus, restriction of the type locality is arbitrarily Charleston, South Carolina, but due to the apparent absence of a type specimen (Brown, 1950), and due to the lack of knowledge about the collector, the type locality is highly questionable.

#### Taxonomic Remarks:

A number of closely related species exist, and *A. carolinensis* has often been confused with these various taxa (Cope, 1894; Barbour, 1910, 1928; Oliver, 1948). These other species have since been allocated to their respective status by Ruibal and Williams (1961), Ruibal (1964), Schwartz and Thomas (1975, 1978), and others (Table I).

ORIGINAL NAME	SYNOPTIC NAME	CURRENT NAME
<u>A. principalis brunneus</u>	<u>A. carolinensis brunneus</u>	<u>A. brunneus</u>
<u>A. smaragdinus</u>	<u>A. c. smaragdinus</u>	<u>A. smaragdinus smaragdinus</u>
<u>A. fairchildi</u>	<u>A. c. fairchildi</u>	<u>A. fairchildi</u>
	<u>A. s. fairchildi</u>	
<u>A. carolinensis lernerii</u>	<u>A. c. lernerii</u>	<u>A. s. lernerii</u>
<u>A. porcatulus</u>	<u>A. c. porcatulus</u>	<u>A. porcatulus</u>
<u>A. maynardi</u>	<u>A. c. maynardi</u>	<u>A. maynardi</u>

Table 1. Anoles formerly assigned as *Anolis carolinensis*, based on Schwartz and Thomas (1975, 1978) and Etheridge (1960)

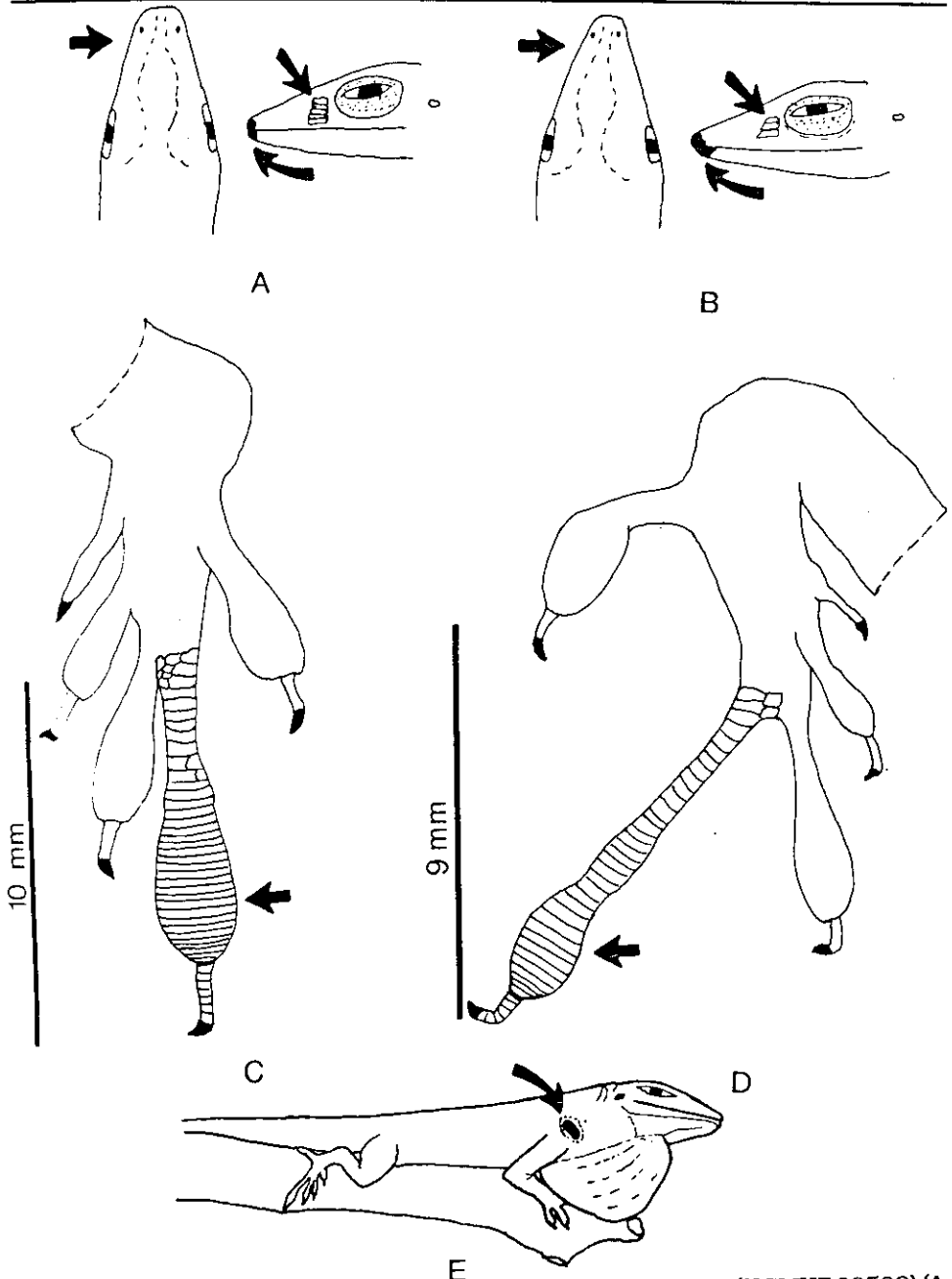


Fig. 3. Morphological variations of *A. carolinensis carolinensis* (UCMVZ 39538) (A and C) and *A. carolinensis seminolus* subsp. nov. (UCMVZ 53793) (B, D, and E) illustrating the shape of the snout, the position of the rostral and mental scales, the number of loreal scales anterior to the eye, width of the 4th toe of the hind foot, and the location of the axillary spot.

Table II. Summary of comparative morphological characteristics of *A. c. carolinensis* and *A. c. seminotus* subsp. nov. Excluded are the data of apparent intergrades of *A. c. carolinensis* X *A. c. seminotus*. \* One individual (FSM #56045) has 5/6 loreal scale rows and another (AMNH 21243) has 4/5 loreal scale rows.

	<i>Anolis carolinensis carolinensis</i>										<i>A. c. seminotus</i> subsp. nov.
	Georgia	So. Carolina	No. Carolina	Alabama	Mississippi	Tennessee	Louisiana	Arkansas	Texas	Florida	
Number of scales on frontal ridge	10/11-15/15	10/10-15/15	10/10-13/14	11/11-14/14	10/13-14/15	12/12	9/9-14/15	11/11-16/15	9/10-15/15	10/10-14/14	
Number of scales on canthal ridge	5/5-6/6	5/5-6/6	5/5-6/6	5/5-7/7	5/5-6/6	5/6	5/5-7/6	5/5-7/7	5/5-7/6	5/5-6/6	
Number of scales betw. frontal and canthal ridge	12/13-25/22	12/12-22/26	14/16-20/21	14/16-20/21	14/14-23/22	20/19	13/16-27/26	16/17-27/26	15/15-27/27	11/11-18/18	
Number of scales betw. frontal ridges	3-17	7-20	8-17	8-21	7-15	15	7-18	8-21	8/6	9-8	
Number of scales surrounding nostril	7/7-9/9	6/6-9/9	6/6-9/9	6/8-9/9	6/8-9/9	8/8	6/7-9/9	6/7-11/11	6/7-9/9	6/6-9/9	
Number of loreal scale rows	4/4-5/6	4/4-7/8	4/4-6/6	4/4-6/8	4/4-7/7	6/6	4/4-6/6	4/4-6/6	4/4-6/6	3/3-4/4*	

Table II. (cont'd) Summary of comparative morphological characteristics of *A. c. carolinensis* and *A. c. seminotus* subsp. nov. Excluded are the data of apparent intergrades of *A. c. carolinensis* X *A. c. seminotus*. \* One individual (FSM #56045) has 5/6 loreal scale rows and another (AMNH 21243) has 4/5 loreal scale rows.

	<i>Anolis carolinensis carolinensis</i>										<i>A. c. seminotus</i> subsp. nov.
	Georgia	So. Carolina	No. Carolina	Alabama	Mississippi	Tennessee	Louisiana	Arkansas	Texas	Florida	
Number of loreal scales	22/22-36/33	19/19-43-45	22/22-35-34	20/19-34/30	22/21-39/40	35/32	20/23-37/38	18/18-39/47	22/21-36/36	15/16-27/26	
Number of 4th hind toe lamellae	37/38-43/45	35/35-47-48	37/38-47-45	37/38-48-44	36/36-47-45	44/40	37/40-50/50	36/35-44/47	37/37-47/47	33/32-35/37	
Head shape	Blunt	Blunt	Blunt	Blunt	Blunt	Blunt	Blunt	Blunt	Blunt	Sharply pointed	
Shape of 4th hind toe pad	1/3-1/2 dilated	1/3-1/2 dilated	1/3-1/2 dilated	1/3-1/2 dilated	1/3-1/2 dilated	1/2 dilated	1/2 dilated	1/2 dilated	1/2 dilated	1/4 dilated	
Axillary spot	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present	
Mental reaches posteriorly of rostral suture	No	No	No	No	No	No	No	No	No	Yes	

*A. porcatus* Gray has been continually included as a subspecies of *A. carolinensis*, but recent investigators have elevated *A. porcatus* to full species with at least two possible subspecies (Ruibal and Williams, 1961; Ruibal, 1964) which remain undescribed.

#### Taxonomic variability:

Variations are not surprising in a reptilian species with the range of *A. carolinensis* (Fig. 3, Table II). Loennberg (1894) casually mentioned the existence of a variation concerning the size and shape of the head, but he referred to these types as "short-snouted" and "long-snouted" with variants between the two. Oliver (1955) noticed that east Florida individuals attained a total length of 6 3/4 inches, whereas individuals 60 miles inland reached only 6 inches. Fitch (1976) presented a report on sexual dimorphism, showing that males may be nearly 79% larger than females; this may have been partly responsible for the Loennberg observation.

Smith (1946) is quoted as saying, "It is also not improbable that the species is composed of at least two geographical races." Duellman and Schwartz (1958) performed the first detailed study of Florida variations, noting that examples from southern Florida had an overall smaller body size and less massive head which agrees with Loennberg (1894). They also made note of other aspects from four different areas of Florida:

1. Lower Keys. - Throat fan pink to red; no stripes on throat, but sometimes indistinctly spotted; head scales strongly keeled; head width less than 17 percent of snout-vent length; ventrals slightly larger than dorsals.
2. Upper Keys. - Throat fan red; numerous longitudinal brown stripes on throat; ventrals and dorsals essentially similar in size; head 17 percent of snout-vent length (average ratio 15.8%).
3. Eastern Mainland. - Throat fan red; throat without stripes, but sometimes with series of dashes or spots in longitudinal rows; ventrals half again the size of dorsals; head scales moderately to heavily keeled; average head width/snout-vent length ratio 16.2 percent.
4. Western Collier County. - Throat fan greenish gray or greenish white; no stripes on throat; ventrals slightly larger than dorsals; head scales moderately keeled; head width/snout-vent length ratio 16 to 18 percent (16.8%).



In addition to the above characteristics, Duellman and Schwartz called attention to a specimen from Collier County, Florida, which differed from all others by having lateral and dorsolateral dark brown stripes, larger dorsal scales than ventrals, and smooth head scales. These features led Duellman and Schwartz to hypothesize the following: the mainland species has a strong tendency to break into variant groups within small areas, the specimens from the four regions of Florida may have resulted from introductions from other insular populations, or they developed as a result of the combination of the first two reasons.

Collette (1961) noted a difference concerning the more numerous right front fourth digital lamellae of females from Key West as compared to those from the Mainland (Miami). He also noticed a similar but less substantive difference in males, and a smaller average body length of mainland examples when compared to Key West individuals.

Williams (1969) suggested that the mainland may harbor more than one taxon of *A. carolinensis* as indicated by the variability of snout sizes noted earlier by Loennberg (1894) and Duellman and Schwartz (1958).

Conant (1975) made the same basic observations as Duellman and Schwartz (1958) concerning dewlap coloration and he offers some additional observations. "Males from southern Florida are variable. They may be longitudinally streaked with slate gray on the nape and anterior part of the trunk. Throat fans vary from virtually white through pinks and magentas to blues and purples. Whether these anomalies represent variation with the species or whether a sibling complex of two or more species is involved is unknown at this time." This was also indicated by Smith and Brodie (1982).

Christman (1980) provided a detailed color description of these south Floridian representatives. He listed colors of the dewlap as: pale gray, darker gray, dark magenta, reddish magenta, pink, red, dark red and bright red. The dewlap colors of dark and reddish magenta were considered as intermediate colors between the gray and red-throated forms. His laboratory experiments revealed attempted mating and territorial displays when sexes of both types were placed together, thus suggesting that the lizards themselves do not recognize the different colored dewlaps. Wilson and Echternacht (1987, 1990) present physiological evidence that this species may be polytypic. They indicate the gray-throated forms are of an average smaller mass than the red-throated variety, and the gray-throated morph may be restricted to Florida because of its inability to adapt to cooler temperatures.

The information presented in the preceding paragraph strongly suggest that *A. carolinensis* is confined, with the exception of the Florida Keys and transports, to the mainland. Strong supportive evidence suggest that this species has undergone differentiation in part of its south Florida range which is an indication that subspeciation has taken place. Figure 4 serves to illustrate the morphological variations of *A. carolinensis*.

In light of the reported and new geographical and morphological variations of *A. carolinensis*, it seems practical to indicate the northern and western populations as:

#### Northern Green Anole (Figs. 1-16, Table II)

##### *Anolis carolinensis carolinensis* Voigt

Definition: A subspecies of *A. carolinensis* characterized by the combination of: long, broad and blunt shaped muzzle, mental scale fails to extend posteriorly of the rostral scale, 4-8 loreal scale rows on the right or left sides, 18-47 loreal scales on the right or left sides, absence of an axillary spot in preserved specimens, 4th toe lamellae of the hind leg number 35-50 from the junction of the toe with the foot and extending to the toenail, digital dilation of 4th hind toe extends  $1/3$ - $1/2$  of toe length, absence of axillary spot.

Dewlap of males and females characteristically red, scarlet, or pink. Heads of individuals east of the Mississippi River are shorter when compared with individuals of the same snout-vent length from west of the Mississippi River, but the author does not consider this significant enough to designate an eastern and western subspecies. They should be considered simply as a short and long headed morphs. The illustration of Cope (1900) is of a short headed morph from an unknown locale.

Description of Neotype: The neotype is an adult male, (Fig. 4), CR 862, collected on September 29, 1929, in Charleston County, South Carolina by collector or collectors unknown. This neotype is designated due to the apparent nonexistence of a holotype.

The snout is somewhat blunt; interparietal is twice as long as ear opening, number of scales on frontal ridge including supraorbital semicircles is 13/13; number of scales on canthal ridge which are in contact with the loreals is 5/6; number of scales between the frontal and canthal ridges are 12/13 which are 1-4 and 1-4 scales wide, respectively; 14 scales between frontal ridges up to the narrowest area between the supraorbital semicircles which is 1-3 scales wide; supraoculars grade down in size posteriorly; temporals are of various sizes; mental barely exceeds the posterior margin of the rostral; 3/3 scales between rostral and nasal scales; 5/6 loreal scale

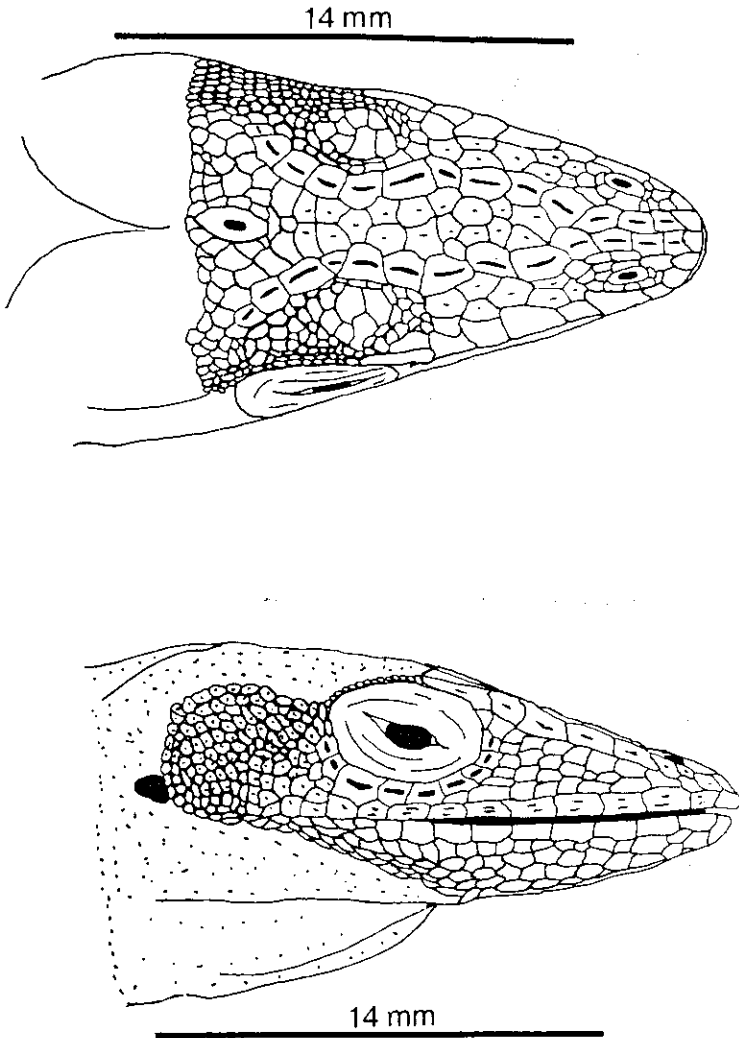


Fig. 4. Line drawings of the dorsal and lateral head aspects of *A. c. carolinensis* (CR 862) from Charleston Co., South Carolina, which illustrates a short headed morph and neotype.

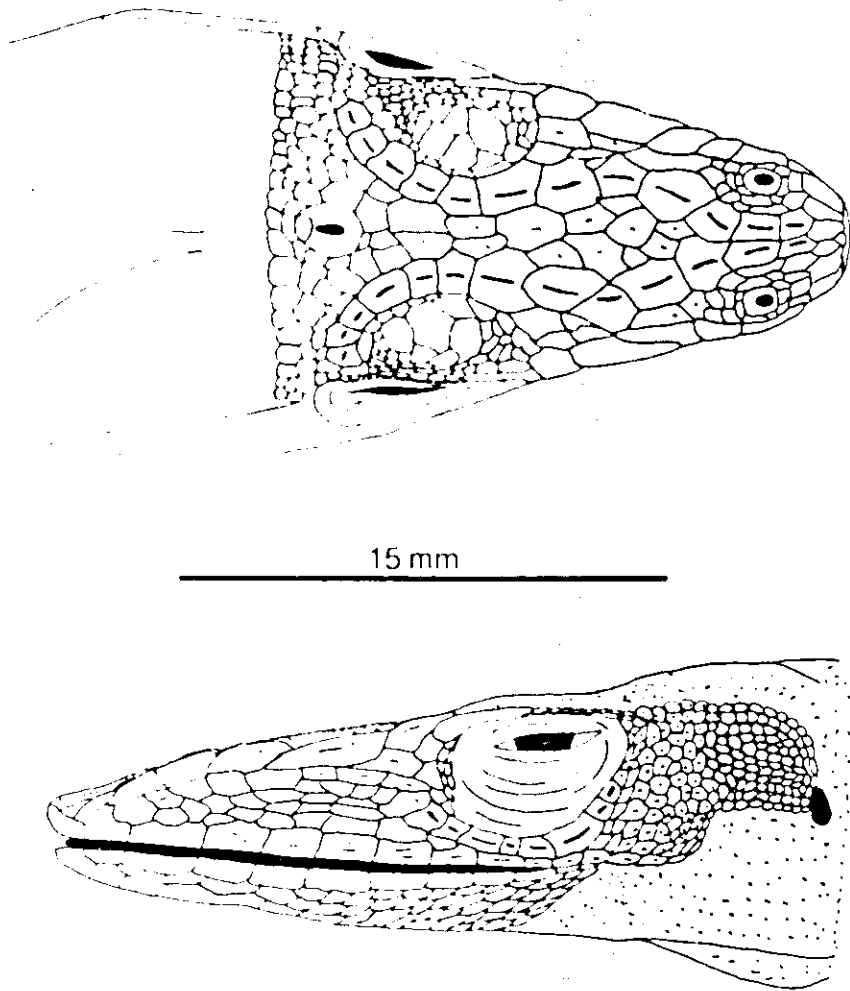


Fig. 5. Line drawings of the dorsal and lateral head aspects of *A. c. carolinensis* (NC 1982.4.12.1L) from Corsicana, Navarro Co., Texas which illustrates a long headed morph.

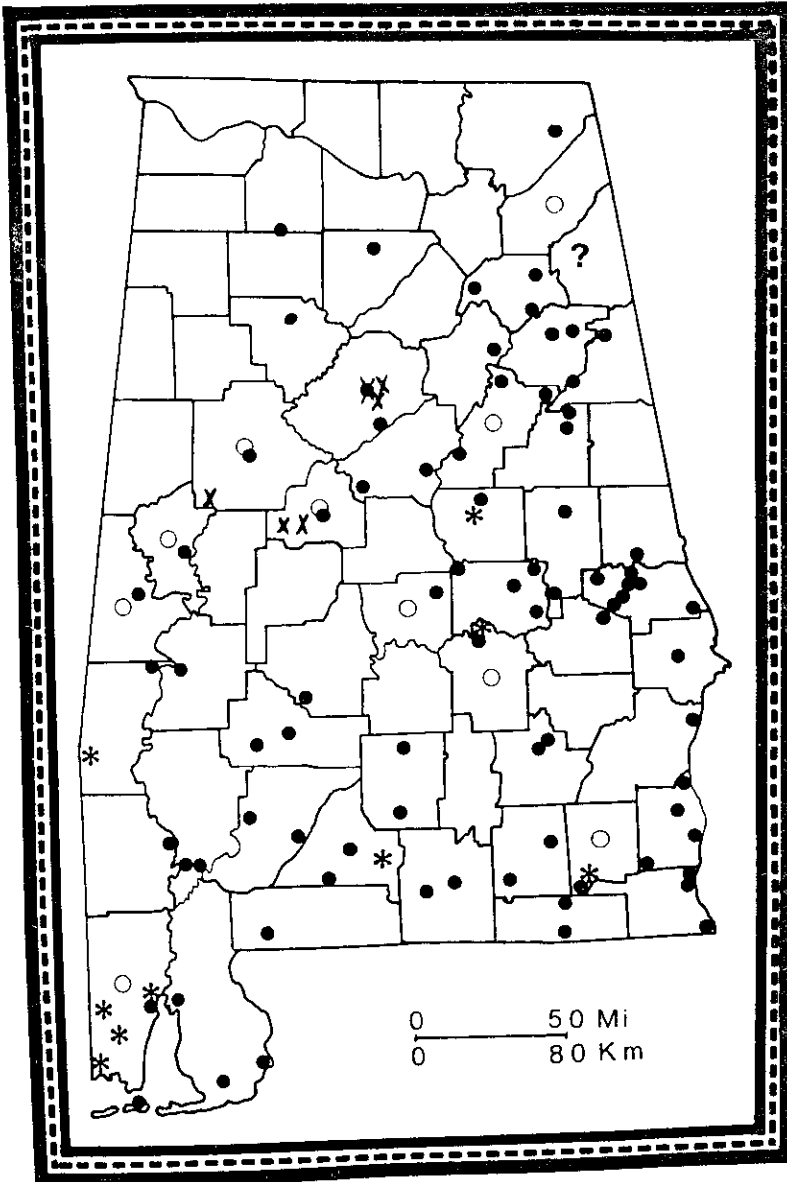


Fig. 6. Locality recording of *A. carolinensis* in Alabama. Hollow circles represent county records while solid circles represent specific localities and the question mark represents a questionable locality. Specimens examined by the author are listed as X's for intergrades and asterisks for *A. c. carolinensis*.



Fig. 7. Locality recordings of *A. carolinensis* in Arkansas. Hollow circles represent county records while solid circles represent specific localities. Specimens of *A. c. carolinensis* examined by the author are represented by asterisks.

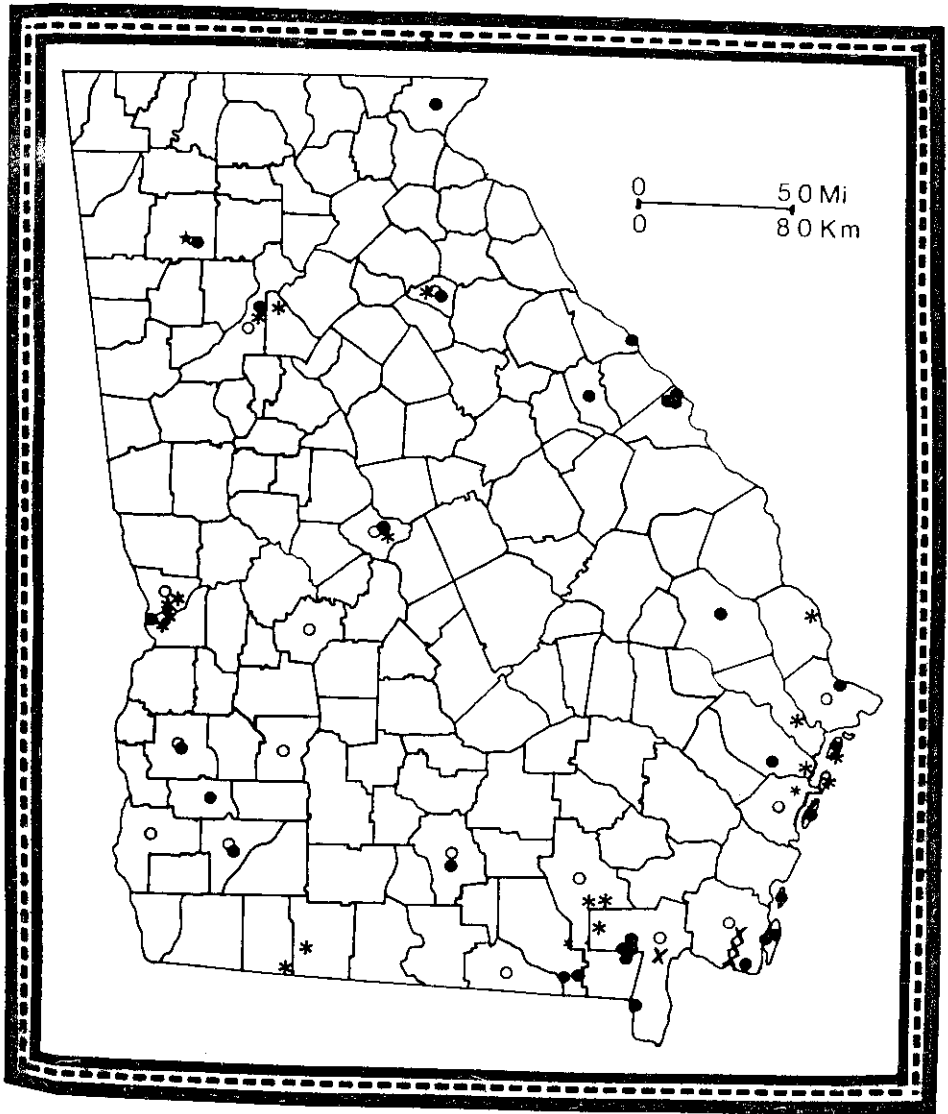


Fig. 8. Locality recordings of *A. carolinensis* in Georgia. Hollow circles represent county records while solid circles represent specific localities and the star represents a fossil record. Specimens examined by the author are listed as X's for intergrades and asterisks for *A. c. carolinensis*.

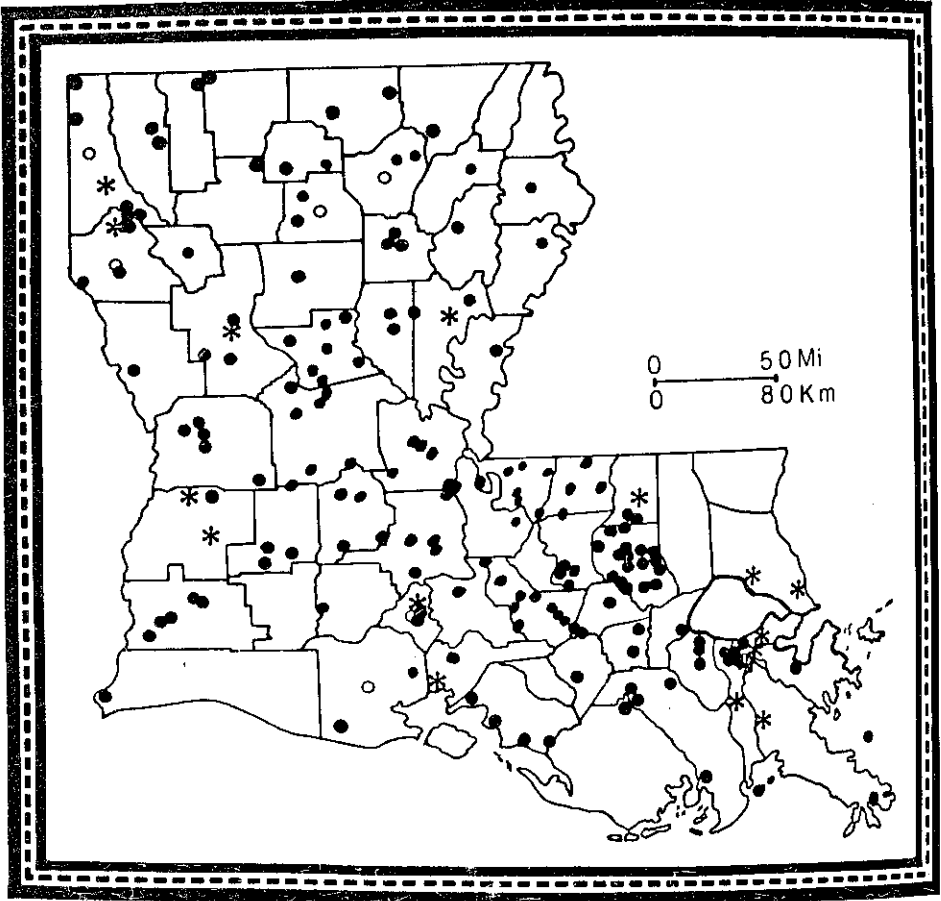


Fig. 9. Locality recordings of *A. carolinensis* in Louisiana. Hollow circles represent county records while solid circles represent specific localities. Specimens of *A. c. carolinensis* examined by the author are represented by asterisks.



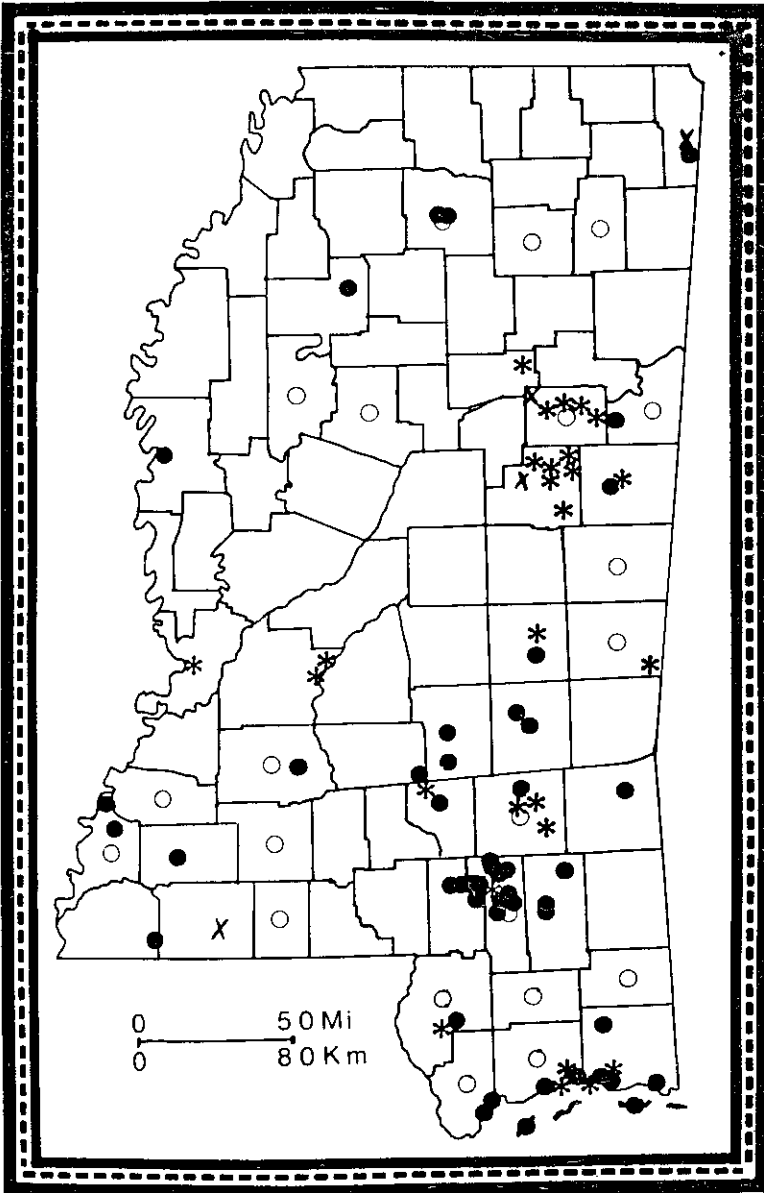


Fig. 10. Locality recordings of *A. carolinensis* in Mississippi. Hollow circles represent county records while solid circles represent specific localities. Specimens examined by the author are listed as X's for intergrades and asterisks represent *A. c. carolinensis*.

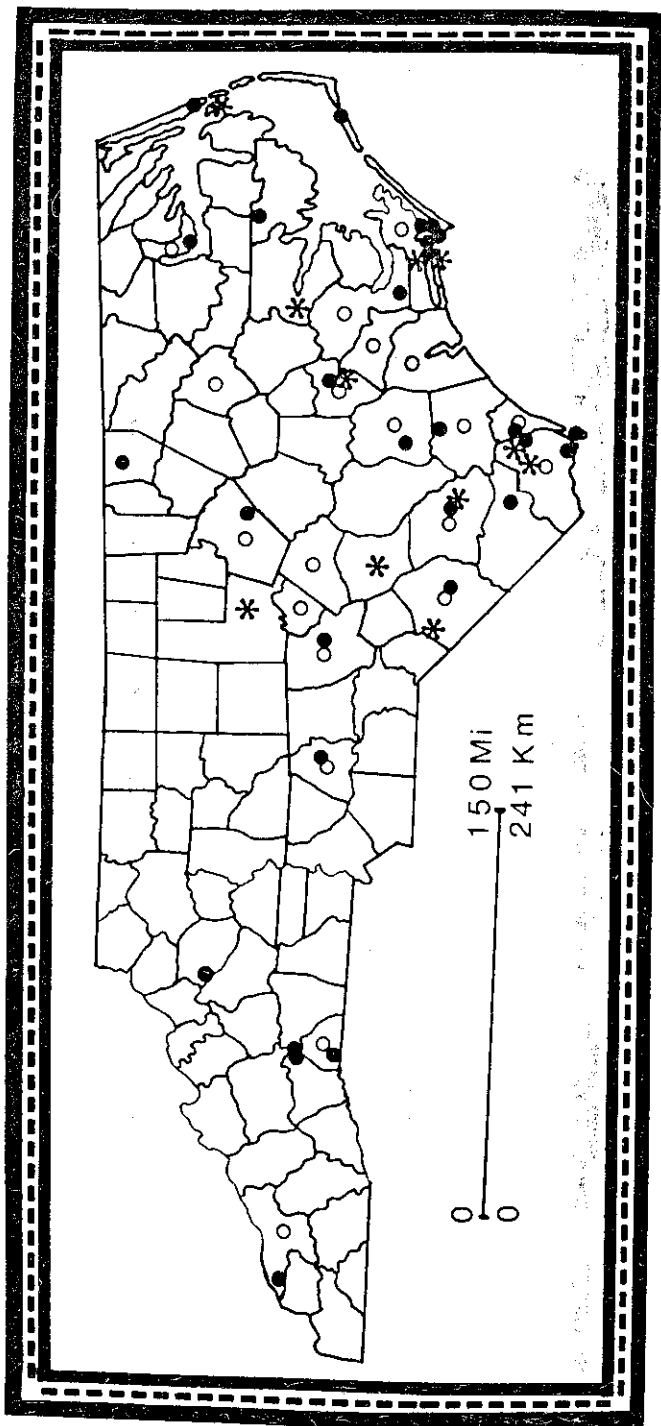


Fig. 11. Locality recordings of *A. carolinensis* in North Carolina. Hollow circles represent county records while solid circles represent specific localities. Specimens of *A. c. carolinensis* examined by the author are represented by asterisks.

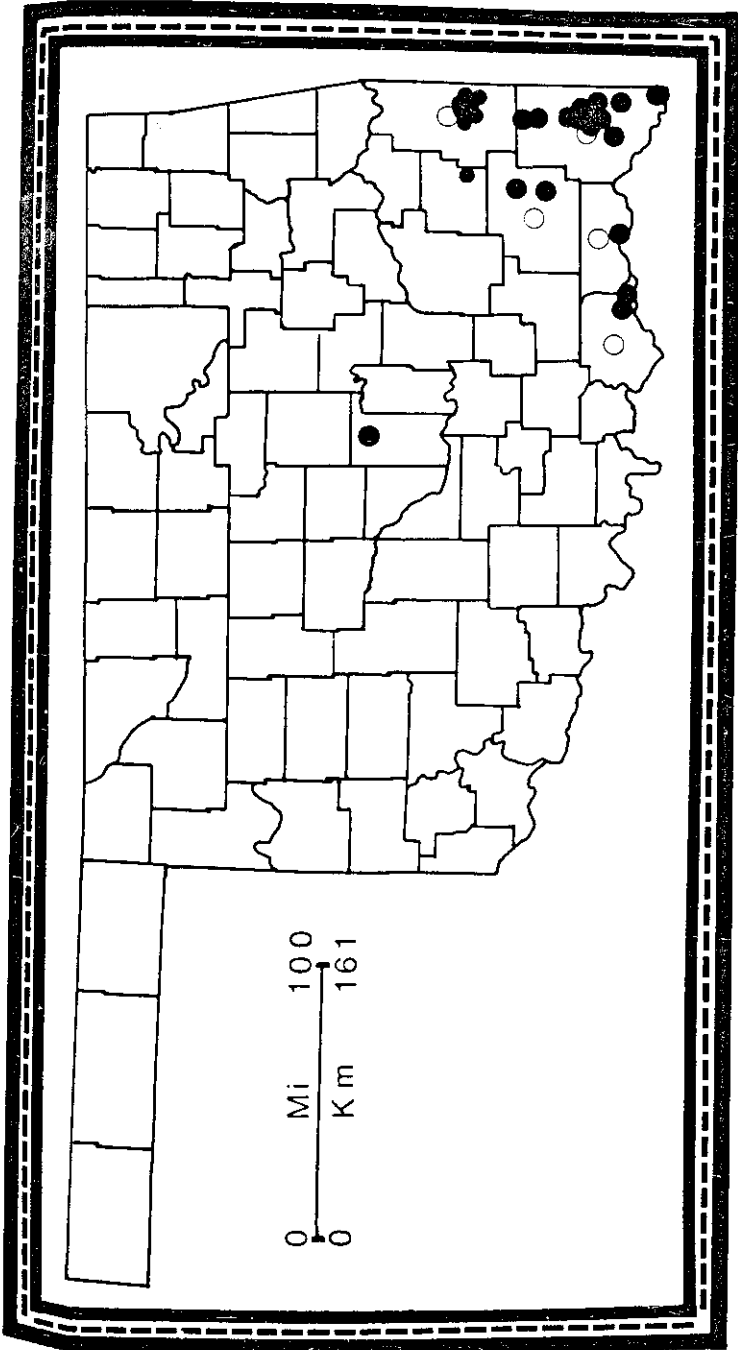


Fig. 12. Locality recordings of *A. c. carolinensis* in Oklahoma. Hollow circles represent county records while solid circles represent specific localities.

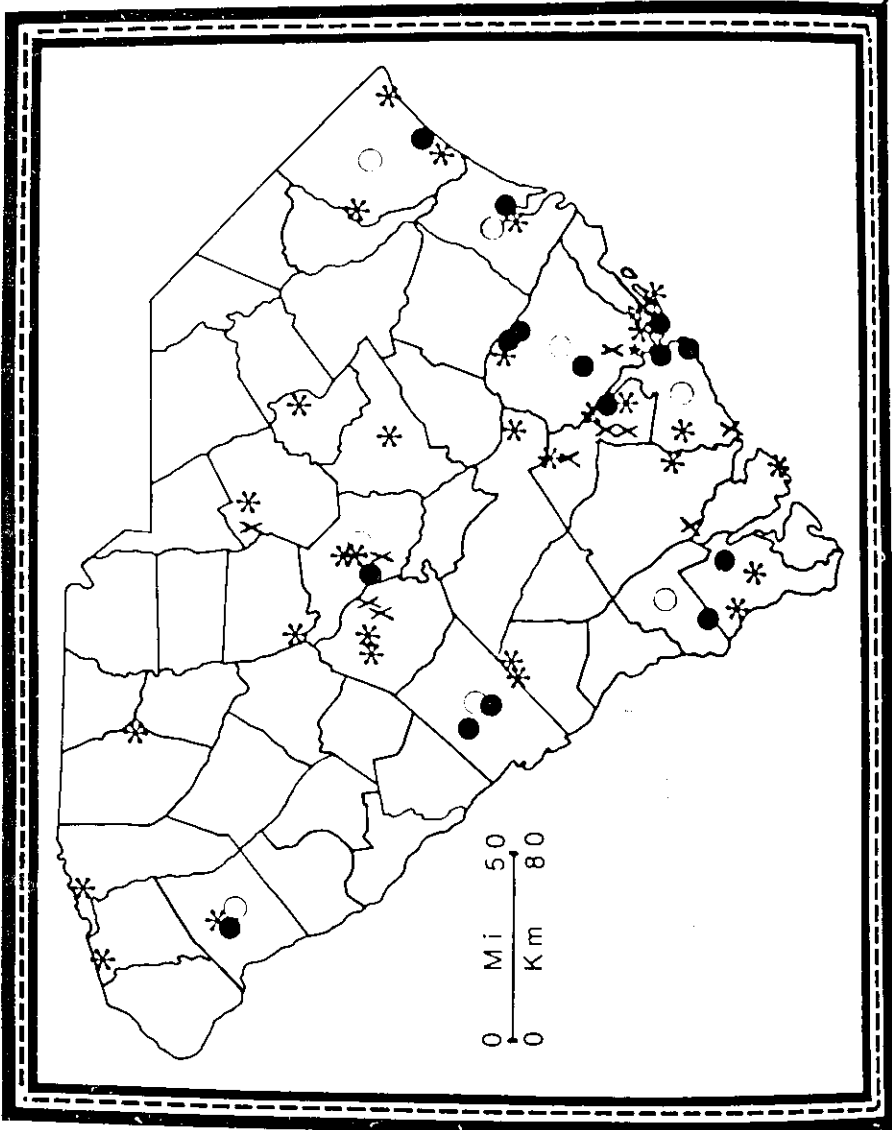


Fig. 13. Locality recordings of *A. c. carolinensis* in South Carolina. Hollow circles represent county records while solid circles represent specific localities. Specimens examined by the author are listed as Xs for intergrades, asterisks for *A. c. carolinensis*, and a star represents the locality of the neotype.

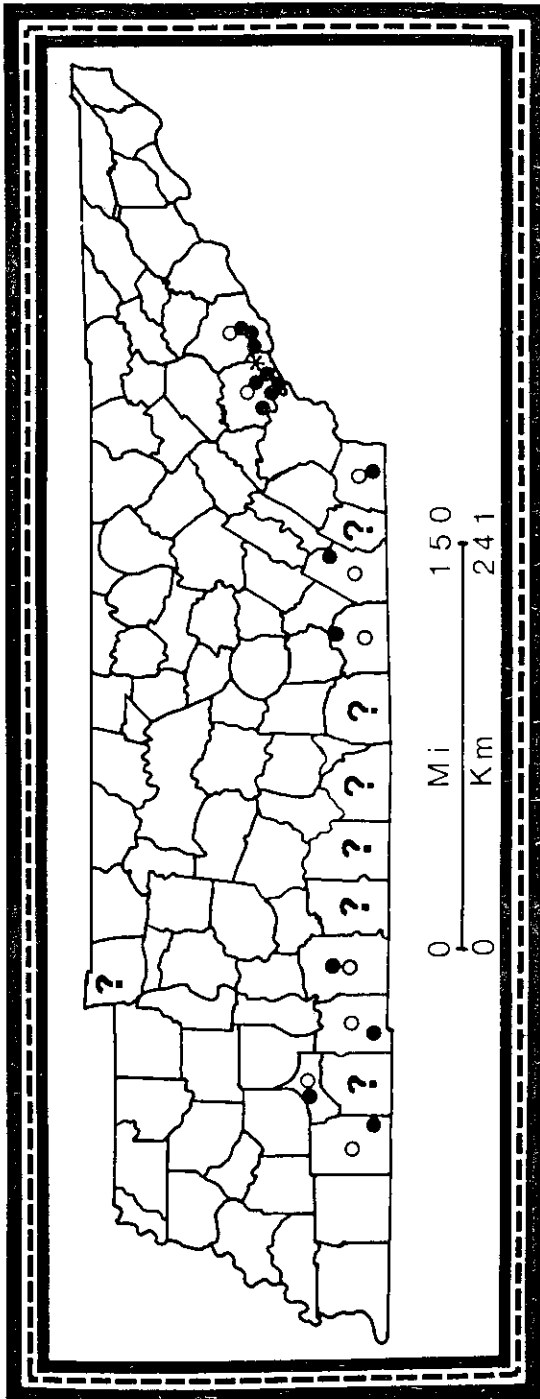


Fig. 14. Locality recordings of *A. carolinensis* in Tennessee. Hollow circles represent county records while solid circles represent specific localities, and the question marks represent unconfirmed county localities. A specimens of *A. c. carolinensis* examined by the author is represented by an asterisk.

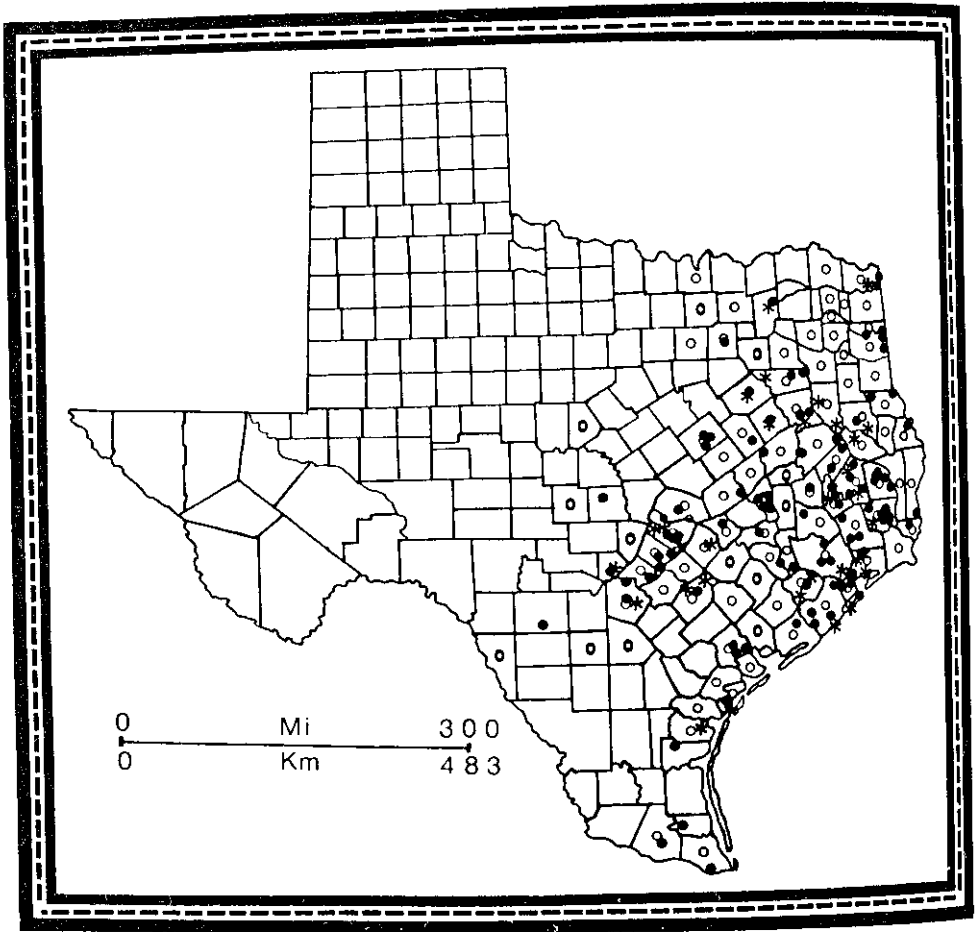


Fig. 15. Locality recordings of *A. carolinensis* in Texas. Hollow circles represent county records while solid circles represent specific localities. Specimens of *A. c. carolinensis* examined by the author are represented by asterisks.

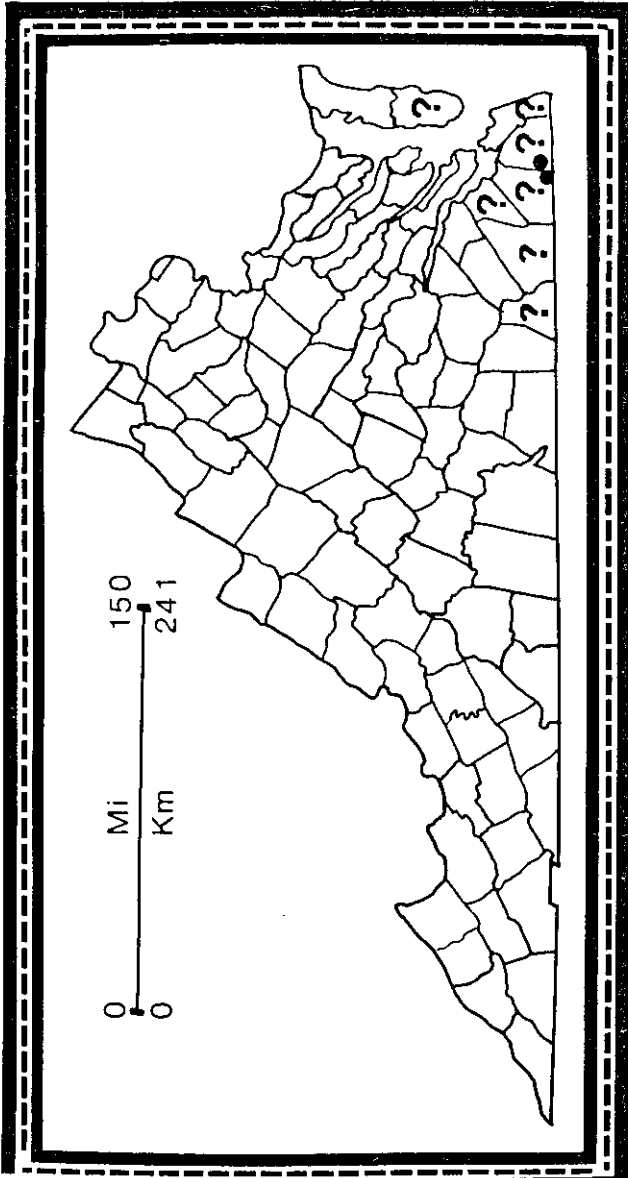


Fig. 16. Locality recordings of *A. carolinensis* in Virginia. Solid circles and question marks represent two questionable recordings.

rows; 28/27 loreal scales; head scales keeled, loreals slightly so; ear opening is oval; 10/10 upper labials; 10/9 lower labials, mental divided; dorsals with blunt keels, ventrals somewhat more strongly keeled, hind leg strongly keeled with sharp keels; presence of 2 postanal scales separated by one scale; adpressed hind leg fails to reach ear opening; digital dilation of 4th toe lamellae of hind leg is between  $1/3 - 1/2$  of the toe length; 41/40 lamellae present on the 4th toes of the hind legs.

Coloration in preservative is as follows: top of head, back and tail dark brown; back and nape of neck with slight evidence of grayish-black reticulations on anterior  $1/4$  of trunk; small dark blotches on posterior  $3/4$  of trunk; dorsal surface of limbs dark brown with evidence of grayish-black blotches; presence of dark brownish-black postocular blotch between the eye and ear opening; absence of axillary spot; ventrum dark beige with evidence of dark brown; thin, longitudinal gular stripes, but abdomen consists of slight indications of small brown dots; ventrum of rear legs somewhat darker than the venter; absence of a dorsal stripe.

Measurements of the neotype are as follows: length of head from interparietal to tip of snout is 14 mm; length of right hind leg is 36 mm; length of right foreleg is 22 mm; snout-vent length is 59 mm; and length of the tail (intact) is 119 mm.

The distribution is presented in Fig. 2 and all the state maps with the exception of Florida (Figs. 6-16) with some new county distribution records noted.

**Etymology:** *A. c. carolinensis* is apparently named after the state of South Carolina where Catesby was known to visit.

#### *Anolis carolinensis carolinensis*

**Specimens examined:** AMNH 28707-09, 65594-95, 66504, 97001, 104740-41, 46729, 1975, 65616, 88355, 92747, 74536, 57978-79, 57981, 104736, 104738, 114550, 110684-93, 114581-82, 66502-03, 118584, 126626, CR 126-128, 158, 479, 490, 826-865, 867-871, 875-898, 900-904, 906-907, 910, 913-922, 980-996, 1000, 1011, 1021-1025, 1029, 1050, 1185, 1187-1188, DMNH 34-35, 84-85, 164-165, 361, 478, 869, 1126, 1139, 1145, 1161-62, 1175-76, 1182-84, 1487, 2025-26, 2838, 2932-33, 3664-68, 3683-84, 3686-94, 4178, FMNH 2700, 5784-87, 8136-38, 18466-67, 21487-89, 27031-32, 34819-27, 37536, 40806, 40941, 41256, 41305-06, 42357, 42506, 48646, 48819, 62041-42, 69321, 74741, 94750-54, 94756, 94761, 94763-65, 162952-60, 171944-50, 192452-55, 192457-67, 192469-71,



192479-80, 192482, 192484, 192488-90, 192496, 194377-80, 194385, 194392-94, LACNHM 3797-3801, 8550, 27224-29, 35056-57, 36440, 36466-67, 15585-92, 61527, 61529-31, 66645-56, 93925-35, 106928-40, 121534, 126270, 130746-53, 121233-39, 131565, 132840-41, 135074, MPM 513,3048-50, 11816-21, 5454-55, 5459-61, 5476, 5478-79, 7006-07, 7187, 8560-62, 10030, 12270, 12932, 13136-37, 13142, 13159, 13328-31, 13142, 15042-49, 15051-57, 15839, 16087, 16147, 16139, 16140, 17162, 17600, 17635-38, 17694-95, 19606, 19622, 19624, NC 1977.10.9.8L, 1978.10.8.23L-.24L, 1979.3.11.1L, 1979.3.15.1L, 1979.4.12.1L, 1979.5.4.1L-.3L, 1980.3.28.1L, 1980.4.2.1L, 1980.6.12.1L, 1980.6.20.1L, 1980.14.12.1L, 1982.9.9.1L, 1982.9.26.1L-.3L, 1983.8.29.1L-.10L, 1984.12.30.1L, 1984.4.20.1L-.2L, 1984.4.29.1L, TMM 9180-82, 9601, 9836, 9122, 9753-59, 9881-82, 41816-18, 20460, 10101, 14232-33, 14268, 14288-89, 14292, 14365, 14367-72, 9610-19, 9602, 673, 1532, 6910-13, 9104-05, 9125, 9133, 13123, 13600-01, 14538, 14540-41, 18995-97, 19001-03, 19010-12, 21187, 21254-65, 22463-67, UAM 68-735-6, 68-735-7, 68-735-9, 68-735-85, 68-735-1620, 68-735-1621, UCMZ 14792-93, 8129-30, 11105, 43395-97, 15058-59, 150154-55, 181158, 53788-89, 53810, 8131-33, 39535-38, 43398-409, 53785-87, 150160, 80046, 39664-66, 64493, 68406-07, 78225, 78245, 98811, 98819-20, 128055-59, 150156-57, 181159-61, 187474-75.

The Florida population is a small one located in southwest Florida which seems to undergo a broad area of intergradation with *A. c. carolinensis* over most of Florida and the neighboring states (Fig. 2).

Although the dewlap of males is considered to be gray, it should not be used alone as an identification feature, yet other features are notable. Therefore, the Floridian population of *A. carolinensis* is designated as:

Southern Green Anole (Figs. 2-3, 17-18, Table II)

*Anolis carolinensis seminolus* subsp. nov.

**Definition:** A subspecies of *A. carolinensis* which is characterized by the combination of: sharply pointed or narrow muzzle; mental scale exceeds past the posterior margin of rostral; 3-4 loreal scale rows on the right or left sides; 15-27 loreal scales on the right or left sides; presence of dark and oval or oblong axillary spot which is bordered by light colored scales in preservative, 4th toe of hind leg is dilated at the extreme 1/4 length of the toe; lamellae of the 4th toe of the hind leg may vary from 32-39 from the junction of the toe with the foot and extending to the toenail. Dewlaps may be gray or perhaps pinkish. Comparative features of this taxon and *A. c. carolinensis* are presented in Table II.

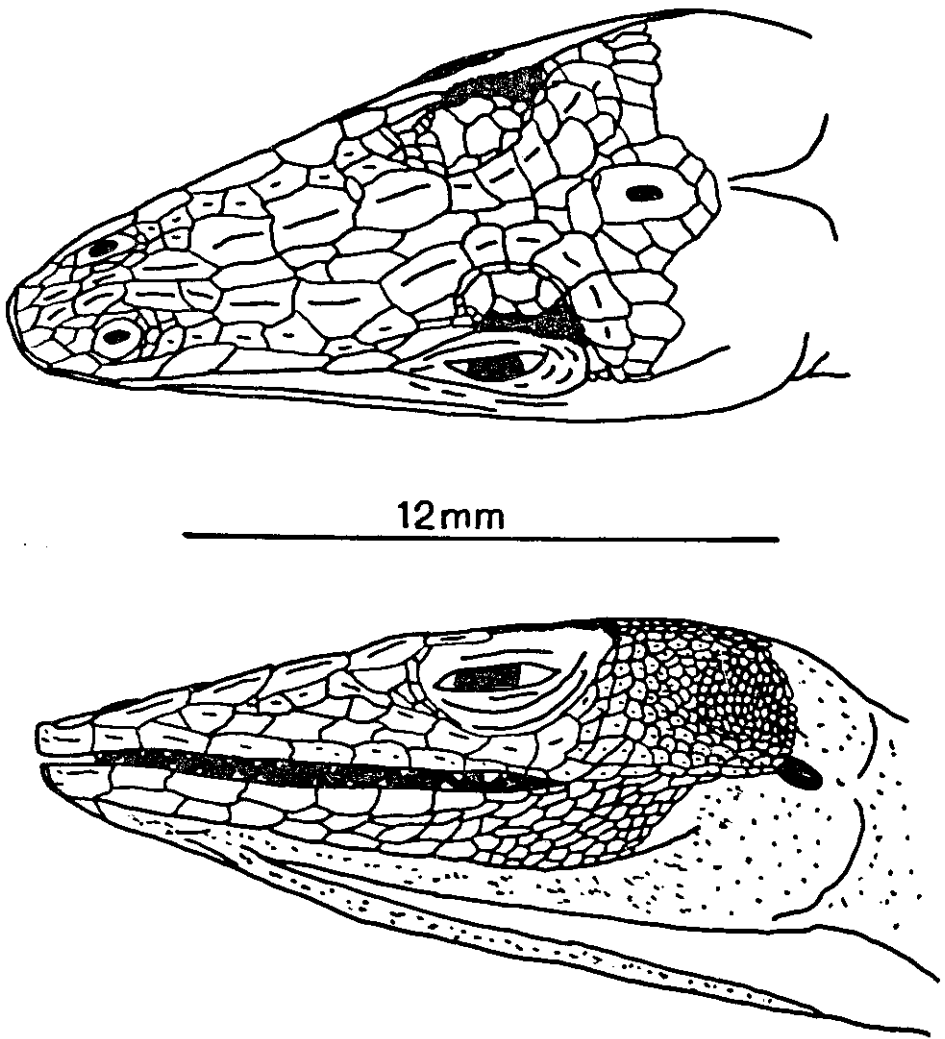


Fig. 17. Line drawings of the dorsal and lateral head aspects of *A. c. seminolus* subsp. nov. (UCMVZ 53793) from 6.8 mi. WNW Murdock, Sarasota Co., Florida, which illustrates the holotype.

**Description of holotype:** The holotype is an adult male (Fig. 17, UCMZ 53793, collected on April 9, 1950, 6.8 miles WNW of Murdock, Sarasota County, Florida, by Robert Stebbins. Paratypes are UCMZ 53792 and 53794-95 with the same collecting data as the holotype.

The snout is sharply pointed; interparietal twice as long as ear opening; number of scales on frontal ridge including supraorbital semicircles 12/12; number of scales on canthal ridge in contact with the loreals 5/4; number of scales between frontal and canthal ridges 16/16 which are 1-3 and 1-4 scales wide respectively; 7 scales between frontal ridges up to the narrowest area between the supraorbital semicircles which are 1-2 scales wide; supraoculars do not grade posteriorly; temporals are of different sizes and shapes; mental reaches beyond posterior margin of the rostral; 3/3 scales between rostral and nasal scales, 4/3 loreal scale rows, 13/15 loreal scales; head scales keeled, loreals slightly so; ear opening oval; 9/9 upper labials; 9/9 lower labials, mental divided; dorsals nearly same size as the ventrals and slightly keeled, ventrals somewhat more keeled than dorsals; laterals smaller than dorsals and ventrals; scales on top of forearm keeled with blunt keels; scales on top of hind leg somewhat keeled; presence of 2 postanal scales which are in contact; adpressed hind leg fails to reach ear opening; digital dilation of 4th toe lamellae of the hind leg is 1/4 length of toe; 37/36 lamellae present on 4th toes of hind legs.

Coloration in preservative is as follows: top of head, neck and rear half of the back and tail dark brown; back and nape of the neck show evidential color (green-black) indicating an injury; the only dorsal markings are occasional dark spots barely evident down vertebral area; dorsum of limbs slightly lighter than back with faint evidence of an axillary spot surrounded by a single layer of white scales; ventrum beige without any noticeable markings; ventrum of rear legs somewhat darker than belly; absence of dorsal strip.

Measurements of holotype are as follows: length of head from interparietal to tip of snout 12 mm; width of head through the center of the eyes 8 mm; length of right hind leg 32 mm; length of right foreleg 21 mm; snout-vent 54 mm; and length of the tail (damaged but still intact) 98 mm.

**Etymology:** *A. c. seminolus* is named after the Seminole Indians of Florida.

Subtle behavioral differences are known to occur when *A. c. carolinensis* and *A. c. seminolus* are compared. Milstead (1967) reports that *A. c. carolinensis* will display from sites on vertical surfaces with the longitudinal axis up, down, or oblique along a tree trunk, yet Christman (1980) notes that the Florida gray-throated forms (*A. c. seminolus*) will usually

perch on reeds and other vertical surfaces facing downward, and when disturbed, will run to the ground to avoid capture. The intergrade anoles (*A. c. carolinensis* X *A. c. seminolus*) will typically perch on larger sticks and tree trunks and, when disturbed, will move upward. The subspecies identifications being those of the current author. Christman (1980) observes that adult males of the gray-throated forms will respond to introduced males with red dewlaps (*A. c. carolinensis* or perhaps *A. c. carolinensis* X *A. c. seminolus*) and with a display followed by an attack in the same way they respond to their own kind. Male gray-throated forms will also display to and mount females regardless if they are gray-throated or red-throated (Christman, 1980).

*Anolis carolinensis seminolus*

Specimens examined: AMNH 107338-39, 21240-41, 21243-44, FMNH 23225-26, 94744, 94749, 192444, FSM 56045, LACMNH 3804, 15596-97, UCMZ 53791-93, 53795, 53803-05.

*Anolis carolinensis carolinensis* X *Anolis carolinensis seminolus*

(Figs. 2, 6, 8, 10, 13, 18)

Specimens examined: AMNH 104737, 85788, 114549, 117851, 88600, 127256, 93788, 6991-95, 22419, 21242, 76-78, 80-82, 36489, 22381, 2422-23, 63907, CR 480-81, 834, 872, 873-74, 899, 905, 908, 909, 911-12, FMNH 5803, 8128, 8130, 42662-65, 94733-35, 94739-40, 94742, 94746, 94755, 16815-18, 192451, 192456, 192468, 194384, 208310, FSM 3214, 56040-44, 56046-49, 8821, 17233-36, 19712, 1433, 2461, 3942, 4150, 6946, 9424, 56021-39, 34430, 34445, 9255, 9836, 55903-99, 56000-03, LACMNH 15605-07, 61500-14, 3802-03, 15593-95, 15598-04, 61528, 74311-13, 116113-115, MPM 504-512, 1947, NC 1985.5.20.1L, UCMZ 36583-86, 53799-800, 53797-98, 53801-02, 53806, 40957-58.

Summary

*Anolis carolinensis* is a wide ranging mainland anole which exhibits enough variation to be considered as a polytypic species. A total of 27 names or variation of names are applicable to this taxon.

Various systematic problems have existed regarding this lizard. The virtual non existence of a holotype along with the lack of a proper type locality

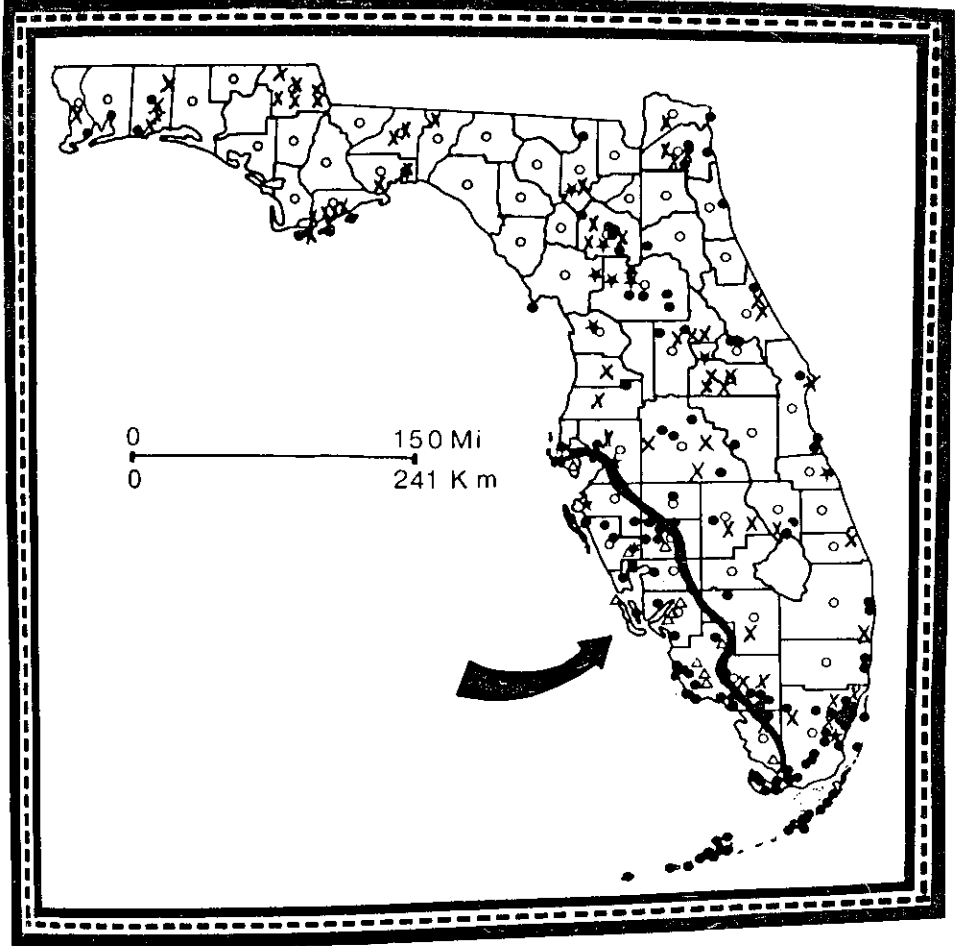


Fig. 18. Locality recordings of *A. carolinensis* in Florida. Hollow circles represent county records while solid circles represent specific localities and stars represent fossil records. Specimens examined by the author are listed as X's for intergrades, hollow triangles for *A. c. seminolus*, and an asterisk represents the type locality.

locality and questionable authorities of the scientific name have caused a great degree of systematic chaos.

This study provides information on 12 morphological characters which are used to describe the mainland populations of *A. carolinensis*. The result is the description of a subspecies from Florida (*Anolis carolinensis seminolus* subsp. nov.) which is readily discernable from the subspecies of the rest of the species range.

In addition, a neotype is designated in absence of a holotype for the species and Voigt is considered as the proper authority. Commonly used names of the 1800's and early 1900's (*A. bullaris* and *A. principalis*) are considered *nomina dubia*. The neotype locality is designated as Charleston, Charleston County, South Carolina.

#### Acknowledgments

Numerous people have provided generous help during the planning and preparation of this report. Even the job of reading and editing the manuscript merits considerable attention.

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