Additional Records of the Giant Beaver, *Castoroides,* from the Mid-South: Alabama, Tennessee, and South Carolina

Paul W. Parmalee and Russell Wm. Graham

ABSTRACT

Four previously unreported records of *Castoroides* provide supportive evidence that the giant beaver probably occurred throughout the southeastern United States, especially along the middle stretch of the Tennessee River. A distal section of an upper right incisor and an incisor fragment of the extinct Pleistocene giant beaver, *Castoroides*, were recovered from Bell Cave, Colbert County, Alabama. Cave ACb-3, also in Colbert County and containing an extensive deposit of late Pleistocene megafauna, yielded a single incisor enamel fragment. A fragment of a left ilium of this beaver was found in a dry stream bed in Ruby Falls Cave, Lookout Mountain, Hamilton County, Tennessee. These four specimens are referred to *Castoroides* sp.

A relatively complete skull of *Castoroides* has been recovered from the Cooper River, near Strawberry Hill, Charleston County, South Carolina. The cranial characters of this specimen make it referable to *Castoroides leiseyorum* Morgan and White, 1995, which was described from the Irvingtonian Leisey Shell Pit, Hillsborough County, Florida. The taxonomy of *Castoroides* from the southeastern United States is uncertain, and at least two different interpretations are possible.

Introduction

The extinct giant beaver, *Castoroides* Foster, 1838, was the largest rodent known in North America during the Pleistocene, reaching a length of about 2.5 m and a weight between 150 and 200 kg (Kurtén and Anderson, 1980). The animal possessed huge convex incisors that in adult individuals extended 75 to 100 mm beyond the gum line. Longitudinal grooves and ridges on the exterior enamel make even small fragments diagnostic. The rounded and blunt tips of the incisors, along with certain features of the skull and relative proportions of postcranial elements, have led several researchers (e.g., Barbour, 1931; Stirton, 1965) to conclude that *Castoroides,* unlike the modern beaver, *Castor canadensis* Kuhl 1820, would not have been effective at felling trees. Considered to have been an inhabitant of lakes and ponds bordered by swamps, the giant beaver was probably more similar in habits to the muskrat, *Ondatra zibethicus* (Linnaeus, 1766), than to *C. canadensis*. "The teeth were used in cutting off and grinding up the coarse swamp vegetation on which the giant beaver fed" (Kurtén and Anderson, 1980:236).

Cahn (1932) summarized distribution records of the giant beaver, based upon reported specimens by state, known at that time. Nearly 50 years later Kurtén and Anderson (1980) noted that it had been reported from 30 local faunas as well as from hundreds of isolated sites. Although its remains have been found as far north as Alaska and as far south as Florida, and from Nebraska to the East Coast, *Castoroides* apparently occurred most abundantly in the region immediately south of the Great Lakes (Faunmap Working Group, 1994). Relatively abundant remains of *Castoroides* also have been recorded in Florida (Martin, 1969, 1975; Morgan and White, 1995). There are, however, few records of this extinct beaver (Faunmap Working Group, 1994) for the mid-South (~33°N–36°N) east of the Mississippi River. The most recent record of *Castoroides* from Alabama, and apparently the first for the state, is of an incisor fragment from the Bogue Chitto Creek site, a late Pleistocene vertebrate assemblage in the coastal plain west of Selma, Dallas County (McCarroll and Dobie, 1994). A large portion of a right lower jaw with full dentition from Shelby County, Tennessee, was first described by Wyman (1850) and was referred to as the "Memphis specimen" by Cahn (1932:234). Parmalee et al. (1976) reported isolated cheek teeth from two caves in east Tennessee: Baker Bluff Cave (Sullivan County) and an unnamed cave along the Clinch River

Paul W. Parmalee, Frank H. McClung Museum, University of Tennessee, Knoxville, Tennessee 37996. Russell Wm. Graham, Earth Sciences, Denver Museum of Natural History, 2001 Colorado Boulevard, Denver, Colorado 80205.

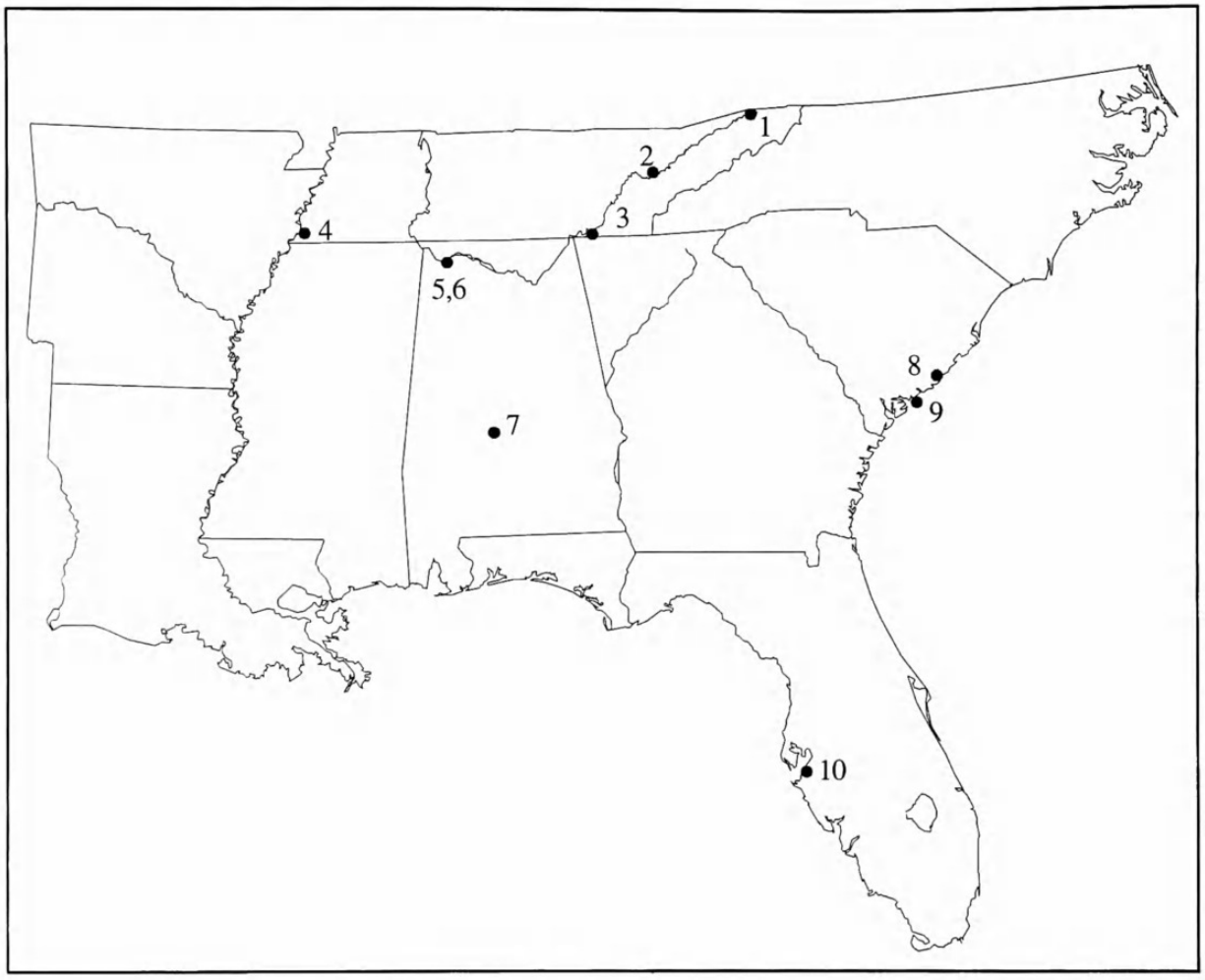

FIGURE 1.—Map showing the location of *Castoroides* localities mentioned in the text: 1=Baker Bluff Cave, Sullivan County, Tennessee; 2=Clinch River Unnamed Cave, Roane County, Tennessee; 3=Ruby Falls Cave, Hamilton County, Tennessee; 4="Memphis specimen," Shelby County, Tennessee; 5=Bell Cave, Colbert County, Alabama; 6=Cave ACb-3, Colbert County, Alabama; 7=Bogue Chitto Creek, Dallas County, Alabama; 8=Strawberry Hill, Charleston County, South Carolina; 9=Edisto Island, Charleston County, South Carolina; 10=Leisey Shell Pit, Hillsborough County, Florida.

(Roane County). *Castoroides* cf. *ohioensis* also has been reported from Edisto Island, a barrier island located 34 km southwest of Charleston, South Carolina (Roth and Laerm, 1980). We herein report four new records for the mid-South region (Figure 1): one from Tennessee (Hamilton County), two from Alabama (Colbert County), and one from South Carolina (Charleston County).

ACKNOWLEDGMENTS.—Special appreciation is extended to Kent Ballew for bringing to our attention bone deposits he discovered in Ruby Falls Cave and for collecting samples for study. We thank Jack Steiner and Ronnie Burk for granting permission to examine the vertebrate material and to publish this record of *Castoroides* from Ruby Falls Cave. Gorden L. Bell and James P. Lamb, directors of the Bell and ACb-3 cave excavations, and Susan Henson, Discovery 2000 (formerly known as Red Mountain Museum), are acknowledged with gratitude for the loan of the giant beaver specimens from these caves and for permission to publish the records. We acknowledge with thanks Patricia P. Adams for assisting with the collection of specimens in Ruby Falls Cave. We appreciate the assistance of Maria Wilson and Malinda Aiello for typing drafts of the manuscript. We thank Jeffrey Saunders for providing access to the *Castoroides* innominate from the Hopwood Farm site. We extend our gratitude to Ruth Holmes Whitehead for bringing to our attention the skull from Strawberry Hill. We also thank James Knight for access to the Strawberry Hill specimen and for permission to describe it. We appreciate the efforts of W. Miles Wright and Marlin Roos for preparation of the photographs. We thank R. Bruce McMillan for his valuable comments on an earlier draft of the manuscript and we appreciate reviews by William Korth and Fred Grady.

Material

During 1991–1993, Kent Ballew from Hixon, Tennessee, was able to investigate several extensive unexplored passage-

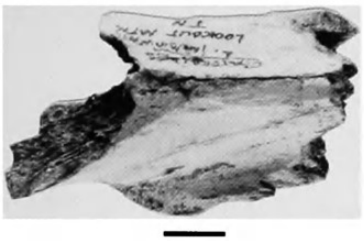

FIGURE 2.—Section of left ilium of *Castoroides* sp. from Ruby Falls Cave, Hamilton County, Tennessee.

ways forming a complex multilevel system of corridors in Ruby Falls, a commercially operated cave in Lookout Mountain, Chattanooga, Hamilton County, Tennessee. This cave, overlooking the Tennessee River, has been inhabited by animals since late Pleistocene times. Many of the more accessible passageways have been greatly modified by human activity in historic times, including mining for saltpeter during the Civil War, and more recently by enlarging and straightening passages to accommodate visitors.

Animal remains occur in many of the passageway floors and streambeds; a varied extant fauna is represented, as well as extinct Pleistocene taxa, such as jaguar (*Panthera onca* (Linnaeus, 1758)) and tapir (*Tapirus* (Brunnich, 1772)). In the fall of 1993, Mr. Ballew recovered a 63.5 mm long section of a left ilium broken just anterior of the acetabulum (Figure 2). It was found lying on the surface of a dry streambed, but the original site of deposition could not be determined. The specimen was compared with a complete *Castoroides* innominate from the Hopwood Farm site, Montgomery County, Illinois (King and Saunders, 1986), housed in the paleontological collections of the Illinois State Museum, Springfield, Illinois. Although slightly smaller and less rugose, the Ruby Falls specimen can be assigned to *Castoroides* with certainty. The size differences in these two specimens may be attributed to sexual dimorphism, ontogenetic development, or geographic variation.

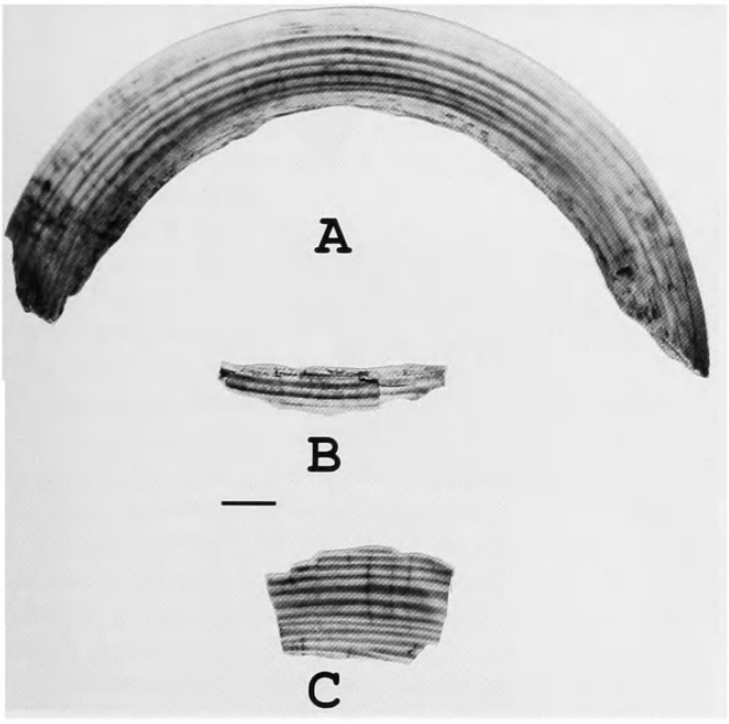

FIGURE 3.—*Castoroides* sp. from Bell Cave, Colbert County, Alabama: A, upper right incisor (RMM 4000); B, incisor fragment (RMM 5547); C, incisor fragment (RMM 6223).

During the summers of 1984 and 1987, paleontologists from the Red Mountain Museum (RMM) dug six excavation units (1 × 1 m) into the floor of Bell Cave, located in the south bluff of the Tennessee River (Tennessee River Mile 248.2 (km 397.1) ~11 km west of Tuscumbia, Colbert County, Alabama). A species-rich vertebrate assemblage was recovered, which included remains of fish, turtles, birds (Parmalee, 1992), and mammals. Many of the extant species, such as fisher (*Martes pennanti* Erxleben, 1777) and caribou (*Rangifer tarandus* (Linnaeus, 1758)) (Churcher et al., 1989), have boreal affinities and no longer occur in the area. In addition to extant mammals, extinct species including tapir (*Tapirus* sp.) and long-nosed peccary (*Mylohyus nasutus* Leidy, 1869) also were represented. Remains of the giant beaver from Bell Cave consisted of a 195.0 mm external section of an upper right incisor (RMM 4000) and a 44.0 × 10.5 mm incisor fragment (RMM 5547) (Figure 3A,B). Radiocarbon dates indicate that the accumulation of vertebrate remains occurred between ca. 25,000 and 11,500 radiocarbon years before present (RCYBP).

Lively et al. (1992) reported Uranium (U)-series dates from travertines associated with a late Pleistocene megafauna recovered in a cave designated as ACb-3 (Colbert County, Alabama). This cave is ~70 m long × 15 m wide and has several huge open rooms. It is situated ~0.5 km west of Little Bear Creek (Tennessee River Mile 249.5 (km 399.2)). ACb-3 was excavated by paleontologists from RMM during the summers of 1985 and 1987. Like Bell Cave, it contained remains of both extant and extinct taxa; included in the latter group were *Tapirus* sp., *M. nasutus,* sabertooth (*Smilodon fatalis* (Leidy, 1868)), beautiful armadillo (*Dasypus bellus* (Simpson, 1930)), and Jefferson's ground sloth (*Megalonyx jeffersonii* (Desmarest, 1822)). Jefferson's ground sloth was represented by a minimum of six individuals, including old adults and infants. *Castoroides* was represented in the assemblage by a single incisor enamel fragment (RMM 6223) measuring 36.5 × 22.0 mm (Figure 3C). According to the U-series dates, ACb-3 "was accumulating small vertebrate remains as early as 228,000 B.P. and was visited by large vertebrates from about 170,000 years to at least 115,000 years B.P. and probably later" (Lively et al., 1992:1).

A skull of *Castoroides* (Figure 4) was recovered by divers from the Cooper River, near Strawberry Hill, Charleston County, South Carolina. It has been reposited under the number SC75.33.1 in the South Carolina State Museum, Columbia, South Carolina. The skull is relatively complete, but both zygomatics (Figure 4A) and both incisors (Figure 4B) have been broken. In addition, the right maxilla and the right palatine bones have been broken just posterior to the alveolus for P4, but the left maxilla is complete with alveoli for the left P4–M3 (Figure 4C). All of the molar and premolar teeth are missing. The left palatine bone is broken and missing. Most of the su-

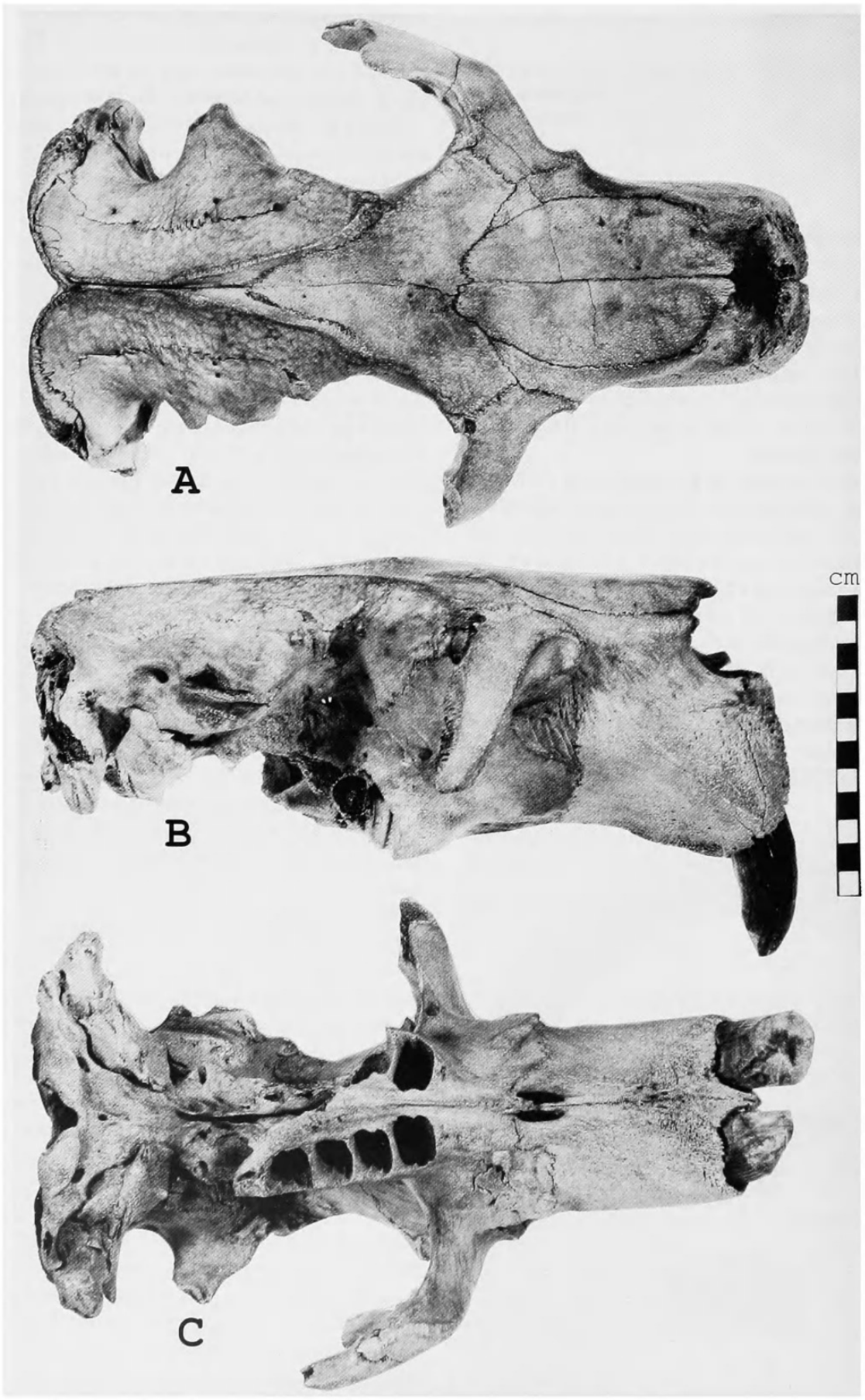

FIGURE 4.—Cranium (SC75.33.1) of *Castoroides leiseyorum* from Cooper River, Strawberry Hill, South Carolina: A, dorsal view; B, right lateral view; C, ventral view.

TABLE 1.—Measurements (in mm) of the cranium (SC75.33.1) of *Castoroides leiseyorum* from Cooper River, Strawberry Hill, South Carolina.

Cranial feature	Unsided	Right side	Left side
1. Greatest length from anterior end of premaxillary to posterior end of occipital condyles	289.4	–	–
2. Basal length from anterior end of premaxillary to inferior notch between occipital condyles	275.2	–	–
3. Greatest length from anterior end of premaxillary to posterior edge of palatine wing of interpterygoid at dorsal choana	238.3	–	–
4. Greatest length from anterior end of premaxillary to anterior edge of incisive foramen	83.5	–	–
5. Greatest length from anterior end of nasals to dorsomedial notch of lamboidal crest	248.6	–	–
6. Greatest length from anterior end of premaxillary to posterior edge of lamboidal crest	–	284.8	283.8
7. Chord from posterior edge of incisor alveolus to anterior edge of P4 alveolus	112.9	–	–
8. Length of alveolar tooth row from anterior edge of P4 alveolus to posterior edge of M3 alveolus	–	67.4	–
9. Length of alveolar molar row from anterior edge of M1 alveolus to posterior edge of M3 alveolus	–	–	49.8
10. Greatest mediolateral diameter of I1 alveolus	–	33.6	33.4
11. Greatest anterodorsal diameter of I1 alveolus	–	31.2	31.8
12. Width from lateral anterior edges of alveoli for P4s	39.6	–	–
13. Greatest width across rostrum from lateral edges of the alveoli for the incisors	74.3	–	–
14. Greatest width of anterior nares at premaxillo-nasal sutures	41.5	–	–
15. Greatest height of anterior nares from nasal suture to premaxillary suture	42.7	–	–
16. Greatest width across rostrum at the maxillo-premaxillary suture at anteroventral edge of the infraorbital foramen	80.9	–	–
17. Least width of postorbital constriction at fronto-parietal sutures	66.1	–	–
18. Greatest width across postorbital processes	85.9	–	–
19. Least width of postzygomatic constriction across squamosals and parietals	81.6	–	–
20. Greatest width between outer edges of mastoid processes	150.6	–	–
21. Greatest width between outer edges of paroccipital processes	115.6	–	–
22. Greatest diameter of foramen magnum at medial edges of occipital condyles	28.0	–	–
23. Greatest height of foramen magnum	19.0	–	–
24. Height of occiput from base of basioccipital to middle of lamboidal crest	68.5	–	–
25. Height of rostrum above incisive foramen	98.0	–	–

tures in the skull have not fused completely, although the size of the skull indicates that the individual was an adult. Cranial measurements are given in Table 1.

Morgan and White (1995) described a new species, *Castoroides leiseyorum,* from the Irvingtonian Leisey Shell Pit, Hillsborough County, Florida. *Castoroides leiseyorum* is biometrically and morphologically similar to *C. ohioensis* (Morgan and White, 1995). *Castoroides leiseyorum* is distinguished from *C. ohioensis,* in part, however, by the absence of the palatine wing of the interpterygoid fossa and the mesopterygoid fossa (Morgan and White, 1995:416). Specifically, *Castoroides* species are unique in possessing two separate openings for the posterior internal nares (see Stirton, 1965:280, fig. 3 for a detailed description). These two openings are referred to as the dorsal and ventral choanae. A large, deep, ovate fossa in the basisphenoid just posterior of the dorsal choana is known as the mesopterygoid fossa, and it is one of the most unusual characters of *C. ohioensis* (Stirton, 1965:280). The mesopterygoid fossa is clearly apparent in figured specimens of *C. ohioensis* from New York (Stirton, 1965, fig. 3) and Iowa (Hay, 1914, pl. 71: fig. 1).

Castoroides leiseyorum has both ventral and dorsal choanae but lacks the mesopterygoid fossa. Instead, the basisphenoid bears a slightly concave, elongated groove along the midline that connects anteriorly to the dorsal choana (Morgan and White, 1995:416). Although the posterior palatine region of the South Carolina specimen (SC75.33.1) is broken, the basisphenoid and dorsal choana are well preserved. The South Carolina specimen, like the Florida specimens of *C. leiseyorum,* lacks a deep, ovate mesopterygoid fossa, but it has a slight concave groove extending into the dorsal choana (Figure 4C).

Morgan and White (1995:420) also stated that "there is a slight ridge along the midline of the basioccipital in the Leisey crania and the portion of the basioccipital lateral to this ridge is only slightly concave." The same is true for the basioccipital of the South Carolina specimen (Figure 4C). In "typical" specimens of *C. ohioensis,* the median ridge is higher and the lateral fossae are well developed (more concave) (Morgan and White, 1995:420).

In addition, the lamboidal crests in *C. leiseyorum* form a distinct V-shaped outline, whereas in *C. ohioensis* the lamboidal crest is sharper and more vertical, and it meets the sagittal crest

at nearly a right angle (Morgan and White, 1995). The lamboidal crest of the South Carolina specimen is V-shaped like that of *C. leiseyorum* (Figure 4A). Because the South Carolina skull shares diagnostic characteristics with *C. leiseyorum* Morgan and White, 1995, it is assigned to this taxon.

Discussion

Because of its size, the distinctive occlusal pattern of the cheek teeth, the unique longitudinally grooved enamel on the anterior and labial surfaces of the huge incisors, and its former extensive range, the giant beaver is one of the most intriguing species constituting the late Pleistocene megafauna of eastern North America. It is thought to have been more like the muskrat in its habits than the modern beaver, inhabiting river bottom lakes, embayments, and associated bogs and swamplands where it probably fed on coarse marsh vegetation. Kurtén and Anderson (1980:236) stated that "there is no evidence that the giant beaver built dams or felled trees." *Castoroides ohioensis* appears to have reached its greatest abundance in areas adjacent to the Great Lakes, especially the region that is now Michigan, Illinois, Indiana, and Ohio. The animal apparently was able to adapt well to a wide variety of environments with aquatic habitats, as evidenced by its extensive temporal (Blancan to Rancholabrean) and geographic (Alaska to Florida and Nebraska to East Coast) ranges.

Just as for the majority of the megafauna species, reasons for extinction of the giant beaver at the end of the Pleistocene are unclear (e.g., Martin and Klein, 1984). In the northern latitudes a combination of a gradual increase in the annual mean temperature, resulting in replacement of a spruce/pine/hemlock forest with a deciduous one, and reduction of backwater marsh and swamp habitat may have brought about the animal's demise. The natural reorganization of biological communities at the end of the Pleistocene may have resulted in the destruction of habitats for many mammal species (Graham and Lundelius, 1984). Cahn (1932) noted that a radical change would not have been required for climatic, biotic, or hydrographic conditions to have a profound effect on a highly specialized form such as *Castoroides*. Competition for habitat with *C. canadensis* as a factor, as has been suggested by Cahn (1932) and others, is questionable in light of apparent differences between the two relative to foods, feeding behavior, and general adaptations to aquatic habitat. Furthermore, these two taxa appear to have coexisted throughout much of the Pleistocene (Kurtén and Anderson, 1980).

Remains of *Castoroides* sp. from Ruby Falls, Bell, and ACb-3 caves provide new records of this extinct beaver for the mid-South and establish its former presence along the middle stretch of the Tennessee River. During the late Pleistocene, floodplain lakes and marshes bordering the middle (northwestern Georgia, northern Alabama) and lower stretches of the Tennessee River were probably extensive. These environments probably persisted into the Holocene. Parmalee (1993:81), in reporting an avian assemblage from Smith Bottom Cave, Lauderdale County, Alabama, (approximately opposite Bell and ACb-3 caves), a primarily Archaic aboriginal deposit 8950± 950 RCYBP, commented that "the predominance of remains of ducks such as the mallard (*Anas platyrhynchos*), teal and closely related species suggests considerable expanses of backwater sloughs, embayments and floodplain lakes within close vicinity to the site."

The taxonomy of *Castoroides* in the southeastern United States is not clear. Morgan and White (1995:420) indicated that the Leisey specimens may represent the early stages in the evolution of *Castoroides,* especially with regard to the development of the basicranial region of the skull. The Leisey fauna correlates most closely with the late early Irvingtonian, 1.6 to 1.0 million years ago (Morgan and Hulbert, 1995). The age of the South Carolina specimen is unknown, but it is quite likely late Pleistocene. It is, therefore, possible that the basicranial features of *C. leiseyorum* are actually geographic variants within *C. ohioensis* rather than characters diagnostic of a chronospecies. The lack of a mesopterygoid fossa may, consequently, be characteristic of a southeastern phenon of *Castoroides*. This hypothesis could be tested, if the South Carolina specimen could be dated by radiocarbon methods (e.g., Stafford et al., 1991). It is interesting to note that all specimens of *Castoroides* documented to have a mesopterygoid fossa, a high median ridge and well-developed lateral fossa on the basioccipital, and a strong lamboidal crest that joins the sagittal crest at right angles (typical *C. ohioensis* features) come from northern states (e.g., New York, Illinois, Iowa).

Martin (1969) described, on the basis of dental parameters, an extinct subspecies of *C. ohioensis, C. o. dilophidus,* from Florida. *Castoroides ohioensis dilophidus* has been found throughout Florida and may persist from the Blancan into the late Rancholabrean (Martin, 1969, 1975). Morgan and White (1995:421), however, noted that the presumed Blancan specimens of *C. o. dilophidus* are from the Santa Fe 1B fauna, which may be a heterochronic mixture of Blancan and Irvingtonian vertebrates. The diagnostic character of *C. o. dilophidus* is the occurrence of two isolated lophs (ids) in place of a single anterior loop in the upper third molar and the lower fourth premolar (Martin, 1969:1035).

Martin (1969) also assigned some postcranial elements to this subspecies, but cranial material of this taxon apparently was not known. In their later review, Morgan and White (1995: 420–421) indicated that other than the two Leisey specimens, there are no crania of *Castoroides* from Florida with a basicranial region. Different diagnostic criteria have been used for the various Florida taxa, so it is difficult to compare *C. leiseyorum* (cranial characters) with *C. o. dilophidus* (dental characters). The only lower fourth premolar from Leisey lacks the isolated lophid characteristic of *C. o. dilophidus* (Morgan and White, 1995:416). Martin (1969:1035), however, indicated that not all upper third molars and lower fourth premolars of *C. o. dilophidus* have the diagnostic isolated lophs (ids). In the original

samples he studied, Martin (1969:1035) found that only 83% (n=6) and 29% (n=7) of the lower fourth premolars and upper third molars, respectively, had the diagnostic feature. Absence of the diagnostic feature in the only lower fourth premolar from Leisey therefore does not significantly distinguish the Leisey sample of *C. leiseyorum* from *C. o. dilophidus*.

Two different interpretations of current knowledge of the taxonomy and evolutionary history of *Castoroides* in the Southeast are possible. On the one hand, it may be that the more typical *C. ohioensis* morphology (sensu stricto Stirton, 1965) is characteristic of more northern populations, and that *C. leiseyorum* and *C. o. dilophidus* are the same southern geographic variant of *C. ohioensis*. Under this scenario, *C. leiseyorum* represents cranial characters and *C. o. dilophidus* typifies dental features of this southeastern phenon. If this proves to be the case, then *C. leiseyorum* should be synonymized with *C. ohioensis*, and, depending upon additional taxonomic evaluations, either *C. o. dilophidus* or *C. dilophidus* would be the appropriate name. On the other hand, if *C. leiseyorum* is shown to be distinct from *C. o. dilophidus*, then it appears that two different phena (*C. leiseyorum* and *C. o. dilophidus*) may have persisted throughout the southeastern United States (at least Florida and South Carolina) for most of the Pleistocene. Further studies of associated cranial and dental material are required before either of these interpretations can be refuted.

Literature Cited

Barbour, E.H.
1931. The Giant Beaver, *Castoroides*, and the Common Beaver, *Castor*, in Nebraska. *Nebraska State Museum Bulletin*, 20(1):171–186.

Cahn, A.R.
1932. Records and Distribution of the Fossil Beaver, *Castoroides ohioensis*. *Journal of Mammalogy*, 13(3):229–241.

Churcher, C.S., P.W. Parmalee, G.L. Bell, and J.P. Lamb
1989. Caribou from the Late Pleistocene of Northwestern Alabama. *Canadian Journal of Zoology*, 67:1210–1216.

Faunmap Working Group
1994. FAUNMAP: A Database Documenting Late Quaternary Distributions of Mammal Species in the United States. *Illinois State Museum Scientific Papers*, 25(1–2): 690 pages.

Graham, R.W., and E.L. Lundelius, Jr.
1984. Coevolutionary Disequilibrium and Pleistocene Extinctions. *In* P.S. Martin and R.G. Klein, editors, *Quaternary Extinctions: A Prehistoric Revolution*, pages 223–249. Tucson: University of Arizona Press.

Hay, O.P.
1914. Pleistocene Mammals of Iowa. *Iowa Geological Survey Annual Report*, 1912:22.

King, J.E., and J.J. Saunders
1986. *Geochelone* in Illinois and the Illinoian-Sangamonian Vegetation of the Type Region. *Quaternary Research*, 25(1):89–99.

Kurtén, B., and E. Anderson
1980. *Pleistocene Mammals of North America*. 442 pages. New York: Columbia University Press.

Lively, R.S., G.L. Bell, and J.P. Lamb, Jr.
1992. Uranium-Series Dates from Travertines Associated with a Late Pleistocene Megafauna in ACb-3, Alabama. *Southeastern Geology*, 33(1):1–8.

Martin, P.S., and R.G. Klein, editors
1984. *Quaternary Extinctions: A Prehistoric Revolution*. 892 pages. Tucson: University of Arizona Press.

Martin, R.A.
1969. Taxonomy of the Giant Beaver *Castoroides* from Florida. *Journal of Paleontology*, 43(4):1033–1041.
1975. Giant Pleistocene Beavers and the Waccasassa River, Levy County, Florida. *Bulletin of the New Jersey Academy of Science*, 20(1): 26–30.

McCarroll, S.M., and J.L. Dobie
1994. Additional Pleistocene Mammals from Bogue Chitto Creek, Dallas County, Alabama. *Journal of the Alabama Academy of Science*, 65(1):16–27.

Morgan, G.S., and R.C. Hulbert, Jr.
1995. Overview of the Geology and Vertebrate Biochronology of the Leisey Shell Pit Local Fauna, Hillsborough County, Florida. *Bulletin of the Florida Museum of Natural History*, 37(I)1:1–92.

Morgan, G.S., and J.A. White
1995. Small Mammals (Insectivora, Lagomorpha, and Rodentia) from the Early Pleistocene (Irvingtonian) Leisey Shell Pit Local Fauna, Hillsborough County, Florida. *Bulletin of the Florida Museum of Natural History*, 37(II)13:397–461.

Parmalee, P.W.
1992. A Late Pleistocene Avifauna from Northwestern Alabama. *Natural History Museum of Los Angeles County, Science Series*, 36: 307–318.
1993. An Archaeological Avian Assemblage from Northwestern Alabama. *ArchaeoZoology*, 5(2):77–92.

Parmalee, P.W., A.E. Bogan, and J.E. Guilday
1976. First Records of the Giant Beaver (*Castoroides ohioensis*) from Eastern Tennessee. *Journal of the Tennessee Academy of Science*, 51(3):87–88.

Roth, J., and J. Laerm
1980. A Late Pleistocene Vertebrate Assemblage from Edisto Island, South Carolina. *Brimleyana*, 3:1–29.

Stafford, T.W., Jr., P.E. Hare, L. Currie, A.J.T. Jull, and D.J. Donahue
1991. Accelerator Radiocarbon Dating at the Molecular Level. *Journal of Archaeological Science*, 18:35–72.

Stirton, R.A.
1965. Cranial Morphology of *Castoroides*. *In* A.G. Jhingran et al., editors, *Dr. D.N. Wadia Commemorative Volume*, pages 273–285. Calcutta: Mining, Geological and Metallurgical Institute of India.

Wyman, J.
1850. Remarks on Finding Bones of *Megalonyx*, *Castor* and *Castoroides* at Memphis, Tennessee. *Proceedings of the Boston Society of Natural History*, 3:281.