THE SYSTEMATICS AND PALEOECOLOGY OF TWO LATE PLEISTOCENE HERPETOFAUNAS FROM THE SOUTHEASTERN UNITED STATES

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ABSTRACT

THE SYSTEMATICS AND PALEOECOLOGY OF TWO LATE PLEISTOCENE HERPETOFAUNAS FROM THE SOUTHEASTERN UNITED STATES

By

Vincent Victor Wilson

Fossils representing late Pleistocene herpetofaunas from Reddick, Florida, and Ladds, Georgia, are identified and reviewed. The known number of reptiles and amphibians is increased from thirty-nine to forty-four at the Reddick site, and is increased from twenty-three to twenty-six at the Ladds site.

Each herpetofauna is discussed separately. Special attention is given to the paleoecological and paleoclimatic significance of the herpetofaunas. Evidence is presented that the winters at Reddick were less cold at the time of fossil deposition than they are now. Little faunal evidence was found to indicate that the late Pleistocene climate at Ladds differed substantially from that of the present.

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By

Vincent Victor Wilson

A DISSERTATION

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For Sally

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Hibbard (1970) presented an interpretation of the Pleistocene and recent environments of the central great plains. His analysis was based primarily on the wealth of data available on the successive faunas from late Cenozoic Kansas and Oklahoma.

The same type of interpretation remains to be done for the southeastern United States. Unfortunately, the Pleistocene faunas of this area have not been studied to the extent of their Great Plains counterparts. This study makes a small attempt to correct that situation.

In the southeastern United States, only northern Florida has been found to have an extensive series of Pleistocene deposits containing local faunas. The largest known Pleistocene fauna is found near Reddick, Marion County, Florida. Only one site containing a sizable Pleistocene terrestrial vertebrate fauna has been reported from another southeastern state. This is the Ladds, Bartow County, Georgia deposit. The study of the herpetofaunas of these two deposits constitutes the basis of this report.

PART I

THE PLEISTOCENE HERPETOFAUNA OF

REDDICK IB, FLORIDA

Reddick I is an abandoned limerock quarry located one mile southeast of Reddick, Marion County, Florida (SW 1/4, NW 1/4, Sec. 14, T. 13 S., R. 21 E.). The quarry is currently on a portion of property owned by Mr. Jimmy Williams.

As a result of previous quarrying operations, four major fossil bearing deposits lie exposed at Reddick I. Gut and Ray (1963) and Hamon (1964) have designated these four deposits as IA, IB, IC, and ID. The fossils occur in the mostly unconsolidated earths which are found in the solution pipes and caverns of the area.

Hamon (1964) describes Reddick IB as a sink filling. The fossils found there probably represent animals that were trapped by falling into, or by taking refuge in the solution pipe(s) of the area. Although other vertebrate fossils occur in the residual clay and sand of the IB site, they are outnumbered by the high concentration of reptile and amphibian fossils found there.

A number of workers have investigated various segments of the Reddick I herpetofauna. Auffenberg (1955, 1956, 1958, 1959, and 1963a and b) has identified the majority of the reptiles found there. Goin and Auffenberg (1955) record an amphibian from the IB site. Holman (1962a) lists several reptiles and amphibians from the IC site.

Detailed stratigraphic treatment of the area can be found in Auffenberg (1963b), Bader (1957), Brodkorb (1957), and Hamon (1964). Auffenberg (1963b) and Brodkorb (1957) have indicated that the site is of Illinoin age. Pinkham (1971), using recent stratigraphic evidence provided by Brooks (1968) as well as correlation by faunas, concludes that Reddick is of Sangamon age.

In June and July, 1968, Dr. J. Alan Holman and Clair Ossian processed matrix and collected fossils from the IB site. A volume of approximately one cubic yard of matrix was removed from one exposure of the fossil bearing stratum. This matrix was processed using a modified version of the washing and screening method of Hibbard (1949). Thousands of vertebrate fossils were recovered by this method and were eventually sorted into their appropriate class. A list of the amphibians and reptiles found in this sample follows.

Class Amphibia

Order Urodela

Family Sirenidae
Siren lacertina Linnaeus
Family Ambystomatidae
Ambystoma tigrinum (Green)

Order Anura

Family Pelobatidae
Scaphiopus holbrooki (Harlan)
Family Ranidae
Rana grylio Stejneger
Rana pipiens Schreber
Rana aerolata Baird and Girard
Family Microhylidae
Gastrophyrne carolinensis (Holbrook)
Family Bufonidae
Bufo terrestris (Bonnaterre)
Bufo woodhousei fowleri (Hinckley)
Bufo quercicus (Holbrook)
Family Hylidae
Hyla cinerea (Schneider)
Psuedacris nigrita (Le Conte)

Class Reptilia
Class Reptilia

Order Testudines

Family Emydidae
Terrapene carolina (Linnaeus)
Family Testudinidae
Gopherus polyphemus (Daudin)
Geochelone crassiscutata (Leidy)
Geochelone incisa (Hay)

Order Squamata

Family Iguanidae
Anolis carolinensis (Voigt)
Family Teidae
Cnemidophorus sexlineatus (Linnaeus)
Family Anguidae
Ophisaurus ventralis (Linnaeus)
Family Scincidae
Eumeces sp. indet.

Family Colubridae
- *Carphophis amoenus* (Say)
- *Elaphe* sp. *indet.*
- *Pituophis melanoleucus* (Daudin)
- *Coluber* or *Masticophis*
- *Drymarchon corais* (Daudin)
- *Heterodon platyrhinos* (Latreille
- *Heterodon simus* (Linnaeus)
- *Storeria dekayi* (Holbrook)
- *Thamnophis sirtalis* (Linnaeus)

Family Elapidae
- *Micrurus fulvius* (Linnaeus)

Family Viperidae
- *Sistrurus miliarius* (Linnaeus)
- *Crotalus adamanteus* Beauvois

In the annotated list that follows, if the species under consideration has not been reported from 1B previously, reference is given to the closest known Pleistocene occurrence of that species. This procedure is followed in all Orders but the Squamata. Since Auffenberg (1963b) has previously reported all of the snakes from the IB site, his record is not repeated under each species account.

ANNOTATED LIST

Class Amphibia

Order Anura

Family Sirenidae

Siren lacertina Linnaeus

Material--Eleven thoracic verbebrae, MSU 640, figures 1A, 1B, 1C, 1D.

Remarks--These typical *Siren* vertebrae are assigned to *Siren lacertina* because of their large size. Vertebrae of *S. intermedia* Le Conte are much smaller. In the two skeletons of *S. intermedia* available for study, the haemal

Figure 1. Reddick amphibian fossils.

A. Fossil _Siren_ _lacertina_ vertebra, anterior, x 2.9.

B. Fossil _Siren_ _lacertina_ vertebra, lateral, x 3.3.

C. Fossil _Siren_ _lacertina_ vertebra, dorsal, x 3.3.

D. Fossil _Siren_ _lacertina_ vertebra, ventral, x 3.3.

E. Recent _Siren_ _lacertina_ vertebra, ventral, x 4.7.

F. Recent _Siren_ _intermedia_ vertebra, ventral, x 4.7.

G. Fossil _Ambystoma_ _tigrinum_ vertebra, lateral, x 5.0.

H. Fossil _Scaphiopus_ _holbrooki_ sphenethmoid, x 2.3.

I. Fossil _Scaphiopus_ _holbrooki_ frontoparietal, x 3.2.

J. Fossil _Scaphiopus_ _holbrooki_ nasal, x 3.5.

K. Fossil _Scaphiopus_ _holbrooki_ ilium, x 3.0.

L. Fossil _Rana_ _grylio_ maxilla, x 2.5.

M. Fossil _Rana_ _grylio_ humerus, x 2.3.

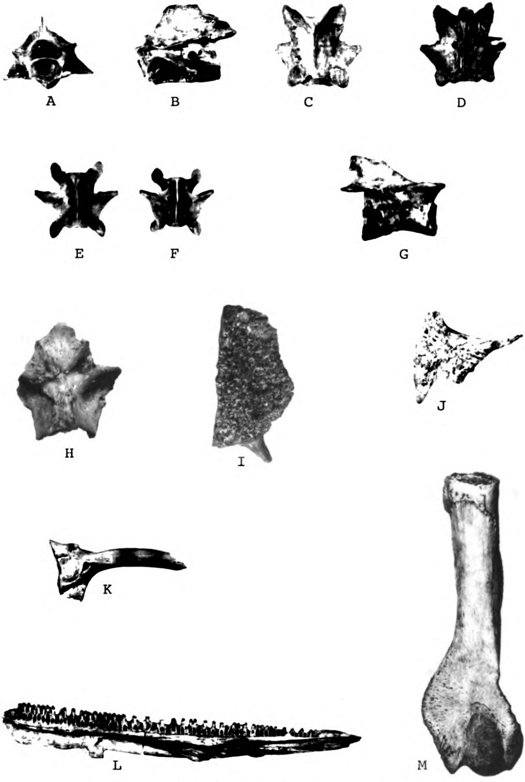


Figure 1. Reddick amphibian fossils.

keel of the vertebrae are wider and do not extend as close to the lip of the cotyle as in _S. lacterina_ (Figures 1E, 1F). The fossil vertebrae resemble _S. lacertina_ in these characters.

Goin and Auffenberg (1955) record _S. lacertina_ from this site.

Family Ambystomatidae

Ambystoma tigrinum (Green)

Material--Thirty-nine vertebrae, MSU 641, figure 1G.

Remarks--The vertebrae of _Ambystoma tigrinum_ are distinct. Besides exhibiting the wide and short proportions as defined by Tihen (1958), the posterior portion of the neural arch is directed upward and extends well beyond the end of the centrum. Holman (1969) has reported the latter feature to be characteristic of _A. tigrinum_.

This is the first report of this species from this site.

Order Anura

Family Pelobatidae

Scaphiopus holbrooki (Harlan)

Material--One nasal, seven frontoparietals, two sphenethmoids, three left ilia, six right ilia, one urostyle, MSU 649, figures 1H, 1I, 1J, 1K.

Remarks--The identified elements are distinct and not easily confused with other species.

This species was first reported from Reddick 1B by Gut and Ray (1963).

Family Ranidae

<u>Rana grylio</u> Stejneger

<u>Material</u>--One maxilla, one pterygoid, one dentary, one scapula, one coracoid, two humeri, one radioulna, one sacrum, two ilia, one femur, one urostyle, MSU 646, figures 1L, 1M.

<u>Remarks</u>--These fossils apparently represent one large male. The entire series was recovered from one small clump of matrix. Species identification was based on several of the elements. The ilia indicate the <u>Rana catesbeiana</u> Shaw, <u>R</u>. <u>hecksheri</u> Wright, <u>R</u>. <u>grylio</u> group of Auffenberg (1957). The maxilla indicates <u>grylio</u>. The section of the maxilla anterior to the nasal process is proportionately higher and shorter in <u>catesbeiana</u> and <u>heckscheri</u> than in <u>grylio</u>. In this character the fossil maxilla resembles <u>R</u>. <u>grylio</u>.

Sex was determined by the presence of a well developed epicondylar flange on the humerus. Chantell (1970) verified the value of this feature in determining sex.

This is the first fossil record of <u>R</u>. <u>grylio</u> from Reddick 1B. Tihen (1952) records <u>R</u>. <u>grylio</u> from the Pleistocene of Alachua County, Florida.

Rana pipiens Schreber

Material--Eight left ilia, seven right ilia, MSU 644, figure 2B.

Remarks--Auffenberg (1957) divides the ilia of New World Rana into two morphological groups based on the slope of the posterodorsal border of the ilial crest. In the pipiens group the slope is more gradual than in the catesbeiana group. The fossils show the pipiens group character. The only two members of the pipiens group appearing in or near Florida today are R. pipiens and R. areolata Baird and Girard. R. areolata ilia can be distinguished from those of pipiens by the more pronounced crainiad expansion of the ventral acetabular expansion that occurs in the latter. This character can be seen by comparing the reference ilia of R. pipiens and R. areolata shown in figures 2A and 2C. The fossil ilia resemble pipiens.

Holman (1962a) records R. pipiens from this site.

Rana areolata Baird and Girard

Material--Three left ilia, four right ilia, MSU 645, Figure 2D.

Remarks--As previously discussed under Rana pipiens, figures 2A and 2C illustrate the difference between the ventral acetabular expansion of Rana pipiens Schreber and R. areolata. This difference was found to be constant in

Figure 2. Reddick anuran fossils.

A. Recent *Rana pipiens* ilium, x 3.0.

B. Fossil *Rana pipiens* ilium, x 3.0.

C. Recent *Rana areolata* ilium, x 3.0.

D. Fossil *Rana areolata* ilium, x 3.0.

E. Fossil *Gastrophyrne carolinensis* ilium, x 4.0.

F. Fossil *Bufo terrestris* nasal, x 3.5.

G. Fossil *Bufo terrestris* squamosal, x 3.5.

H. Fossil *Bufo terrestris* frontoparietal, x 3.1.

I. Fossil *Bufo woodhousei fowleri* ilium, x 5.5.

J. Fossil *Bufo terrestris* ilium, x 5.5.

K. Fossil *Bufo quercicus* ilium, x 5.0.

L. Fossil *Bufo woodhousei* fowleri ilium, x 5.5.

M. Fossil *Bufo terrestris* ilium, x 5.5.

N. Fossil *Hyla cinerea* ilium, x 4.4.

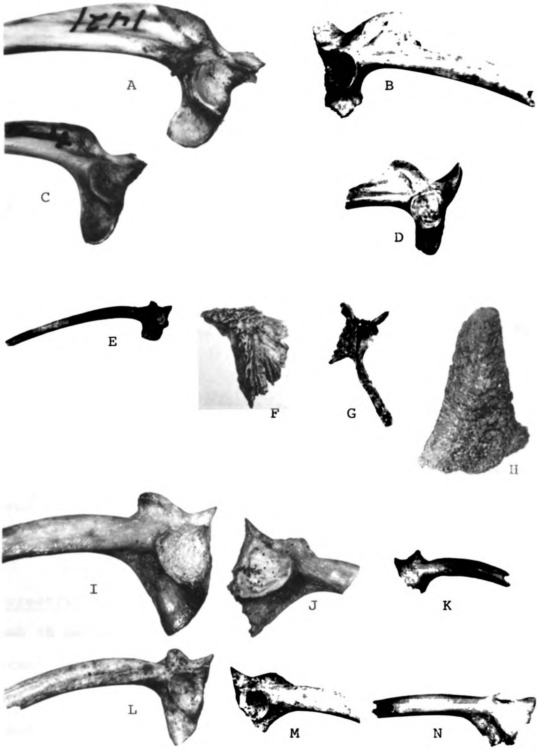


Figure 2. Reddick anuran fossils.

the nine skeletons of areolata and seventy skeletons of pipiens available for study.

This is the first fossil record of R. areolata.

Family Microhylidae

Gastrophryne carolinensis (Holbrook)

Material--Ten left ilia, four right ilia, MSU 651, figure 2E.

Remarks--The ilia of Gastrophryne carolinensis are easily recognized by their rectangular ventral acetabular expansion.

This species has been reported from Reddick 1B by Holman (1962a).

Family Bufonidae

Bufo terrestris (Bonnaterre)

Material--One nasal, twenty-three frontoparietals, seven squamosals, twelve left ilia, fifteen right ilia, MSU 642, figures 2F, 2G, 2H, 2J, 2M.

Remarks--Tihen (1962) states that in Bufo terrestris the height of the ilial prominence is never more than 30 percent of its base. Measurements made on fourteen recent MSU B. terrestris skeletons (twenty-eight ilia) support his findings. The MSU ilia showed a range of twenty-one to twenty-nine percent for this character. All fossil Bufo ilia with ilial prominence height to base ratios of less than 30 percent were assigned to

B. terrestris. All other bufonids of the eastern United States show ratios above 30 percent (Tihen, 1962).

The frontoparietal, squamosal, and nasal of B. terrestris are distinctive. The anterior dorsal portion of the squamosal of B. terrestris is proportionately larger than that of either B. americanus Holbrook or B. woodhousei fowleri (Hinckley). The frontoparietal of B. terrestris exhibits a crainial crest which is more rounded and knoblike than the corresponding member of the latter two species. The dorsal ridges on the nasal of B. terrestris are more clearly defined than those of B. americanus or B. w. fowleri.

Tihen (1962) records this species from Reddick 1B.

Bufo woodhousei fowleri (Hinckley)

Material--Eight left ilia, seven right ilia, MSU 643, figures 2I, 2L.

Remarks--Fifteen typical Bufo ilia with ilial prominence height to base ratios of .30 to .42 are assigned to Bufo woodhousei fowleri. Although the ilia of Bufo americanus Holbrook also show similar ratios, the base of the ilial protuberance in B. americanus is wider than that of equal sized ilia of B. w. fowleri (Holman, 1967). This character distinguished the fossils as B. w. fowleri.

Tihen (1962) indicates having seen "one or a few" ilia from various florida Pleistocene localities that should be referred to this species. Reddick 1B is mentioned as one of the localities. *B. w. fowleri* does not occur in Florida today.

Bufo quercicus Holbrook

Material--One left and one right ilium, MSU 650, figure 2K.

Remarks--These two small *Bufo* ilia are difficult to distinguish from juvenile *Bufo woodhousei fowleri* (Hinckley). Since they lack the porosity characteristic of juveniles of the latter, they are assigned to *B. quercicus*.

Tihen (1962) records this species from the present site.

Family Hylidae

Hyla cinerea (Schneider)

Material--One left ilium, MSU 647, figure 2N.

Remarks--The large size and oval shape of the dorsal protuberance, its relatively great distance from the acetabular fossa, and the relatively acute angle with which the anterior edge of the ventral acetabular expansion meets the ilial shaft are characteristic of *Hyla cinerea*.

This is the first fossil record of *H. cinerea* at the Reddick 1B site. Lynch (1965) records this species from the Pleistocene of Alachua County, Florida.

Pesudacris nigrita (Le Conte)

Material--One right ilium, MSU 648, figure 3D.

Remarks--The ilium of Pseudacris nigrita exhibits a wider ventral acetabular expansion than is found in either P. ornata (Holbrook) or P. triseriata (Wied) and can be separated from those two species on that basis. This feature is shown in figures 3A, 3B, and 3C.

This is the first fossil record of this species.

Family Emydidae

Terrapene carolina (Linnaeus)

Material--One proneural, four partial hyoplastrons, three partial hypoplastrons, two humeri, one scapula, two femora, MSU 668, figures 3E, 3F.

Remarks--Auffenberg (1958), Holman (1967), and Milstead (1967), discuss characteristics of Terrapene carolina.

Auffenberg (1959), working with complete shells from this area, has indicated that the Reddick 1B Terrapene probably represents an intergradient population of T. c. carolina or T. c. bauri and the extinct T. c. putnami (Hay). However, Blaney (1971) has placed T. c. putnami in the snyonomy of T. c. major (Aggasiz).

Gopherus polyphemus (Daudin)

Material--One partial mandible, four humeri, five femora, MSU 669, figures 3G, 3H, 3I.

Figure 3. Reddick amphibian and reptile fossils.

A. Recent *Pseudacris triseriata* ilium, x 6.0.

B. Recent *Pseudacris ornata* ilium, x 6.0.

C. Recent *Pseudacris nigrita* ilium, x 6.0.

D. Fossil *Pseudacris nigrita* ilium, x 6.0.

E. Fossil *Terrapene carolina* humerus, x 2.0.

F. Fossil *Terrapene carolina* femur, x 1.5.

G. Fossil *Gopherus polyphemus* humerus, x 2.4.

H. Fossil *Gopherus polyhpemus* femur, x 2.0.

I. Fossil *Gopherus polyphemus* mandible, x 1.4.

J. Fossil *Geochelone crassiscutata* dermal ossicle, x 3.3.

K. Fossil *Anolis carolinensis* frontal, x 4.0.

L. Fossil *Anolis carolinensis* dentary, x 5.0.

M. Fossil *Cnemidophorus sexlineatus* dentary, x 5.0.

N. Fossil *Ophisaurus ventralis* precadal vertebra, x 4.0.

O. Fossil *Ophisaurus ventralis* caudal vertebra, x 3.8.

P. Fossil *Ophisaurus ventralis* dentary, x 5.0.

Q. Fossil *Eumeces*, sp. indet. dentary, x 5.0.

R. Fossil *Elaphe*, sp. indet. verbetra, lateral, x 4.0.

S. Fossil *Elaphe*, sp. indet. vertebra, dorsal, x 4.0.

T. Fossil *Elaphe*, sp. indet. vertebra, ventral, x 4.0.

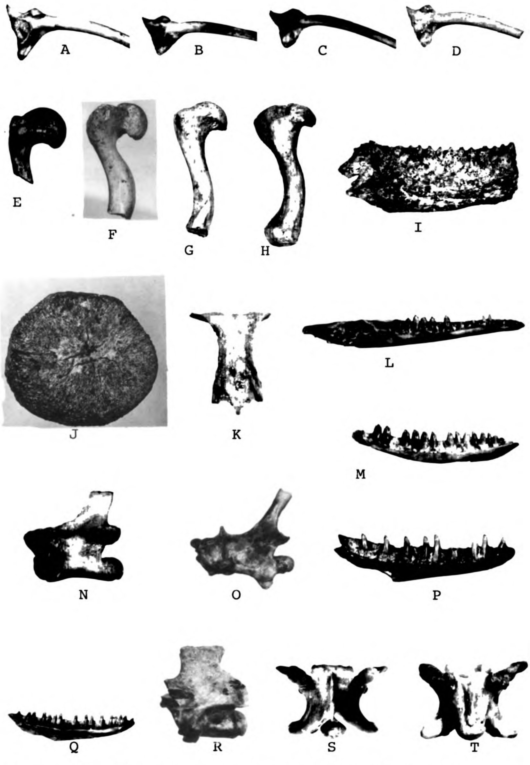


Figure 3. Reddick amphibian and reptile fossils.

Auffenberg (1959) records *Gopherus* from this site.

Order Testudines

Family Testudinidae

Geochelone, cf. *G. crassiscutata* (Leidy)

Material--One dermal ossicle, MSU 670, figure 3J.

Remarks--The size of the ossicle (3 cm.) indicates the presence of a large tortoise. Only *G. crassiscutata* is known to reach such a size in the Pleistocene of Florida.

Auffenberg (1963b) records this species from this site.

Geochelone, cf. *G. incisa* (Hay)

Material--Fragmented carapacial elements, MSU 671.

Remarks--Several carapacial elements, too fragmentary for positive specific identification exhibit the rugosity and thickness characteristics of this species.

Auffenberg (1963b) records this species from this site.

Order Squamata

Family Iguanidae

Anolis carolinensis Voigt

Material--Five dentary fragments, five frontals, MSU 652, figures 3K, 3L.

Remarks--*Anolis* dentaries are easy to identify. They are long, low, and have a reduced or absent Meckelian Groove. The heterodont teeth are singly cusped anteriorly, tricusped posteriorly. I cannot distinguish the fossils from recent *Anolis carolinensis* dentaries.

The frontal of *Anolis* is also distinctive. The fossil frontals are assigned to *A. carolinensis*.

Auffenberg (1956) records *A. carolinensis* from Reddick 1B.

Family Teidae

Cnemidophorus sexineatus (Linnaeus)

Material--Three dentaries, two vertebrae, MSU 653, figure 3M.

Remarks--The fossils are indistinguishable from corresponding elements of *Cnemidophorus sexlineatus*. On this basis and on zoogeographic grounds, the fossils are assigned to that species.

Auffenberg (1956) records a single dentary fragment from Reddick 1B.

Family Anguidae

Ophisaurus ventralis (Linnaeus)

Material--Eight precaudal vertebrae, five caudal vertebrae, MSU 655, figures 3N, 3O, 3P.

Remarks--Auffenberg (1955) and Etheridge (1961) have discussed methods for identifying the vertebrae of the three species of *Ophisaurus* occurring in eastern North

America. They have found that precaudal vertebrae of _O. compressus_ Cope can be distingushed from those of _O. attenuatus_ Baird and _O. ventralis_ by the shorter and wider appearance of the latter two species. _O. attenuatus_ precaudal vertebrae can be separated from those of _O. ventralis_ by using the angle formed by the posterior border of the neural spine and the longitudinal axis of the centrum. These angles have been reported to be 45° to 65° (mean--58°) for _O. attenuatus_, and 65° to 84° (mean--73°) for _O. ventralis_. The angle between the anterior border of the caudal transverse processes and the longitudinal axis of the centrum is used to diagnose the caudal vertebrae of all three species. These angles have been reported to be 70° to 75° (mean--73°) in _O. ventralis_, 75° to 85° (mean--81°) in _O. attenuatus_, and 50° to 65° (mean--55°) in _O. compressus_.

Using the criteria given above, the fossils were identified as _O. ventralis_. In the course of identifying the fossils, four prepared skeletons of _O. attenuatus attenuatus_ were examined. The neural spine-longitudinal axis angle in these specimens varied from 68° to 81° (mean--72°) thus causing the known variation of this measurement to overlap with the known variation in _O. ventralis_. Assuming that Etheridge and Auffenberg used the eastern subspecies of _O. attenuatus_ (_O. a. longicauda_) as their reference material, it may be possible to use vertebral angles to separate _O. ventralis_ from

O. attenuatus longicauda. Making this assumption these fossils are identified as _O. ventralis_.

Auffenberg (1955) records _O. ventralis_ from this site.

Family Scincidae

Eumeces, sp. indet.

Material--Two partial dentaries, MSU 654, figure 3Q.

Remarks--Auffenberg (1956) provisionally lists _Eumeces fasciatus_ (Linnaeus) from Reddick 1B. His identification was based on a single complete dentary containing twenty-seven teeth. The recent skeletons available to him gave dentary teeth counts of twenty-one to twenty-five in _Eumeces laticeps_ Schneider and _Eumeces inexpectatus_ Taylor, and twenty-five to twenty-six in _E. fasciatus_. Since the number of teeth found in _E. fasciatus_ most closely approached the number found in the fossil, the fossil was assigned to that species.

Two additional fossil dentaries from the Reddick 1B site are assigned to _Eumeces_. One fossil dentary is nearly complete and has a tooth-alveolar count of twenty-four, placing it in the _laticeps_ and _inexpectatus_ group of Auffenberg. However, eight MSU skeletons of _E. fasciatus_ yielded tooth counts of twenty-three to twenty-four, indicating that the fossil might represent any of those three species.

The other fossil dentary is too fragmentary for a complete tooth count. I am unable to carry this identification of either fossil dentary to the species level.

Family Colubridae

Carphophis amoenus (Say)

Material--Eleven precaudal vertebrae, MSU 660.

Remarks--Diadophis, Tantilla, and Rhadinea are other small colubrids whose vertebrae might be confused with those of Carphophis. Auffenberg (1963) presented data showing the neural spine of Carphohpis vertebrae is proportionately longer and lower than that of Diadophis or Rhadinea. He further indicates that Tantilla vertebrae have a narrower haemal keel than those of Carphophis. Using these criteria, the fossils were identified as Carphophis amoenus.

Elaphe, sp. indet.

Material--Twenty-seven precaudal vertebrae, MSU 659, figures 3R, 3S, 3T.

Remarks--Auffenberg (1963b) found the reference skeletons of Elaphe guttata (Linnaeus) and Elaphe obsoleta (Say) available to him could be separated by a regression curve of ratios of the neural spine length to neural spine height. Enough overlap in this character has been found in MSU specimens to invalidate its usefulness in diagnoses. I am unable to separate these two species by vertebra characters.

Pituophis melanoleucus (Daudin)

Material--One sphenoid, twenty precaudal vertebrae, MSU 657, figures 4C, 4D, 4E.

Remarks--The broad, short appearance of the sphenoid makes it distinctive. The proportionately high neural spine of eastern *P. melanoleucus* serves to distinguish it from other large colubrids. From *Elaphe* with which it is most easily confused it can be distinguished its proportionately larger neural canal and the more vaulted appearance of its neural arch. Figures 4A and 4B illustrate these differences.

Coluber or *Masticophis*

Material--Thirty-one precaudal vertebrae, MSU 658, figures 4F, 4G.

Remarks--I am unable to distinguish between the vertebrae of *Coluber constrictor* Linnaeus and *Masticophis flagellum* (Shaw), the two extant members of these genera in Florida.

Drymarchon corais (Daudin)

Material--One maxilla, one palatine, one basisphenoid, one articular-surangular-prearticular complex, thirty-one precaudal vertebrae, MSU 656, figures 4H, 4I, 4J, 4K.

Remarks--The crainial elements are distinctive and not easily confused with other species. The vertebrae are

Figure 4. Reddick snake fossils.

A. Recent *Elaphe obsoleta* verbetra, posterior, x 3.2.

B. Recent *Pituophis melanoleucus* vertebra, posterior, x 3.2.

C. Fossil *Pituophis melanoleucus* sphenoid, x 3.0.

D. Fossil *Pituophis melanoleucus* verbetra, dorsal, x 2.5.

E. Fossil *Pituophis melanoleucus* vertebrae, lateral, x 2.5.

F. Fossil *Coluber* or *Masticophis* vertebra, lateral, x 2.6.

G. Fossil *Coluber* or *Masticophis* vertebra, dorsal, x 3.0.

H. Fossil *Drymarchon corais* maxilla (upper), palatine (lower), x 2.7.

I. Fossil *Drymarchon corais* sphenoid, x 1.9.

J. Fossil *Drymarchon corais* vertebra, lateral, x 2.0.

K. Fossil *Drymarchon corais* vertebra, dorsal, x 2.1.

L. Fossil *Heterodon platyrhinos* sphenoid, x 4.0.

M. Fossil *Heterodon platyrhinos* vertebra, anterior, x 4.0.

N. Fossil *Heterodon simus* vertebra, anterior, x 4.0.

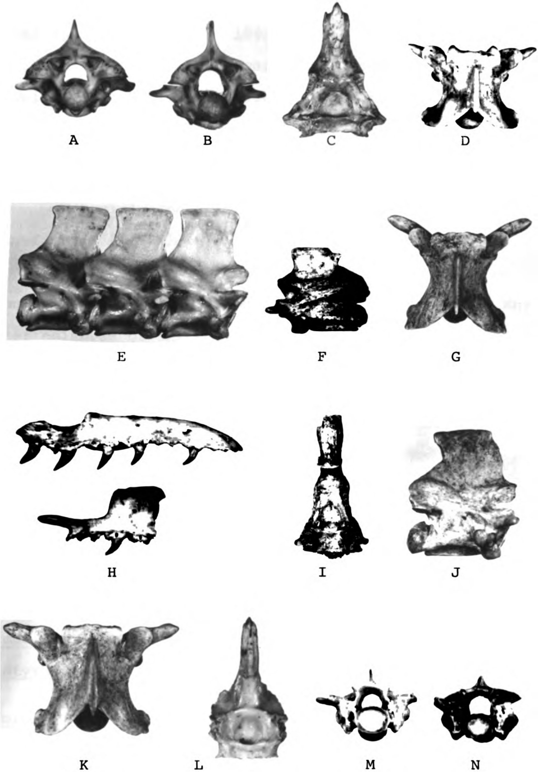


Figure 4. Reddick snake fossils.

easily identified by the beveled anterior edge of their neural spine (Auffenberg, 1963b).

All of these bones were found together in one shovelful of matrix. The size of the various elements indicates that they all may have come from one adult snake.

Heterodon platyrhinos Latreille

Material--One sphenoid, twenty-one verbebrae, MSU 661, figures 4L, 4M.

Remarks--The sphenoid is dinstinctive. Its pleurosphenoid portion is more convex in outline than any other colubrid of the southeastern United States. Heterodon vertebrae are easily identified by their flattened and broadened haemal keel (Holman, 1959).

Heterodon simus (Linnaeus)

Material--One precaudal vertebra, MSU 662, figure 4N.

Remarks.--In addition to the characters used by Auffenberg (1963b) to separate H. simus from H. platyrhinos, the shape of the neural canal can be used also. In H. simus the canal is more dorsally expanded than in H. platyrhinos.

Storeria dekayi (Holbrook)

Material--Two precaudal vertebrae, MSU 663.

Remarks--The two fossils appear to be middle precaudal vertebrae. Using the criteria of Auffenberg (1963b), the fossils are assigned to *S. dekayi*.

Thamnophis sirtalis (Linnaeus)

Material--One sphenoid, sixty-three precaudal vertebrae, MSU 664, figures 5E, 5F, 5G.

Remarks--The sphenoids of various large natricines are very similar. Holman (1967) points out that sphenoids of *T. sirtalis* have more pointed, better developed posterior processes than those of *Natrix sipedon* (Linnaeus) and *T. sauritus* (Linnaeus). The fossil sphenoid is similar to *T. sirtalis* in this character and are assigned to that species.

Holman (1962b) and Auffenberg (1963b) have discussed the vertebral characteristics of *Thamnophis*. As they point out, the large natricines with which *Thamnophis* vertebrae are most easily confused are *Natrix sipedon* (Linnaeus) and *N. fasciata* (Linnaeus) both of which have higher neural spines than *T. sirtalis*. Figures 5A, 5B, and 5C illustrate this point.

Besides the characters mentioned by Holman (1962b), *T. sirtalis* vertebrae can be separated from those of *T. sauritus* by the lower neural spine and proportionately wider neural arch of the latter.

Figure 5. Reddick snake fossils.

A. Recent Natrix fasciata vertebra, lateral, x 4.0.

B. Recent Natrix sipedon vertebra, lateral, x 4.0.

C. Recent Thamnophis sirtalis vertebra, lateral, x 4.0.

D. Recent Thamnophis sauritus vertebra, lateral, x 4.0.

E. Fossil Thamnophis sirtalis sphenoid, x 4.0.

F. Fossil Thamnophis sirtalis vertebra, lateral, x 3.6.

G. Fossil Thamnophis sirtalis vertebra, dorsal, x 3.0.

H. Fossil Micrurus fulvius vertebra, lateral, x 3.6.

I. Fossil Micrurus fulvius vertebra, dorsal, x 3.9.

J. Fossil Sistrurus miliarius vertebra, lateral, x 3.1.

K. Fossil Sistrurus miliarius vertebra, dorsal, x 4.9.

L. Fossil Crotalus or Sistrurus fang and premaxilla, x 3.7.

M. Fossil Crotalus adamanteus vertebra, lateral, x 2.0.

N. Fossil Crotalus adamanteus vertebra, dorsal, x 1.8.

O. Fossil Crotalus adamanteus vertebra, anterior, x 2.0.

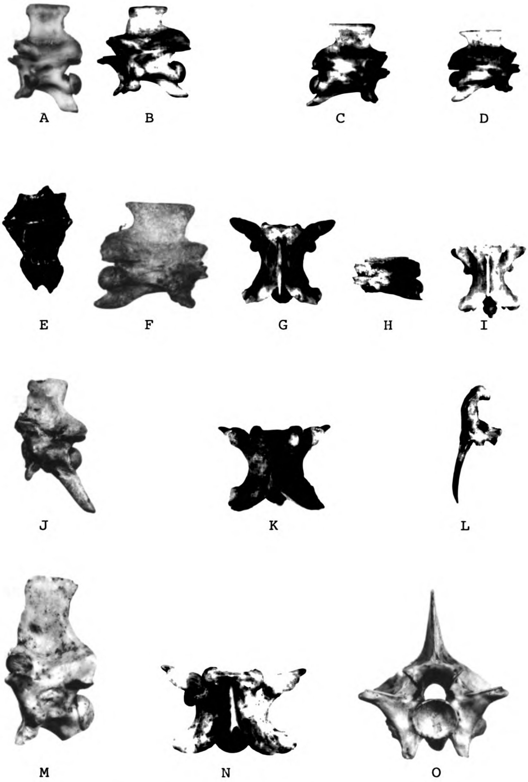


Figure 5. Reddick snake fossils.

Family Elapidae

Micrurus fulvius (Linnaeus)

Material--One-hundred sixty-six precaudal vertebrae, MSU 665, figures 5H, 5I.

Remarks--These are typical *Micrurus* vertebrae with well developed hypapophyses, and a long, low neural spine. On zoogeographic grounds they are assigned to *M. fulvius* from which they cannot be distinguished.

This was the single most common reptilian element found in the samples. Whether the vertebrae represent few or many individuals is uncertain.

Family Viperidae

Sistrurus miliarius (Linnaeus)

Material--Thirty-five precaudal vertebrae, MSU 666, figures 5J, 5K.

Remarks--The fossils are typical *Sistrurus* vertebrae, being of the viperid type and having a relatively long and narrow centrum. On zoogeographic grounds they are assigned to *S. miliarius* rather than *S. catenatus*.

One viperid maxilla with its attached fang was found. Its small size suggests that it may represent this species. But, I am unable to distinguish between *S. milarius* and *Crotalus adamanteus* Beauvois using this element. The squarish outline of the maxilla indicates that the fossil does not represent *Agkistrodon*. Holman (1959), has pointed out that Agkistrodon maxillae have a more rounded outline. This fossil is illustrated in figure 5L.

Crotalus adamanteus Beauvois

Material--Ten precaudal vertebrae, MSU 667, figures 5M, 5N, 5O.

Remarks--Auffenberg (1963b), discusses the vertebral characteristics of C. adamanteus. Several of the vertebrae represent large individuals, but they do not exhibit the wide proportions of the extinct C. giganteus Brattstrom.

DISCUSSION

The Herpetofauna

In their check list of 1963, Gut and Ray list thirty-eight species of reptiles and amphibians as being found at Reddick I. With the exception of Pseudobranchus robustus Goin and Auffenberg, and Rhineura floridana Baird and Girard, all of the species listed by Gut and Ray were found at the IB site. Holman (1962a) originally recorded P. robustus and R. floridana from Reddick IC.

The present study adds five species to the known herpetofauna of Reddick IB, Ambystoma tigrinum, Rana grylio, Rana areolata, Hyla cinerea, and Pseudacris nigrita. This is also the first fossil record of Rana areolata and Pseudacris nigrita.

The herpetofauna from the Reddick I site is comprised of at least forty-three species, of which all but two occur at the IB site. *P. robustus*, *G. crassiscutata*, and *G. incisa* are the only extinct forms. Thus approximately 40 percent of the ninety-three extant species of reptiles and amphibians found in central Florida are represented in the Reddick fossil fauna.

Paleoecology

Although it is generally agreed that the Reddick 1 fossils accumulated in a large cave (Brodkorb, 1957; Auffenberg, 1963b, Hamon, 1964), various investigators have expressed divergent opinions as to the nature of the surrounding paleocommunity. Based on the avifauna, Brodkorb (1957) and Hamon (1964) suggest that a typical wet grassland or freshwater marsh was nearby. Brodkorb (1957) lists the following species of fossil birds from Reddick 1 as being characteristic of such a habitat: piedbilled grebe, six species of duck, six species of rails, killdeer, lesser yellowlegs, burrowing owl, sedge wren, yellow throat, red-winged blackbird, meadowlark, and Henslow's sparrow. He also notes that the remaining avian members of the fossil fauna are in harmony with a marsh community. The absence of birds which are confined to deep water and the total absence of fish remains were interpreted as meaning that the marsh contained no sizeable body of open water and that the marsh probably became dry periodically.

Auffenberg (1963) interprets the reptilian faunal elements as suggesting a dry, open forest, but not necessarily scrub. He points out that the absence of aquatic genera such as Natrix suggests that no ponds were nearby. He further notes that the bulk of Brodkorb's bird fossils came from site 1A, while the reptiles (primarily snakes) came from site 1B which is situated approximately 260 feet to the southwest. This leads him to speculate that these two sites may not be contemporaneous, and may represent different ecological conditions.

The fossil herpetofauna being discussed in this paper was taken from one small area of locality 1B. The possibility that this sample represents a heterochronic assemblage rather than a unit fauna still exists, but that likelihood is reduced due to the small volume of the sample and the localized nature of the sampling technique.

Most of the species found in the present sample have wide ecological tolerances and may be found in a variety of habitats. It is the species whose habitats are restricted that give the best clues to the paleohabitat. In the latter category are Siren lacertina, Pituophis melanoleucus, and Gopherus polyphemus. S. lacertina requires an aquatic habitat, but can estivate in moist burrows during droughts (Carr, 1940). P. melanoleucus and G. polyphemus are largely restricted to high pine, although G. polyphemus is occasionally found in upland hammock situations (Carr, 1940). Thus in this one sample elements are present which are strong indicators of the dry open forest postulated by Auffenberg and the freshwater marsh of Brodkorb.

Of the remaining members of the fauna, Carr (1940) characterizes twelve as being characteristic of or occurring frequently in high pine, while seven are listed as being characteristic of or occurring frequently in upland hammocks (see Table 1). Nearly all of the fauna can be found at least occasionally in either the high pine or upland hammock habitats. The addition of a nearby marsh to either habitat would allow for the presence of the aquatic members of the fauna.

It is entirely possible that a high, well-drained forest could be associated with a lower marsh area. Such conditions are found in central Florida today. Hamon (1964) states that the mean surface elevation of Reddick 1 is ninety-three feet. He also furnishes a relief map of this area which indicates the presence of a shallow basin. The center of this basin lies within one thousand feet of the Reddick 1 quarry and is at an elevation of seventy feet. Some of the terraine surrounding the basin and quarry rises to an elevation of 120 feet. Under suitable conditions the basin could become a shallow pond with a radius of several hundred feet.

Considered as a unit fauna, the sample suggests that both Auffenberg and Brodkorb's views of the paleo-ecology of the Reddick 1 site may be partially correct. A synthesis of their two paleoecological interpretations seems

Table 1.--Habitat preferences of the Reddick 1B herpetofauna.

Species	High Pine	Upland Hammock	Marsh
Siren lacertina	-	-	c
Ambystoma tigrinum	-	O	O
Scaphiopus holbrooki	f	c	
Rana grylio	-	-	c
Rana pipiens	-	O	c
Rana areolata	c	O	
Gastrophyrne carolinensis	O	f	
Bufo terrestris	f	c	
Bufo w. fowleri	O	O	
Bufo quercicus	f	O	
Hyla cinerea	O	O	
Psuedacris nigrita	O	O	
Terrapene carolina	O	f	
Gopherus polyphemus	c	O	
Anolis carolinensis	O	f	
Cnemidophorus sexlineatus	f	O	
Ophisaurus ventralis	f	O	
Carphophis amoenus	-	O	
Pituophis melanoleucus	c	O	
Coluber or Masticophis	f	c	
Drymarchon corais	c	O	
Heterodon platyrhinos	f	O	
Heterodon simus	O	O	
Storeria dekayi	-	O	
Thamnophis sirtalis	O	O	
Micrurus fulvius	O	f	
Sistrurus miliarius	O	O	
Crotalus adamanteus	f	O	

Note: f = frequent; c = characteristic; O = occasional; - = rare or absent. Data from Carr (1940), and Conant (1958).

to be the most satisfactory explanation of the apparent ecological incompatibility of the species found at Reddick 1.

Zoogeography and Pleistocene Climate

Were it not for the presence of G. crassiscutata, B. w. fowleri, and C. amoenus, the fossil herpetofauna of Reddick 1B would offer no suggestion that the environmental conditions under which they lived differed in the least from the present conditions in that area. However, B. w. fowleri and C. amoenus presently occur no farther south than several hundred miles to the north of Reddick (figure 6). G. crassiscutata, a giant tortoise, is now extinct. The giant tortoise which occurs closest to the Reddick site is found in the Galapagos Islands. This information implies that the ecological relationships between the faunal members, and possibly the existing climatic conditions, differed from current conditions.

Several authors have given their interpretation of the paleoclimate at Reddick 1. Brodkorb (1957), believing that the Reddick 1 fauna represented the Illinoian glacial stage, suggested that when the fossils were deposited the climate of northern Florida was at least as cool as that of northern Virginia. His conclusion was based on finding the bones of nestling Tachcineta speleodytes Brodkorb, an extinct swallow. The closest living relative of T. speleodytes breeds no farther south than Virginia. Among

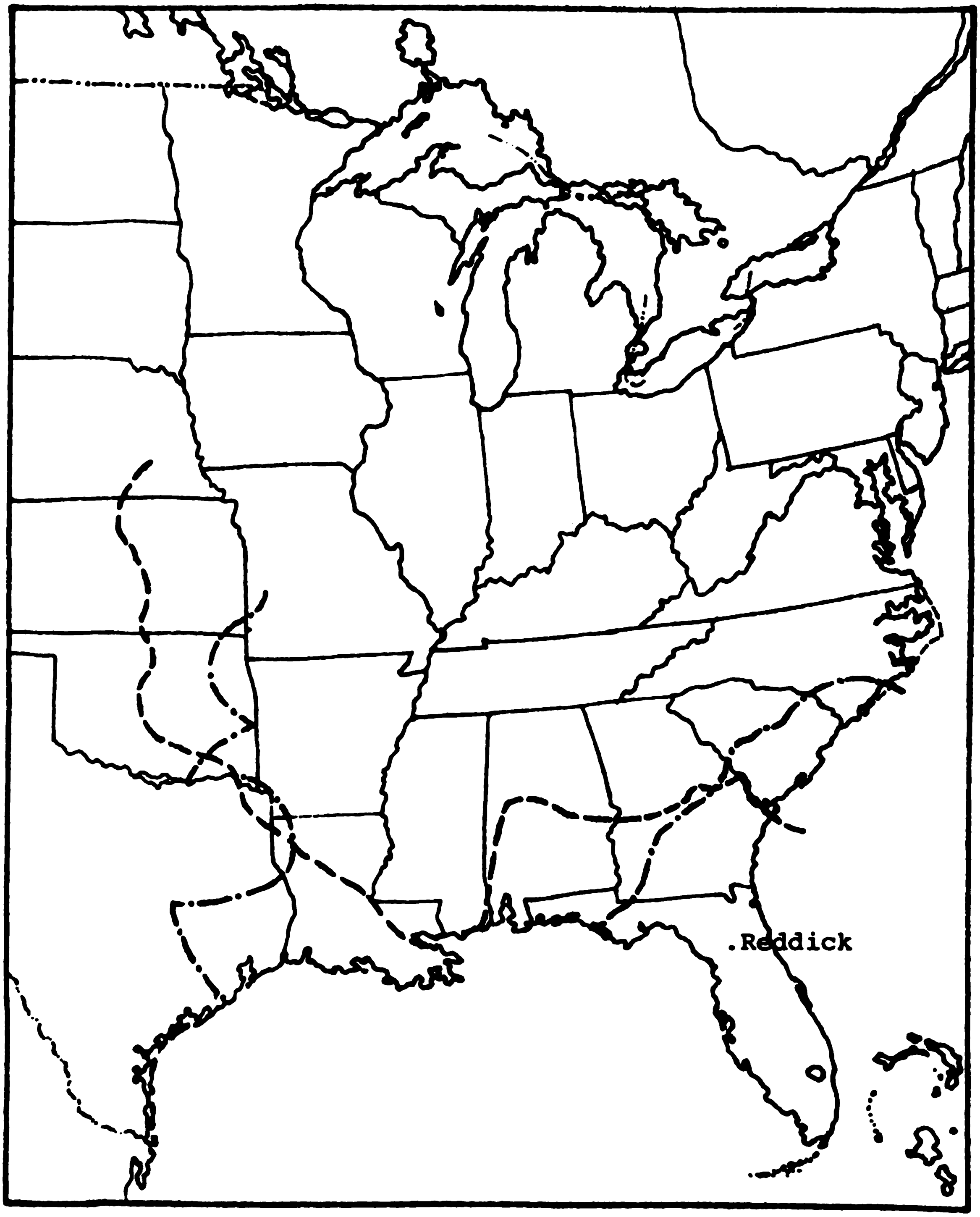


Figure 6. Southern range limits of Carphophis amoenus and Bufo w. fowleri.

---- C. amoenus

-·-·- B. w. fowleri

the fossil mammals found at Reddick 1, Brodkorb points to *Synaptomys australis* and notes that today the genus *Synaptomys* finds its southern limits in Maryland, although isolated populations occur in Virginia and North Carolina.

Hamon (1964) attempted to determine the July and January mean temperatures at Reddick at the time of fossil preservation. He mapped the present southern limits of *Synaptomys*, *Tachycineta*, and *Cistothorus*, three boreal elements found in the deposit of Reddick. An average July mean temperature of 74.9 degrees Fahrenheit was found to occur along these borders. That temperature was compared with a July mean temperature of 81.1 degrees Fahrenheit at Ocala, Florida, a location ten miles south of the fossil site. Hamon concluded that during the time of fossil deposition the summers at Reddick were about six degrees cooler than now.

To determine the January mean temperature the process was repeated using the northern range of a southern element. *Alligator mississipiensis* was chosen as this southern element. The average January mean temperature along the northern limits of its range was found to be 50.4 degrees Fahrenheit. This temperature was equated with the January mean temperature of Reddick at the time the fossils were being deposited. The current January mean temperature at Ocala, Florida was stated to be 57.2 degrees Fahrenheit, about seven degrees warmer than Reddick at fossil deposition time. Thus, both Brodkorb and Hamon concluded that at the time the fossils were being deposited, summer and winter temperatures were lower than now. These conclusions and the methods used to arrive at them are open to criticism.

Loosely paraphrased, Merriam's temperature laws state that animals and plants are restricted in northward distribution by the total quantity of heat during the season of growth and reproduction, and that their southward distribution is determined by the intensity of heat during the hottest period of summer. Either knowingly or unknowingly, both Brodkorb and Hamon used these laws, or a facsimile thereof, to arrive at an estimation of the paleoclimate at Reddick. Since these laws have been largely discredited (Kendeigh, 1932; Shelford, 1932), their use in the determination of paleoclimates must be questioned.

The use of the alligator's northern range limits to estimate paleotemperatures at Reddick must be questioned, also. The present range of the alligator extends to the north of Reddick (Conant, 1958, Map 1). Therefore, it is meaningless to equate the average the January mean temperatures along its northern limits with the January mean temperature of Reddick at the time of fossil deposition. To arrive at an estimation of the January mean at Reddick in a manner analogous to that which was used to estimate the July mean temperature, a southern element should have been chosen whose northern range now lies to the south of the Reddick site. This might be possible to do if the January paleotemperatures were warmer than at present. But again, the practice could be criticized due to the questionable validity of Merriam's temperature laws.

In recent years, other workers (Dalquest, 1965; Hibbard, 1970; Slaughter & Hoover, 1963) have made interpretations of Pleistocene paleoclimates of the United States. Their works have centered on the Great Plains region, and have been based largely on faunal evidence. In particular, fossils representing species having northern distributions have been used as temperature indicators. When such a fossil was found to the south of the current southern range limits of the species it represented, it was interpreted as an indication that cooler summer temperatures prevailed at the paleohabitat. As already discussed, such interpretations are loosely based on Merriam's temperature laws, and therefore, they are based on faulty assumptions.

Nevertheless, the importance of temperature effects cannot be overlooked as a possible factor, perhaps even the major factor, in contributing to faunal mixing as found in Pleistocene deposits. However, other factors may also contribute to the phenomenon. Humidity, seasonal patterns of rainfall, predation, and competition are just a few of the factors that may act independently or in concert with other environmental factors to delimit a species' range. As yet, just how these factors may interact to affect distributions is only partly understood. Until such interactions are more fully investigated, it seems unwarranted to ascribe all faunal mixing to temperature effects alone, as has been done.

Therefore, although the presence of *B. w. fowleri* and *C. amoenus* does not conflict with the hypothesis that cooler summer temperatures prevailed at Reddick during the time of fossil deposition, neither does it offer positive evidence for it. Clark (1970), studying the natural history of *Carphophis* in detail, attributes the occurrence of *Carphophis* in Pleistocene Florida to the better soil drainage that was presumed to be present then. The same or a similar non-temperature factor may account for the presence of *B. w. fowleri*, also.

The foregoing discussion might seem to make an estimation of paleotemperatures based on faunal elements impossible. This is not necessarily the case. If it can be shown that a particular species' distribution is determined entirely or largely by temperature, then that species could be used as a temperature indicator. Some progress has been made in this direction.

Brattstrom (1961) notes that mild, equable climates are necessary for the existence of giant tortoises. Without such climatic conditions and some shade, the tortoises reach lethal temperatures when exposed to the sun. In a cool climate their great bulk takes too long to warm up, and they cannot become active. In addition, Brattstrom shows that tortoises have always have a tropical or subtropical distribution.

Hibbard (1960) also suggests that giant tortoises are good indicators of equable climates. He notes that specimens of the giant tortoises brought from the Galapagos Islands were not able to survive in colonies near the southern border of the United States. Even specimens located on Lignum Vitae Island, Florida, died from enteritis, a condition caused by the tortoises being too cool to digest their food.

Hibbard's use of the giant tortoises as indicators of climate is conservative. His summarizing statements on their use for this purpose bears repeating.

> The large Pliocene and Pleistocene land tortoises could not stand freezing, but they may have existed in an area where very few light frosts occurred at night but with temperature during the day warmed to 60 degrees or more Fahrenheit.
>
> The young of these large species may have taken shelter on cool nights in burrows until they were large enough so that their body heat would protect them from temperatures near 32 degrees F. The fact that there is no evidence that these tortoises burrowed or entered burrows during winter months, and the fact that they grew to such large size, suggests that they lived and reproduced in an equable climate.
>
> It is therefore assumed that they lived chiefly in areas of frost free environments. It is not logical to assume that these large land tortoises lived in an environment where they became torpid from cold and dotted the landscape as boulders through a long cold season (Hibbard, 1960, p. 9).

Geochelone crassiscutata is a giant tortoise whose remains have been found at the Reddick 1B site. Auffenberg (1963b) records a specimen of this species whose carapace measured 1210mm in total length. He also states that fragments of much larger specimens have been found.

The presence of *G. crassiscutata* in the Reddick fauna suggests that when this species lived there, the climate was equable and frost free. This would seem to indicate that winter temperatures were not quite so cold as they are now. Data taken from the *United States Weather Bureau Climatic Summary Supplement*, 1932-62, showed that at Ocala, Florida, the temperature drops below thirty-two degrees Fahrenheit on an average of twelve days per year. Presumably, this would make the area uninhabitable by the giant tortoise.

SUMMARY

Five species have been added to the faunal list of fossil reptiles and amphibians found at the Reddick 1 site. The total recorded herpetofauna now stands at forty-four species, including three extinct species.

The fossils identified at site 1B indicate that the surrounding area once contained a well-drained, open forest and a marsh.

The presence of the extinct giant tortoise *Geochelone crassiscutata* suggests that the winters at Reddick during the Sangamon Age were not as cold as present.

PART II

THE PLEISTOCENE HERPETOFAUNA OF LADDS, GEORGIA

The only site between north-central Florida and north-central Tennessee which has yielded an extensive Pleistocene herpetofauna is found near Ladds, Georgia. The Ladds deposit is in a limestone quarry located 2.3 miles west south-west of Cartersville, Bartow County, in Land Lot 591, Fourth District, Third Section of the Georgia Land Survey of 1832. The quarry is developed at the southeastern end of an isolated dolomite ridge, Quarry Mountain. The ridge stands about five hundred feet above the surrounding countryside and reaches an elevation of nearly eleven hundred feet.

Solution cavities of the dolomite contain flowstone and red cave earths which may surround or encrust the fossils. Due to blasting and other quarrying operations, ample opportunity for the mixing of heterochronic elements has occurred (Ray, 1965; Lipps & Ray, 1967).

Faunal evidence suggests the deposit is late Pleistocene. Ray (1967), reported that nearly 25 percent of the mammals found in the deposit are extinct. He reports the presence of late Pleistocene indicators such as *Equus* and *Didelphis*.

For the most part, collecting of fossils has been done by personnel affiliated with Shorter College, Rome, Georgia, under the direction of Dr. Lewis Lipps. Standard collecting techniques have been used, including washing for microfossils.

Beginning in 1963, fossils were collected, sorted, and shipped from Shorter College to the Smithsonian Institution. There, Dr. Clayton Ray separated the material into various taxonomic classes and shipped the reptile and amphibian portion to Dr. J. Alan Holman for study. Holman (1967) reported on the fossils which were collected in 1963 and 1964 and were studied by him.

Since then, a wealth of new reptile and amphibian fossils from the Ladds site have been received for study. These fossils, dated pre-1968, 1968, and 1969, are the subject of this account.

The following is a list of the reptiles and amphibians represented by the fossils identified in the samples labeled pre-1968, 1968, and 1969.

Class Amphibia

Order Urodela

Family Ambystomatidae
Ambystoma tigrinum (Green)
Family Plethodontidae
Plethodon cf. *Plethodon glutinosus* (Green)

Order Anura

Family Ranidae
Rana pipiens Schreber
Family Bufonidae
Bufo americanus Holbrook
Bufo terrestris (Bonnaterre)

Class Reptilia

Order Testudines

Family Emydidae
Clemmys insculpta (Le Conte)
Terrapene carolina (Linnaeus)
Chrysemys picta (Schneider)
Pseudemys sp. indet.

Order Squamata

Family Colubridae
Diadophis punctatus (Linnaeus)
Carphophis amoenus (Say)
Coluber or *Masticophis*
Elaphe sp. indet.
Lampropeltis getulus (Linnaeus)
Lampropeltis triangulum (Lacepede)
Natrix sipedon (Linnaeus)
Storeria dekayi (Holbrook)
Thamnophis sirtalis (Linnaeus)
Family Viperidae
Crotalus horridus (Linnaeus)

ANNOTATED LIST

Class Amphibia

Order Urodela

Family Ambystomatidae

Ambystoma tigrinum (Green)

Material--Eight vertebrae, USNM 209175.

Remarks--These *Ambystoma* vertebrae are assigned to *A. tigrinum* since the posterior portion of the neural arch of each is upswept and extends well beyond the end of the centrum. Holman (1969) has found this character to be peculiar to *A. tigrinum*.

As pointed out by Holman (1967) *A. tigrinum* does not occur in north-western Georgia today, although it is found in nearby southeastern Tennessee.

Family Plethodontidae

Plethodon, cf. *Plethodon glutinosus* (Green)

Material--Fifty-two vertebrae, USNM 209176.

Remarks--*Plethodon glutinosus* vertebrae are amphicoelus. They can be separated from the vertebrae of *Leurognathus* and *Desmognathus* which are opisthocoelous, and from *Pseudotriton* and *Gyrinophilus* vertebrae which are falsely opisthocoelous (Soler, 1950). Holman (1969) separates *Plethodon glutinosus* vertebrae from those of *Eurycea bislineata* (Green), *E. longicauda* (Green), and *E. lucifuga* (Rafinesque) on the basis of the shorter and wider dimensions of the former. He also notes that adult *P. glutinosus* vertebrae are larger than those of *Plethodon cinereus* (Green), *E. bislineata* and the troglodyte species of *Eurycea*. Using these criteria, the fossil vertebrae are assigned to *Plethodon glutinosus* from which they cannot be separated.

Order Anura

Family Ranidae

Rana pipiens Schreber

Material--Twelve right and six left ilia, USNM 209177.

Remarks--Auffenberg (1957) separates *Rana* ilia into two groups. The *pipiens* group is characterized by a less acute angle formed by the posterodorsal border of the idial crest and the dorsal acetabular expansion. The fossils represent members of the *pipiens* group. Holman (1967) separated *R. pipiens* from *R. palustris* Le Conte on the basis of the former's steeper slope of the posterodorsal border of the ilial shaft into the dorsal acetabular expansion. He further separated *R. pipiens* from *R. sylvatica* Le Conte in that the former has a larger, less produced and less roughened prominence for the origin of the vastus externus head of the triceps femoris muscle. The fossil ilia agree with *R. pipiens* in these characters.

Family Bufonidae

Bufo americanus Holbrook

Material--Three left and three right ilia, USNM 209178, figure 7a.

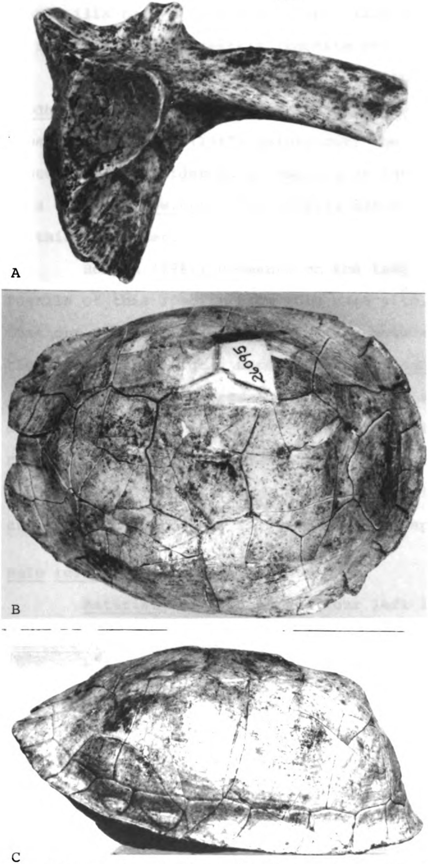
Remarks--All six fossil ilia are much larger than ilia of *Bufo quercicus* Holbrook, and they lack the characteristic ilial protuberance of that species. However, the

Figure 7. Ladds amphibian and reptile fossils.

A. Fossil *Bufo americanus* ilium, x 3.7.

B. Fossil *Terrapene carolina* carapace, dorsal, x 0.6.

C. Fossil *Terrapene carolina* carapace, lateral x 0.6.



A

B

C

Figure 7. Ladds amphibian and reptile fossils.

fossil ilia have a better developed ilia protuberance than is found in Bufo terrestris (Bonnaterre).

The fossils are difficult to separate from Bufo woodhousei fowleri (Hinckley) and Bufo americanus. However, as Holman (1967) points out, the base of the ilial protuberance is wider in B. americanus than in equal sized ilia of B. w. fowleri. The fossils agree with B. americanus in this character.

Holman (1967) comments on the large size of the fossils of this species from this same site. He points out that one of the fossils represent a specimen that exceeds the size of the largest recorded B. americanus. Two of the ilia examined in the present study of the Ladd's site match or slightly exceed the size of the large ilium examined by Holman. However, except for their large size, these ilia do not appear to differ from B. americanus in any respect, and therefore cannot be assigned to a new species.

Bufo terrestris (Bonnaterre)

Material--Five right and four left ilia, USNM 209179.

Remarks--The ilia of Bufo terrestris are easily separated from Bufo american, B. quercicus Holbrook, and B. w. fowleri. B. terrestris has a low ilial prominence with a wide base. The other three species of Bufo have higher, narrower based ilial prominences.

This is the first record of this species from the Ladds site.

Class Reptilia

Order Testudines

Family Emydidae

Clemmys insculpta (Le Conte)

Material--One right epiplastron, USNM 209180.

Remarks--The epiplastron of *Clemmys insculpta* is distinct from other North American emydid turtles. Besides being characteristically narrow and thick, it has a characteristic deep gutter next to the gular lamina (Holman, 1967).

Terrapene carolina (Linnaeus)

Material--Two right and one left femora, a fusion consisting of a partial proneural, several partial peripherals, and one partial pleural, USNM 209181; one nearly complete carapace, USNM 26095, figures 7b, 7c.

Remarks--Holman (1967) separates *Terrapene* femora from other North American emydid turtles by their stouter, more bowed appearance. The fossil femora are similar in those characters to living *Terrapene carolina* from which I am unable to separate them. The fossil consisting of the fused anterior carapacial elements cannot be separated from *Terrapene carolina*, either. Therefore it is referred to that species.

Of considerable interest is the nearly complete carapace of T. carolina. Only a small portion of the proneural bone is missing from this fossil. Today, northern Georgia is inhabited by T. carolina carolina, but the Ladds site is only several hundred miles removed from the range of T. c. bauri Taylor, T. c. major (Agassiz) and T. C. triunguis (Agassiz). Of these subspecies, the fossil most closely resembles T. c. carolina and T. c. triunguis. The fossil lacks the characteristic hump behind the third vertebral scute of triunguis and it does not show the high degree of vaulting often found in triunguis. However, both these characters may be lacking in triunguis and thus the fossil cannot be referred to T. c. carolina with assurance. I prefer to refer to it as Terrapene carolina, subspecies indeterminate.

Chrysemys picta (Schneider)

Material--One left epiplastron, USNM 209182.

Remarks--The epiplastron of Chrysemys picta is easily distinguished from other North American emydid turtles. It differs from Clemmys species in being broader and thinner. It is broader than Deirochelys reticularia. It differs from Emydoidea in having a well developed, laterally directed process immediately anterior to the gular lamina. In C. picta the gular and abdominal scutes cover a large portion of the dorsal surface of the epiplastron, and produce a wide flat border on it. This wide, flat border is lacking in Malaclemmys, Graptemys species, and Pseudemys species. The fossil epiplastron possesses this character and is hence referred to C. picta.

Pseudemys, sp. indet.

Material--One right partial hypoplastron USNM 209183.

Remarks--This large fossil hypoplastron has the general conformations of a large Pseudemys, but because of its fragmentary nature I am unable to carry the identification to the species level.

Holman (1967) described a large fossil proneural from this site. He provisionally referred the specimen to Pseudemys concinna (Le Conte) and made note of its large size. He estimated that the fossil proneural represented a turtle with a carapace length of at least fourteen inches.

The fossil hypoplastron is five inches long (127 .0 mm). A turtle of the Pseudemys group would have a corresponding carapace length of at least sixteen inches. Conant (1958) records only P. concinna, P. floridana, and P. rubriventris as approaching or exceeding this size.

Order Squamata

Family Colubridae

Diadophis punctatus (Linnaeus)

Material--Twelve precaudal vertebrae, USNM 209184.

Remarks--Holman (1967) remarks on characters which separate Diadophis punctatus from Carphophis amoenus

(Say). *D. punctatus* is characterized as having a neural spine which is thicker, higher, and with more of a posterior overhang than *C. amoenus*. The fossils resemble *D. punctatus* in these characters.

Carphophis amoenus (Say)

Material--Four precaudal vertebrae, USNM 209185.

Remarks--These vertebrae were distinguished from *Diadophis punctatus* using the criteria cited under that species.

Coluber or *Masticophis*

Material--Ten precaudal vertebrae, USNM 209186.

Remarks--The vertebrae probably should be assigned to *Coluber constrictor* Linnaeus or *Masticophis flagellum* (Shaw), but I am unable to distinguish between the vertebrae of these two species.

Elaphe, sp. indet.

Material--Eight precaudal vertebrae, USNM 209187.

Remarks--Holman (1965) notes that the vertebral neural spines of *Elaphe vulpina* (Baird and Girard) are lower than those of *Elaphe guttata* (Linnaeus) and *Elaphe obsoleta* (Say). The fossil vertebrae have high neural spines and thus represent one of the latter two species. I am unable to separate the vertebrae of those two species.

Lampropeltis getulus (Linnaeus)

Material--Sixteen precaudal vertebrae, USNM 209188.

Remarks--Auffenberg (1963b) and Holman (1965) have discussed the vertebral characters of *Lampropeltis*. Because of their high neural spines, the fossil vertebrae are assigned to *L. getulus*.

Lampropeltis triangulum (Lacepede)

Material--One hundred seven precaudal vertebrae, USNM 209189.

Remarks--These *Lampropeltis* fossils possess low neural spines and are assigned to *L. triangulum*. Many of the fossils represent a large individual or individuals, possibly the northern subspecies *L. t. triangulum*.

Natrix sipedon (Linnaeus)

Material--Seven precaudal vertebrae, USNM 209190.

Remarks--*Natrix* vertebrae are most easily confused with *Thamnophis* vertebrae. *Natrix* vertebrae are proportionately wider than *Thamnophis* vertebrae of equal width. In addition, most *Natrix* vertebrae possess a proportionately higher neural spine. The fossil vertebrae resemble *Natrix* in both characters. The fossil vertebrae are referred to *N. sipedon* since they possess neural spines which are longer than high. This is characteristic of *N. sipedon*. Other *Natrix* species of the southeastern United States [*N. cyclopion floridana* Goff, *N. erythrogaster* Forster, *N. fasciata* Cope, *N. rhombifera* (Hallowell), and *N.*

taxispilota Holbrook] have neural spines which are higher than long (Holman, 1967).

Storeria dekayi (Holbrook)

Material--One precaudal vertebra, USNM 209191.

Remarks--The precaudal vertebrae of the small natricines are difficult to identify. Auffenberg (1963b) points out that Storeria differs from Seminatrix in having a longer centrum. He separates Storeria from Haldea by the ratio of the neural spine length to the zygosphene width, Storeria showing a ratio greater than 1.21 and Haldea showing a ratio less than 1.21. The fossil has a value of 1.25 for this ratio, placing it in the genus Storeria. For the two species of Storeria, Auffenberg lists the neural spine length to zygosphene width ratio as 1.23 to 1.36 for S. dekayi and 1.60 to 1.64 for S. occipitomaculta. This would place the fossil in the dekayi group. However, the ratios quoted are for middle precaudal vertebrae only. If ratios on all precaudal vertebrae are tabulated there is considerable overlap of values. Thus the correct identification of the vertebrae rests in the ability to distinguish the middle precaudal vertebrae in disarticulated skeletons. The fossil vertebra appears to be a middle precaudal vertebra, and is therefore identified as S. dekayi.

Thamnophis sirtalis (Linnaeus)

Material--Six precaudal vertebrae, USNM 209192.

Remarks--*Thamnophis* can be separated from the other moderate sized natricines of North America by their long, narrow, vertebral centra (Auffenberg, 1963). Holman (1962b) separates *T. sirtalis* from *T. sauritus* (Linneaus) using the angle made by the prezygopophyseal processes and the longitudinal axis of the centrum. Unfortunately, these processes are missing in the Ladds fossils. Examination of recent skeletons of ten *T. sirtalis* and eight *T. sauritus* indicates that the neural spine of *T. sauritus* is lower and longer than that of *T. sirtalis*. On that basis the fossils were identified as *T. sirtalis*

Family Viperidae

Crotalus horridus Linneaus

Material--Sixty-nine precaudal vertebrae, USNM 209193.

Remarks--Holman (1967) detailed how *Crotalus horridus* vertebrae may be distinguished from *Crotalus adamanteus* Beauvois, *Agkistrodon contortrix* (Linneaus), and *Agkistrodon piscivorus* (Lacepede). The fossil vertebrae conform to his diagnosis of *C. horridus* in having low neural spines and shallow pits on either side of the cotyle.

DISCUSSION

The Herpetofauna

The present study adds *Bufo terrestris*, *Chrysemys picta*, and *Storeria dekayi* to the known Pleistocene herpetofauna of the Ladds site. The total herpetofauna now consists of at least twenty-six species.

Species not found in this sample, but previously reported by Holman (1967), are *Desmognathus* or *Leurognathus*, *Gyrinophilus* sp. indet., *Pseudotriton ruber* (Sonnini), *Hyla crucifer* Wied, *Anolis carolinensis* Voigt, *Sceloporus undulatus* (Latreille), and *Heterodon platyrhinos* Latreille.

Paleoecology

The members of the herpetofauna indicate that a moist woodland habitat was present near the deposition site. *Desmognathus*, *Gyrinophilus*, and *Pseudotriton* species are usually associated with a clear woodland stream or brook (Conant, 1958). The other members of the herpetofauna could all be found in a moist deciduous forest which contained or bordered an open, brushy area. The presence of *Pseudemys concinna* and *Clemmys insculpta* suggests the forest also contained a large pond or a large body of running water. Such habitats can be found in the Ladds area today.

Zoogeography and Pleistocene Climate

With the exception of *Clemmys insculpta* and *Bufo terrestris* all the species of the Ladds fossil herpetofauna can be found living in or near the area today. At present, the range of *C. insculpta* extends no further south than northernmost Virginia. *B. terrestris* is found no further north than mid-Georgia, approximately one hundred miles south of the Ladds site. These distributions are shown in figure 8.

Ray (1965), and Lipps and Ray (1967) point out that there is every opportunity for fossil mixing at the Ladds site. Ray (1967) and Holman (1967) indicate that the occurrence of northern species and southern species in the same deposit may be indicative of faunal mixing. However, both acknowledge the possibility that the assemblage could represent a unit fauna.

Even interpreted as a unit fauna, little climatic significance can be credited to the sympatric occurrence of *C. insculpta* and *B. terrestris*. The manner in which Pleistocene variations in precipitation and temperature may have affected distributional patterns of various organisms is poorly known. Not until the physiological and ecological tolerances of the critical species are known better, can definitive faunal-based interpretations of the paleoclimate be made.

Figure 8. Range limits of Clemmys insculpta and Bufo terrestris.

-·-·- Northern limits of B. terrestris
----- Southern limits of C. insculpta

SUMMARY

Three species have been added to the faunal list of reptiles and amphibians found at the Ladds, Georgia site. The total recorded herpetofauna now stands at twenty-six species.

The species represented by the fossils found at the Ladds site suggest that a moist deciduous forest was present when the fossils were deposited.

The herpetofauna gives little indication that the paleoclimatic conditions were much different from the climatic conditions that prevail in the area today.

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