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QUATERNARY DISTRIBUTION OF THE TIMBER RATTLESNAKE (*Crotalus horridus*) IN SOUTHERN INDIANA

Ronald L. Richards
Indiana State Museum, Department of Natural Resources,
202 North Alabama Street, Indianapolis, IN 46204

ABSTRACT: The timber rattlesnake (*Crotalus horridus*) is most frequently reported from Brown, Monroe, and Morgan counties, with fewer reports from other south-central counties, and only two records from southeastern Indiana. Skeletal remains of the timber rattlesnake have recently been recovered from thirty-two caves in Decatur, Greene, Harrison, Jennings, Lawrence, Monroe, Owen, Shelby, and Washington counties, a Harrison county Indian midden, and an alluvial deposit in Daviess county. Although the timber rattlesnake may always have had a spotty distribution in Indiana, the skeletal remains firmly establish its former presence in extreme southern and parts of southeastern Indiana. The Decatur and Shelby county cave remains are north of the range previously suspected for the species. Distribution of *C. horridus* in Indiana appears to be limited more by the availability of dry, hill country, preferably cloaked in oak-hickory forest, than by climatic factors.

INTRODUCTION

The timber rattlesnake (*Crotalus horridus*) has been reported only south of the Wisconsinan glacial boundary in Indiana, particularly in hills of the Norman and Crawford Uplands in the south-central section (Minton, 1972). Previous records include Clark, Jackson, Lawrence, Martin, and Orange Counties, and more recently Harrison and Perry counties, but the timber rattlesnake has always been reported regularly from Brown, Monroe, and Morgan counties (Minton, 1972; Minton, *et al.*, 1983; Figure 1). Allyn (1937) knew of approximately twenty-five specimens that were collected from Brown county and vicinity between 1931 and 1936. There are four unconfirmed records from Clay, Dearborn/Ripley, Franklin, and Posey counties, each extra-limital to the distribution based upon actual specimens (Minton, 1972). The timber rattlesnake appears to have a spotty distribution in Indiana, finding optimum habitat on high, dry ridges cloaked in oak-hickory forest with occasional open areas (Minton, 1972). They are said to show no preference for cliffs, ledges, or massive outcrops, and are rarely reported from the lowlands (Minton, 1972).

Crotalus horridus fossils have been recovered from Kansan-aged deposits (ca. 600,000 B.P.) at Cumberland Cave, Maryland, and Trout Cave, West Virginia (Holman, 1977; Holman, 1982). More recent Rancholabrean fossils are known from Arkansas, Georgia, Missouri, Pennsylvania, Tennessee, and Virginia (Holman, 1981; Lundelius, *et al.*, 1983). Studies of Quaternary snake fossils from Indiana, however, are few. Unidentified snake bones were first noted among the debris of a woodrat (*Neotoma floridana*) den in Sullivan Cave, Lawrence county, (Bader, and Hall, 1960) and snake remains (presently identified as *C. horridus*) were later listed from a Monroe county cave (Richards, 1970). Snake remains that were associated with woodrat bones were identified to family level, recording colubrids from eight, natricines from one, and crotalids from six south-central Indiana cave deposits (Richards, 1972). The smooth

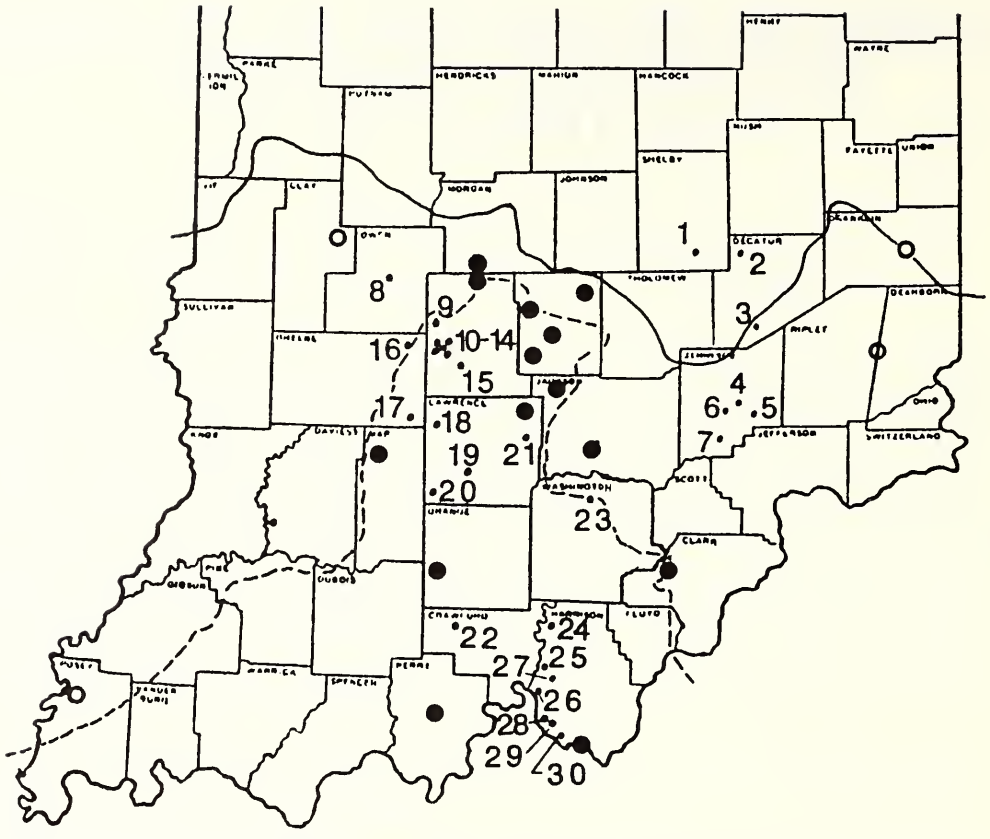

Figure 1. Modern and fossil occurrence of the timber rattlesnake (*Crotalus horridus*) in Indiana. Modern occurrences: Solid circles, confimed occurrences (after Minton, 1972, and Minton, *et al.*, 1983); hollow circles, unconfirmed records (after Minton, 1972). Fossil and sub-recent localities numbered as in Table 1. Solid line, southern limit of Wisconsinan glaciation. Dashed line, southern limit of glacial deposits.

green snake (*Opheodrys vernalis*) was recorded extralimitally from late Pleistocene deposits in Anderson Pit Cave, Monroe county (Holman, and Richards, 1981). Extralimital remains of *Crotalus horridus* were noted from Flat Rock and Dead Man's Caves in conjunction with a second survey of fossil woodrat remains (Richards, 1987). An extensive late Pleistocene and Holocene herpetofauna (Prairie Creek Site, Daviess county) that includes remains of *C. horridus* and other snakes is presently under study (Holman, and Richards, in prep.).

Because the author had recovered viperid vertebrae from numerous cave deposits, including several sites in Harrison County where the timber rattlesnake was at the time unrecorded (pers. comm., Sherman Minton, July 1979), as well as from deposits in two caves north of the suspected range, a study of Indiana's viperid remains seemed timely. A recent inquiry by Dennis Brown, Hoosier Herpetological Society, about the distribution of *Crotalus horridus* fossils in Indiana has prompted the present treatment.

METHODS

Caves had been routinely sampled throughout south-central and southeastern Indiana, with special emphasis more recently placed on caves in the peripheries of both karst areas, in conjunction with the survey of woodrat fossils in the state (Richards, 1987). Snake remains had been gathered where they lay exposed on cave floors or on ledges, but the majority were collected over the years as part of entire faunal samples recovered by the washing of cave sediments through fine-meshed (ca. 1.2 mm) hardware cloth.

Identification was based upon characters of the abundantly recovered trunk vertebrae, as well as of the less commonly preserved cranial elements. Viperid vertebrae are readily recognized by their short length, long, straight, thick ventral hypapophyses, large condyles, and short accessory processes (Auffenberg, 1963; Meylan, 1982; Figure 1). Trunk vertebrae of *Crotalus* (rattlesnakes) and *Agkistrodon* (copperheads and cottonmouths) are very similar, but Holman (1963) noted that those of *Agkistrodon* usually have a distinct pit with one moderately large fossa on either side of the cotyle. Trunk vertebrae of *Crotalus* usually lack those pits, and the one or more fossae that occur are minute. Holman later noted that the pits are *more deeply* excavated in *Agkistrodon* than in *Crotalus* (Holman, 1965). Meylan (1982) suggested that Holman's characters were reliable only for one-third of the mid-body trunk vertebrae, as the anterior and posterior trunk vertebrae of two *Crotalus* reference columns displayed pitting, and one column contained a single large fossa in each pit throughout the series. Meylan relied upon discriminant analysis of the ratios of vertebral measurements. Trunk vertebrae of *Sistrurus* (massasaugas and pygmy rattlesnakes) are recognized by the presence of a small prominence just anterior to the neural spine (Holman, 1964) and by having prezygapophyses which tilt upward to a greater degree than in *Crotalus* or *Agkistrodon* (Holman, 1965). *Crotalus horridus* trunk vertebrae can be distinguished from those of other eastern and southern North American rattlesnakes (*Crotalus adamanteus*, eastern diamondback rattlesnake, and *Crotalus atrox*, western diamondback rattlesnake) by the much lower neural spine of *C. horridus* (Holman, 1982). Cranial elements reported to be diagnostic for *C. horridus* include the maxilla (Holman, 1959), articular (= compound = mandible) (Holman, 1967), dentary (Holman, 1967), and pterygoids, among other elements (Brattstrom, 1964). Terminal caudal vertebrae of rattlesnakes in general are coalesced into a solid shaker, or style (Klauber, 1956) that are occasionally recovered in fossil deposits.

Faunas from Megenity Peccary Cave and Fair-to-Middl'in Well are deposited at the Indiana State Museum, (INSM). Materials from Prairie Creek are on file at the Glenn A. Black Laboratory of Archaeology, Indiana University Bloomington. Other rattlesnake remains, largely from undescribed faunas, are on file with the author.

RESULTS

Crotalus horridus remains were identified from eleven south-central and southeastern Indiana counties, including 32 caves, one Indian midden, and an alluvial deposit (Table 1; Figures 1 and 2). Some of the cave remains occurred as a disarticulated mingle or as scattered bones of a single individual within the entrance area, or 15 or so meters within the cave (e.g., Hendershot cave, Wayne cave, and an unnamed Lawrence county cave); this suggested that some of the rattlesnakes once crawled to position inside the cave. Other deposits beyond the twilight zone occasionally produced commingled remains of a large number of snakes that included more delicate cranial elements (e.g., Dead Man's, Flat Rock, and Henchman caves); this suggested that crevices, fissures and other cover within those caves were repeatedly used in denning. Many isolated vertebrae had been rodent gnawed and dispersed to various loci (often ledges) in the caves (e.g., Brinegar, and Sullivan caves), indicating the activities (or former activities) of woodrats. Remains also occurred in sedimentary deposits where bone had accumulated through carnivore scat, pitfall entrapment, and/or other processes.

Notably, timber rattlesnake remains were recovered from Crawford, Daviess, Decatur, Greene, Jennings, Owen, Shelby and Washington counties where the species had

Table 1. Quaternary localities, occurrence, and remains of *Crotalus horridus* in southern Indiana.

Cave / Site	Quadrangle	County	Occurrence[1]	Materials[2]
1. Flat Rock Cave	Waldron	Shelby	D	Five areas in cave: basioccipital; L dentary; R frontal; L prefrontal; 2L pterygoids; 114 trunk vertebrae (incl. 3 juvenile vertebrae).
2. Dead Man's Cave	Adams	Decatur	D	Three areas: 7 basioccipitals; 2 basisphenoids; 4L, 6R compounds; 11L, 8R dentaries; 5L, 5R ectopterygoids; 2L, 4R exoccipitals; 1L, 6R frontals; 6L, 8R maxillae; 2 parietals; 8L, 11R prefrontals; 3L, 4R pro-otics; 7L, 3R pterygoids; 6L, 6R squamosals; 6 styles; 676 vertebrae (incl. 46 small/juvenile).
3. Faultz Cave	Westport	Decatur	S	3 trunk vertebrae (incl. 1 juvenile).
4. Muscatatuck Caverns	Butlerville	Jennings	S	Two areas: R prefrontal; R pterygoid (viperidae cf. *C. horridus*); L squamosal; 2 trunk vertebrae.
5. Henchman Cave	Vernon	Jennings	D	Five areas: R dentary; L maxilla; L prefrontal; 261 trunk vertebrae (incl. 3 juvenile).
6. Crawl Cave	Vernon	Jennings	S	L compound; L squamosal; 4 trunk vertebrae (incl. 1 juvenile).
7. Biehle Cave	Vernon	Jennings	S,W	Three areas: 7 trunk vertebrae
8. Jesse Tate Cave	Deputy	Jennings	W	1 trunk vertebra
9. Hendershot Cave	Spencer	Owen	L,S	Two areas: 6 trunk vertebrae
10. Hidden Pit Cave	Whitehall	Owen	S	2 juvenile trunk vertebrae; viperidae cf. *C. horridus* (juvenile): 3 cervical, 3 trunk vertebrae.
11. Freeman Pit	Whitehall	Monroe	S	Three areas: L compound; 1 cervical, 128 trunk, 5 caudal vertebrae; viperidae cf. *C. horridus* (juvenile): R compound; 1 trunk vertebra.
12. Wayne Cave	Whitehall	Monroe	L	88 trunk, 4 caudal vertebrae; style
13. Thundermug Cave	Whitehall	Monroe	W	1 trunk vertebra
14. Brinegar Cave	Stanford	Monroe	W	1 trunk vertebra
15. Showcase Pit Cave	Standford	Monroe	S	5 trunk vertebrae (incl. 3 juvenile)
16. Bee Tree Cave	Stanford	Monroe	S	Two areas: basisphenoid; parietal; 10 trunk vertebrae; viperidae cf. *C. horridus*: 1 adult, 24 juvenile trunk vertebrae.

17. Anderson Pit Cave	Clear Creek	Monroe	S	Three areas: 24 trunk vertebrae
18. Mill Cave	Stanford	Greene	S	3 trunk vertebrae
19. Batey Cave	Owensburg	Greene	S	1 cervical, 1 trunk vertebrae.
20. Sullivan Cave	Owensburg	Lawrence	S,W	Two areas: L compound; supraoccipital (juvenile); 97 trunk vertebrae (incl. 15 juvenile); viperidae cf. *C. horridus*: 2 trunk vertebrae.
21. Carcass Crypt Pit Cave	Bedford West	Lawrence	S	1 trunk vertebra
22. Connelly Cave	Huron	Lawrence	S	1 trunk vertebra
23. Cave, name unknown	Norman	Lawrence	L	51 trunk, 6 caudal vertebrae; style
24. Megenity Peccary Cave	Taswell	Crawford	S,W	Under study: numerous vertebrae in several rooms at different stratigraphic levels.
25. Suicide Cave	Kossuth	Washington	S	2 trunk vertebrae; viperidae cf. *C. horridus* (juvenile): 10 trunk vertebrae.
26. Waterfall Cave	Smedley	Washington	S	1 juvenile trunk vertebra
27. King Leo Pit Cave	DePauw	Harrison	S	17 trunk vertebrae
28. Devils Staircase Pit Cave	Leavenworth	Harrison	S	1 trunk vertebra
29. Passenger Pigeon Cave	Leavenworth	Harrison	L,S	Two areas: L compound; L maxilla; 4 cervical, 194 trunk (incl. 14 juvenile), 1 caudal vertebrae.
30. Parker Pit Cave	Corydon West	Harrison	S	1 trunk vertebra
31. N. Jim Cave	Mauckport	Harrison	S	L compound; L,R dentaries; L frontal; R maxilla; L,R palatines; L prefrontal; R pro-otic; L squamosal; 11 trunk vertebrae (incl. 5 juvenile); viperidae cf. *C. horridus*: supraoccipital.
32. Fair-to-Middl'in Well Pit	Mauckport	Harrison	S	L maxilla; 37 trunk vertebrae (incl. 33 small and juvenile).
33. Indian Midden	Mauckport	Harrison	S	1 trunk vertebra
34. Prairie Creek Site	Washington	Daviess	S	2 trunk vertebrae

1, Predominant occurrence of bones: L: Living snake apparently once crawled to position in an entrance area of cave (much of a solitary skeleton). D, probable den site (as in L, but with multiple skeletons sometimes deeper in cave). W, bone apparently transported by woodrat. S, sedimentary deposits accumulated by pitfall trapping, carnivore refuse, and other means (including L and W).

2, Many of the remains are fragments of the elements listed.

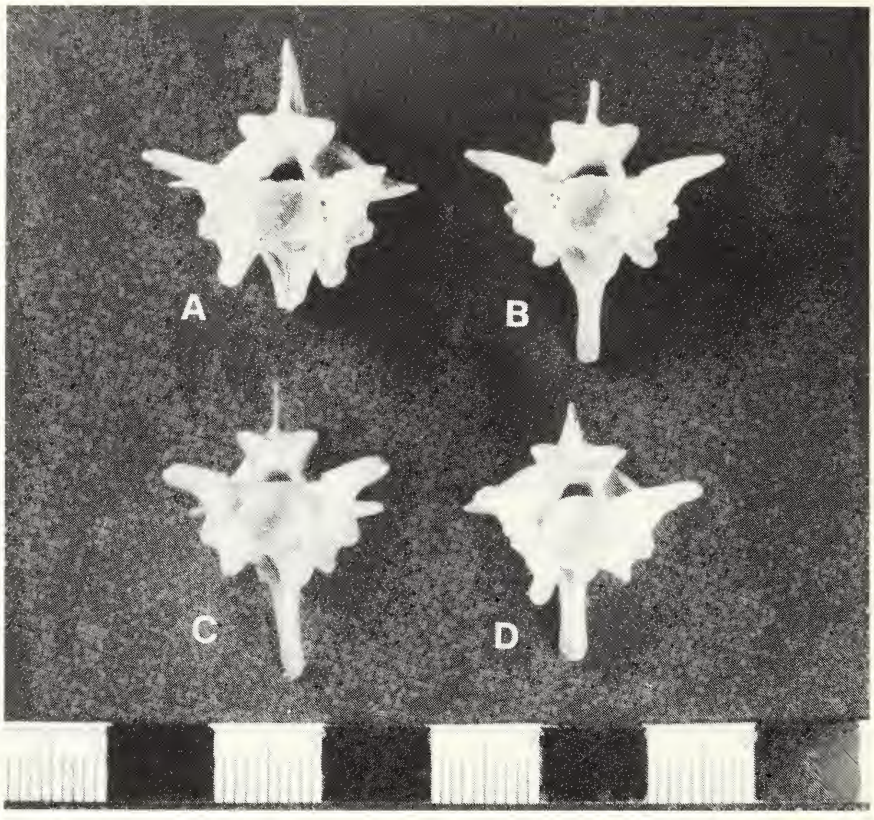

Figure 2. Trunk vertebrae of large Indiana specimens of the timber rattlesnake, *Crotalus horridus*. A,B: Flat Rock Cave, Shelby County; C, modern comparative specimen, Brown County, 5+ 8″ (1727 mm) total length; D, Dead Man's Cave, Decatur County. Scale in millimeters.

not previously been recorded. The Flat Rock Cave (Shelby county) and Dead Man's Cave (Decatur county) localities are north of the range previously suspected for the species.

Identifications were facilitated with comparative skeletal material (*Crotalus h. horridus*, 2; *C. h. atricaudatus*, 3; *Agkistrodon contortrix mokeson*, 3; *A. c. laticinctus*, 2; *Agkistrodon p. piscivorus*, 2) using many of the characters noted above. Fossil cranial elements proved to be relatively distinct, but the separation of *Crotalus* and *Agkistrodon* vertebrae required some experience and judgement. Interestingly, the anterior edge of the ventral hypapophysis was found to be more rounded, and its base less projected from the centrum (except in the cervical region) in *Crotalus* than in *Agkistrodon*, which has a sharper margin and a narrower, more projected base. The distinct pits on either side of the cotyle noted by Holman (1963, 1965) were better developed in comparative materials of *Agkistrodon piscivorus* than in *A. contortrix*, and weakly developed in adult *Crotalus horridus*. As noted by Holman (1963) the foramina in these pits were usually multiple and of small size in *Crotalus* and typically singular and of larger size in *Agkistrodon*. *Crotalus*, however, frequently posessed singular, large foramina in vertebrae of the cervical and posterior trunk and caudal region, but most of the posterior trunk vertebrae could be better identified by characters of the ventral hypapophysis. Juvenile vertebrae of *Crotalus* tended to have much deeper pits on either side of the cotyle than adults, but the multiple foramina were usually quite distinct. Juvenile vertebrae of *Agkistrodon* tended to have more rounded anterior edges on the ventral hypapophyses than adults, but there was usually a singular, relatively large foramen. Fossil vertebrae were identified using a cluster of the above (and previously stated) characters in the following sequence: 1. character of the anterior edge and base of the ventral

hypapophysis, 2. size and number of foramina, 3. nature of pitting, 4. presence of a spur anterior to the base of the neural spine (*Sistrurus*), 5. height of the neural spine, 6. presence of epizygapophyseal spines (frequently occurring in *Agkistrodon*; Auffenberg, 1963), and other more subtile characters not presented. Not all vertebrae of the two genera could be separated, but those of *Crotalus* posessed more distinctive features (including larger size) than those of *Agkistrodon*, in which many trunk vertebrae were similar to posterior cervical vertebrae of *Crotalus*.

Because of the recent discovery of isolated populations of the cottonmouth (*Agkistrodon piscivorus*) in south-central Indiana (Forsyth, *et al.*, 1985), particular alert was given for the possibility of its presence among the recovered fossils, but nothing attributable could be recognized.

DISCUSSION

Cave remains firmly document the former presence of *Crotalus horridus* in several Indiana counties where it was previously unknown, including those in southeastern parts of the state. Fossil remains are not readily available from Brown or Morgan counties where (including Monroe county) the rattlesnake is most commonly encountered today, because of the absence of caves suitable for faunal accumulation. Clearly, the cave remains document only that portion of rattlesnake range that occurs in cavernous regions, rather than the full extent of its distribution.

Dead Man's Cave at the southeast corner of Saint Paul, Decatur county, is particularily interesting as it appears to have served as a rattlesnake den over a long period of time. The remains of no less than ten rattlesnakes, two copperheads, one racer (*Coluber constrictor*), a milk snake (*Lampropeltis triangulum*), and a northern water snake (*Nerodia* cf. *N. sipedon*) were comingled in a crevice 1.2 m above the relatively horizontal cave floor approximately 17 m inside the cave. Both juvenile and adult rattlesnakes were present. Other rattlesnake remains were found in the cave. The cave entrance is south-southwest facing, along a ca. 8 m high rocky bluff outcropping ca. 4 m above and 14 m away from the bank of Flatrock River. This confirms reports that rattlesnakes were once in the area around Saint Paul (pers. comm., Sherman Minton, November 1989). Flat Rock Cave (Shelby county) and Henchman Cave (Jennings county), appear also to have once served as dens. These caves similarly contained numerous rattlesnake skeletons, have relatively horizonal passages, southern or southeastern entrance exposures, and occur at the bases of rocky bluffs in the dry floodplains of streams. Although rattlesnakes are rarely reported from lowlands, it is apparent that they will at least seasonally occupy those habitats when suitable cave or rock outcrops are available for denning. Notably, snake remains record only mortality at the den, rather than the size of the local population.

Mr. James Smith of Shelby county presented a vivid account of his encounter with rattlesnakes (Anonymous, 1887; Chadwick, 1909) that could have applied equally to Decatur or Jennings counties:

> "While en route home from Edinburg in the summer of 1834, near the present site of the Baptist Church, in the Scott neighborhood, my attention was attracted by a noise in the leaves near the roadside. I stopped suddenly, and soon discovered that it was a combat for life between a rattlesnake and a black snake. Drawing near, the black snake became frightened at my presence, and quickly disappeared in the brush. The rattlesnake after a few seconds of apparent rest

> crawled slowly away to the base of a small cliff near the creek bank. Following but a few paces behind, and as I came near the cliff, I discovered what appeared to me at first sight to be hundreds of those venomous reptiles. I immediately repaired to the nearest house, and with the father, sons and dogs, we returned to the spot armed with various implements of warfare, where we killed many rattlesnakes of all ages and sizes''.

Klauber (1956) noted that where available *C. horridus* selects a rocky den with a southern exposure for hibernation. He related that where suitable den sites are widely separated, populations at individual sites tend to run larger. Den populations in western Pennsylvania have been estimated to vary from 20 to 200 rattlesnakes, though much larger populations have been reported. Both rattlesnakes and copperheads den together in Pennsylvania and Virginia, and black rat snakes, king snakes, milk snakes, black racers, and garter snakes have been noted in rattlesnake denning areas (Klauber, 1956).

Crotalus horridus is distributed into such northerly latitudes as southeastern Minnesota, southwestern Wisconsin, and northeastern Iowa, and ranges into New York, southern Vermont, and southern New Hampshire (Conant, 1975), regions with precipitation similar to, but winters longer and cooler than those of, Indiana (Visher, 1945). Yet *C. horridus* is restricted to the hill country south, or just north of the Wisconsinan glacial boundary in southern Indiana. It occurs most abundantly (9 of Minton's 14 specimen records) in the Brown County Hills natural region Section (10B) (Homoya, *et al.*, 1985) where the Norman Upland is cloaked in the presently quite variable oak-hickory forest (Petty, and Jackson, 1966; Schneider, 1966). The Crawford Upland Section (9A), also generally in oak-hickory forest, produced three of Minton's remaining five, and the newer Perry county records. Oak-hickory associations in the less dissected lowlands of southwestern Indiana (Southwestern Lowlands Natural Region), however, have generated only one unconfirmed record of the timber rattlesnake. The Knobstone Escarpment (10C) and Shawnee Hills Escarpment (9B), in oak-hickory and western mesophytic forest associations, repectively, have contributed the remaining two, and the newer Harrison County (9B) records. The present distribution of *Crotalus horridus* in Indiana certainly appears to be limited more by the availability of some oak-hickory forest association in combination with hill country, rather than by climatic factors. Accordingly, the Knobstone Escarpment Section (1OC) and Switzerland Hills Section (11C) would appear at one time to have provided suitable *C. horridus* habitat.

Quaternary-aged rattlesnake remains were most abundantly preserved in the Shawnee Hills Escarpment Section (9B) (Chester Escarpment) and occasionally on the Crawford Upland Section (9A) where cave development is most notable. Interestingly, rattlesnake remains have been recovered from caves in Decatur, Jennings, and Shelby counties where topographical relief is low and beech-maple is today the predominant forest. Rattlesnakes were apparently able to colonize this marginal habitat because of the availability of rocky bluffs dissected along river valleys.

The dynamics of floral and faunal reorganization during the late Pleistocene produced unique associations of relatively temperate-zoned reptiles and amphibians that coexisted with both temperate-zoned and more boreal mammals (Graham, 1976; Graham, 1985; Graham, and Mead, 1987; Holman, and Richards, in prep.; Lundelius, *et al.*, 1983). This suggests that herptile distributions in general have remained relatively ''inert'' when populations were not directly displaced by glacial ice (Fay, 1984a, 1984b, 1986a, 1986b; Holman, 1986). Several *Crotalus horridus* vertebrae were recovered from deposits associated with, and occuring below, two commingled flat-headed peccary

(*Platygonus compressus*) skeletons in Megenity Peccary Cave, Crawford County. Peccary bone collagen produced a radiocarbon date of Wisconsinan age (30,880 ± 500 B.P.) (Richards, 1989). Two other radiocarbon dates associated with *C. horridus* in Indiana are of late Holocene age (Freemans Pit, Monroe County, 2,315 ± 65 B.P.; Prairie Creek Site, Daviess County, 3,180 ± 100 B.P.) (Holman, and Richards, in prep.; Richards, 1983). Particular herptile species populated or repopulated formerly glaciated areas in central and northern Indiana after the recession of Wisconsinian ice based upon the "individualistic" tolerences of each species (Holman, and Richards, in prep.; King, and Graham, 1981). These tolerance levels allowed the eastern massassauga (*Sistrurus catenatus*) to occupy suitable habitat in central and northern Indiana, while the timber rattlesnake remained relatively inert in its distribution among the surviving dissected uplands of southern Indiana.

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