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A HISTORY OF RUMINANTS: PART 2

S. David Webb

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S. David Webb

The first part of this history of ruminants presented the general features of the group and distinguished them from their sister group, the Camelidae. PLASTER JACKET No. 45 also indicated the times of North American appearance of eight different ruminant families that presumably dispersed into the New World from Asia. This second, concluding part of ruminant history reviews the special features of Florida's fossil record of the group beginning in the Oligocene and proceeding through the Pleistocene. As noted previously, all eight of the ruminant families known in North America are also represented in Florida.

Late Oligocene

The earliest ruminant fossils known in Florida were found when Interstate Highway 75 was being built through Gainesville. A small fissure deposit, cut into the Eocene age Ocala Limestone, sampled terrestrial and estuarine vertebrates some 30 million years old. When the sea stood at that elevation (some 90 feet above present sea level) Florida land may have consisted of a modest archipelago scattered southward from the southern Appalachian Mountains. Despite such

Dr. Webb is Curator in Vertebrate Paleontology at the Florida State Museum and Editor of the Plaster Jacket.

possible isolation, the terrestrial vertebrates broadly resemble those much better known in contemporaneous depqsits from the Big Badlands of South Dakota.

The early ruminants from the I-75 local fauna represent the Leptomerycidae and Hypertragulidae, the two earliest families of ruminants known in North America. To judge from the small samples of isolated teeth, Florida species were closely comparable to those well described and figured by Scott (1940) in his great monograph series on "The Mammalian Fauna of the White River Oligocene." Members of both families retained brachydont dentitions and small body size. They may be supposed to have lived like their distant cousins, the living Tragulidae of tropical Africa and southeastern Asia, which they closely resembled.

Early Miocene

The same two families of ruminants continued their residence in North America into the early Miocene, and they are recorded then also in Florida. At the Buda Site in Alachua County, fairly extensive samples of dental elements and a few limb bones represent Nanotragulus loomisi, a species described and better known from the High Plains. This tiny hornless ruminant resembled the Asiatic Mouse Deer in many respects, but had a far more hypsodont dentition than any living tragulid. As in the living tragulids, it had very short front legs and evidently ran like a jack rabbit, with a flexible back, rather than like a deer.

The next important ruminant records in Florida come from Thomas Farm, about 20 million years ago. By then, three new ruminant families had appeared in North America, namely the Moschidae with no horns, the Dromomerycidae with simple skin-covered horns, and the Antilocapridae which at this early stage were represented by the subfamily Merycodontinae with branched horns from which the horny sheaths were shed annually. The Moschidae and the Dromomerycidae are represented by jaws and isolated limb elements at Thomas Farm; but the merycodontine Antilocapridae are unknown in Florida, in contrast with their great abundance in many midwestern and western sites.

In the early Miocene of North America the moschids, represented today only by Moschus (the Musk Deer of China), consisted of two distinct lineages. One group, characterized by long snouts and short premolars, is represented by Machaeromeryx; the other group, characterized by short snouts and long premolars, is represented by Blastomeryx. Excellent material of the latter genus is known from Thomas Farm and has been named Blastomeryx floridanus (well figured by Maglio, 1966). The other group is presumably represented by the species named Machaeromeryx gilchristensis, but unfortunately the material assigned to this taxon is sparse and does not appear to have appropriately short premolars.

The family Dromomerycidae likewise includes at least two major lineages in the early Miocene of North America. Unfortunately, however, the limited material representing this family at Thomas Farm has not been described and does not yet include horns or complete enough dentitions to determine its generic assignment. This is one of many good reasons to continue work at Thomas Farm and other early Miocene sites.

Late Miocene

By the late Miocene the primitive ruminant families Hypertragulidae and Leptomerycidae had become extinct. One new family, the hornless Gelocidae, appeared in the late Miocene of North America. The three most characteristic ruminant families continued to be the Moschidae, the Dromomerycidae, and the Antilocapridae.

The best evidence of Dromomerycidae in eastern North America comes from the Love Bone Bed in the

late Miocene phosphatic sediments of central Florida. There Pediomeryx hamiltoni is represented by an excellent sample of cranial dental and limb elements. The remarkable three-horned skull is illustrated in Figure 1. The long jaws with broad low teeth are also figured (Fig. 2). The shallow depth of the jaw, the long diastema in front of the cheek teeth, and the low-crowned teeth with crenulated enamel are all features reminiscent of a giraffid jaw. And, indeed, the North American family Dromomerycidae may include the New World's nearest relatives of the giraffoids of the Old World. The presence of a long median occipital horn, in addition to the paired frontal horns, characterizes the subfamily Cranio- ceratinae of the North American Miocene (Webb, 1983). The neck and limbs were heavily built and moderately elongate (though not nearly as elongate as in a giraffe). The body size and shape were roughly comparable to those of a moose. A few specimens of the smaller earlier genus, Cranioceras, occur in the lower strata of the Bone Valley District.

The Moschidae are known from a few dental fragments in the late Miocene of Florida. In the lower part of the Bone Valley there is limited evidence of the genus Blastomeryx.

In Florida late Miocene records of the family Antilocapridae (the family is based on Antilocapra, the pronghorn antelopes that survive in western North America) are extremely rare. One or two specimens may represent the older subfamily Merycodontinae in the lower part of the Bone Valley. The more progressive younger subfamily Antilocaprinae is represented at the Love Bone Bed by a few teeth and isolated limb elements. Similar scrappy records come from two other late Miocene sites, McGehee Farm and Withlacoochee River 4A. These sparse records contrast strikingly with the rich fossil samples from midwestern and western sites where extinct pronghorns

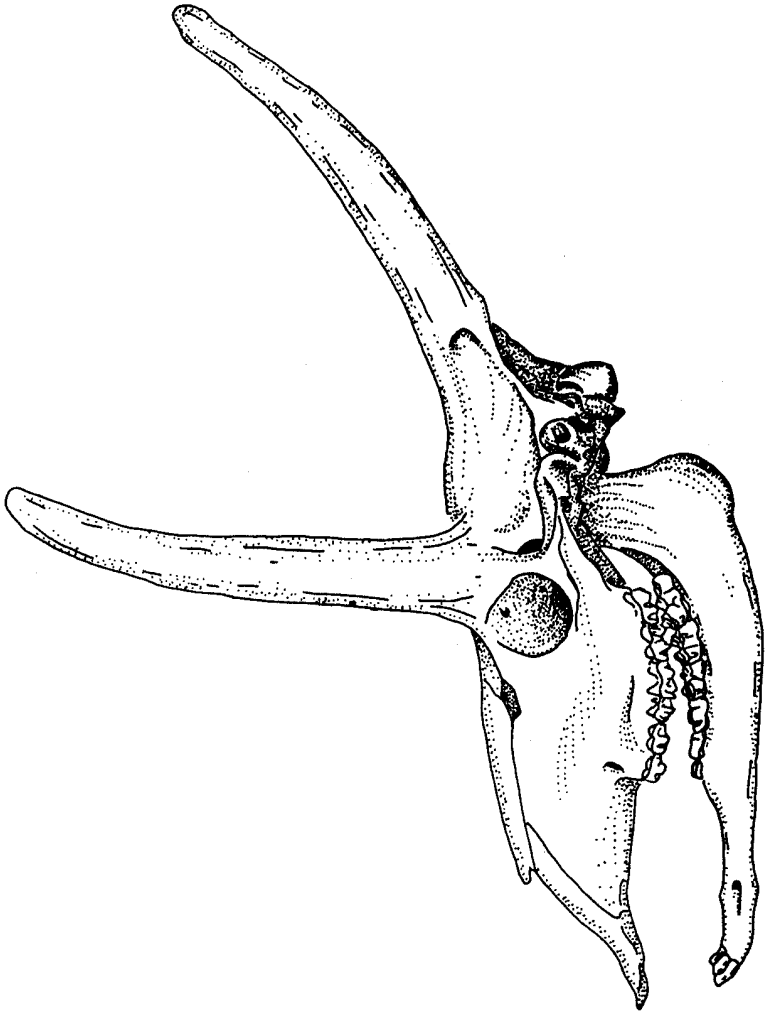

Figure. 1. Skull of Pediomeryx hamiltoni from Love Bone Bed, with paired frontal horns and median occipital horn. This genus includes the largest Tertiary ruminants known in North America.

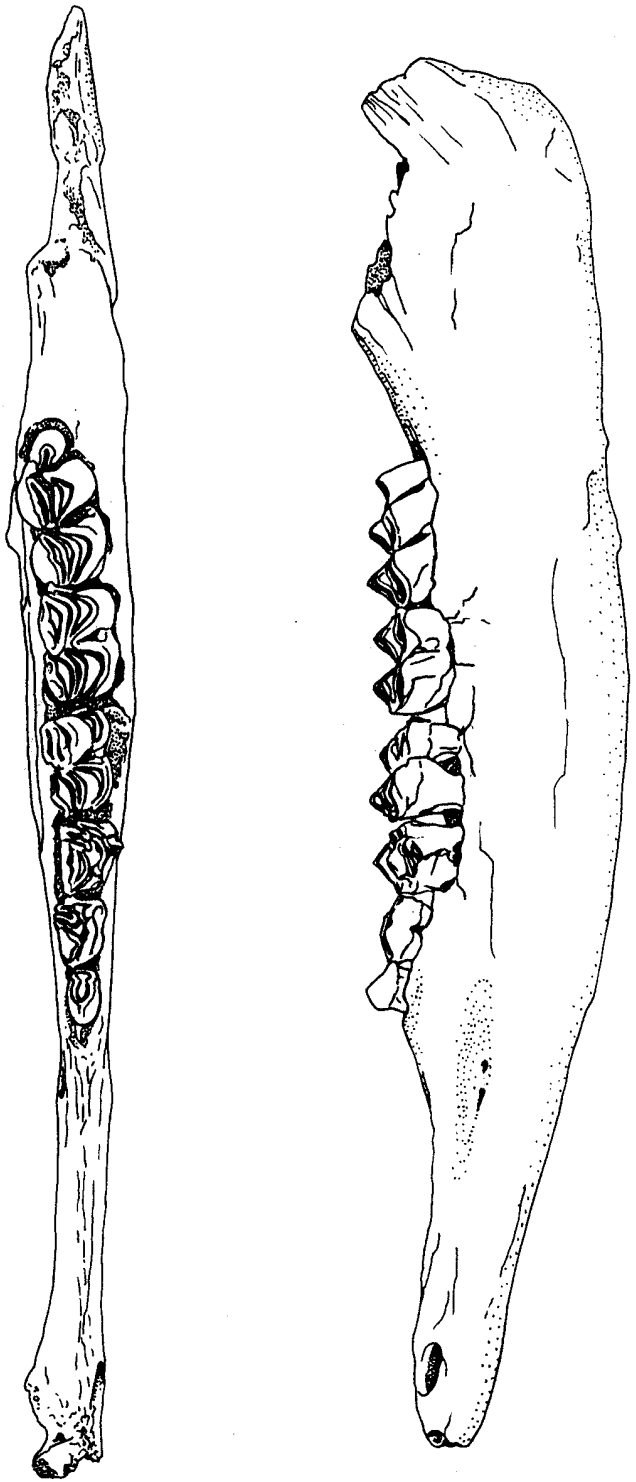

Figure 2. Left mandible of Pediomeryx hamiltoni. In lateral view note long low profile and long diastema between sockets for incisiform teeth and shortened premolars.

often dominate the faunas in which they occur. This is especially surprising since the pronghorns were almost surely herd animals throughout their history, and since depositional environment in two of these Florida sites are stream systems broadly similar to those in the west. One speculation that might explain the paucity of pronghorns in Florida late Miocene sites is that the herbaceous vegetation on which pronghorns grazed might have carried sufficient moisture throughout the year that they never approached streams for water. In that case even large herds might have lived in savanna settings and remained remote from stream sites where they would have been more vulnerable to predation.

An opposite preservational bias may explain the remarkable wealth of Florida Gelocidae. The late Miocene immigration of that family of small hornless ruminants is represented by sparse material of the genus Pseudoceras in no more than a dozen sites in all of North America. At the Withlacoochee 4A site in Florida, however, Pseudoceras is the commonest animal, represented by hundreds of limb bones, dozens of jaws, and several crania. A plausible explanation for its unique abundance at this one site may be that, like the Water Chevrotain in equatorial Africa, it lived in dense forests near water, and that the green clay beds at Withlacoochee 4A represent a forest pond.

Dentally Pseudoceras bears resemblances both to ruminants and to camelids, but poscranially it is wholly comparable to primitive ruminants. Frick (1937) had regarded his genus as a camelid because it had an upright lower canine and narrow premolars, and because he did not have the advantage of knowing it had a ruminant skeleton. The large collection of Florida mandibles also shows that only about half of the mature specimens had upright lower canines; the other half had incisiform canines as in other ruminants. Evidently the males had larger vertical canines for fighting, whereas the females had smaller procumbent canines for feeding. The narrow premolars are a primitive character for ruminants, still evi-

dent in Gelocidae as in Camelidae, but not retained in any higher ruminant groups. The preponderance of characters clearly indicates that Pseudoceras is a small hornless ruminant (Fig. 3).

Pliocene

By the end of the Miocene the Dromomerycidae and the North American Moschidae had vanished. During the Pliocene and Pleistocene North America received representatives of two additional families, the Cervidae (deer) and the Bovidae (including such diverse groups as sheep, goats, cattle, and antelopes). In fact, each of these families was represented by separate dispersals of several species from Asia in the course of the Pliocene and especially the Pleistocene. Florida's Pliocene deposits produce the oldest North American record of the true (antlered) Cervidae, no records of Bovidae, and two unique kinds of Antilocapridae.

The most significant discoveries of Florida Pliocene ruminants have been collected from the upper phosphatic gravel member of the Bone Valley Formation in Polk and Hillsborough counties. These deposits accumulated in river mouths and estuaries and also sampled coastal savannas some five million years ago (during the early Pliocene).

A large sample of antlers, jaws, and some cranial and limb fragments from the upper Bone Valley represent the oldest antlered ruminants in the New World. Studies currently in progress indicate that this sample represents a primitive member of the Odocoileinae, the subfamily that includes the familiar white-tailed deer (Odocoileus virginianus) the only surviving member of the group in the eastern United States. Eight or more additional genera of this subfamily, however, occur in the Pleistocene and Recent of North and South America. Some, such as the Andean Pudu, are much smaller than typical white-tailed deer and bear spike antlers even in mature

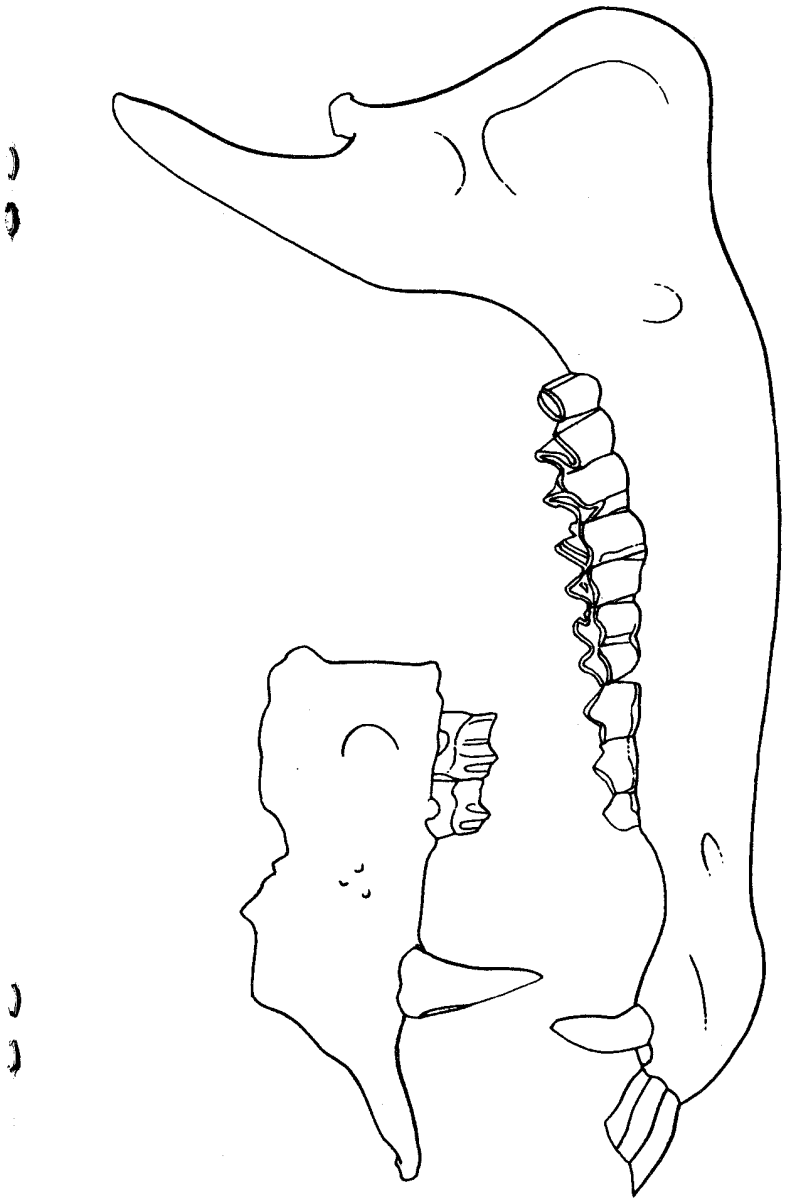

Figure. 3. Left side view of Pseudoceras mandible and rostrum. In this male the upright lower canine occludes and sharpens itself against the anterior face of the large upper canine. About half of the mature mandibles from Withlacoochee 4 A have procumbent incisiform canines.

bucks; while others, such as the caribou, have very elaborate antlers which uniquely in that species also occur in the does. Much remains to be learned about the fossil record of New World Cervidae.

The two kinds of Antilocapridae found in the upper Bone Valley Formation are both uniquely known from those deposits. The larger and more common of the two is Hexameryx simpsoni, a large six-horned antilocaprine. This extraordinary animal, endemic to central Florida as far as present records show, has been taken as the symbol of the Florida Paleontological Society, Inc. (see cover). As in modern Antilocapra americana, each prong was sheathed with a separate horn that tapered slightly toward the tip. This allowed each horn to be shed annually, as is true in Antilocapra and presumably in extinct antilocaprines, but not in Bovidae where the heavy horn is permanent. Among Hexameryx horns from the Bone Valley, two distinct size groups are evident, and furthermore two subtly different patterns of forking are also evident (Fig. 4). Although these were originally recognized as separate species, I suggested (Webb, 1973) that the smaller horn sets in which the middle horn is more closely allied with the anterior horn were Hexameryx cows, whereas the larger ones with the middle horn more centrally placed were Hexameryx bulls. This view tends to be corroborated by a similar dimorphism in samples of the closely related genus, Hexobelomeryx, from the early Pliocene of Chihuahua, Mexico. It is interesting to note this curious low-latitude distribution of the two known groups of six-horned antilocaprids.

The other Bone Valley antilocaprid is even rarer than Hexameryx and is known as Antilocapra (Subantilcapra) garciae. It is thus regarded as an endemic Pliocene subgenus of the genus Antilocapra. The horncore of A. (Subantilocapra) consists of a flattened dense plate of bone with short unequally forked tips. This seems to fit neatly as an intermediate stage in the evolution of the living American Prong-

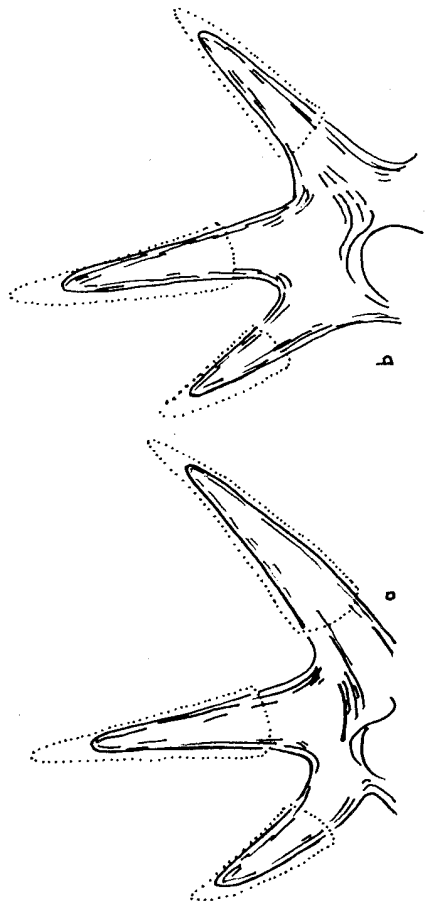

Figure 4. Left side view of Hexameryx horn rack. On the left (a) represents a presumed male which is larger, has a relatively longer posterior horn, and a more central anterior horn than the presumed female on the right (b). The dotted lines indicate the approximate outlines of the horn sheaths; only the bony cores are actually preserved.

horn Antelope (Fig. 5). From late Miocene deeply bifurcate small horns in Plioceros the trend was evidently toward taller, more compressed horns with a shallower bifurcation at the top, as in the Pliocene subgenus. And then, from A. (Subantilocapra) the next step was total suppression of the anterior tip of the bony core, although the horny sheath of medern male Antilocapra still bears an indication of the anterior fork.

Dentitions of both antilocaprid genera are also known from the Bone Valley district. It is traditional in fossil antilocaprid studies to base the taxonomy primarily on horn core morphology, and most type specimens (which bear the names) are designated as horns. Nevertheless, other parts of the skeleton are of great importance as well. In the Bone Valley no teeth are actually associated directly with horncores, but on the basis of size, two distinct groups of dentitions can be securely assigned to the two groups named on horncores. The dentitions of Hexameryx are about 20% larger in all dimensions than those of Antilocapra (Subantilocapra). For their size they are also less compressed transversely and somewhat less high-crowned. As in the living pronghorn, however, both genera had hypsodont teeth that were surely well-adapted to a diet of coarse herbs and grasses taken in with abrasive sand adhering.

Pleistocene

Florida's Pleistocene record of ruminants is extensive, but not particularly diverse. Three families are involved: the Cervidae and Antilocapridae continue (albeit with other genera) and, for the first time in known Florida records, the Bovidae appear.

The small antilocaprid genus Capromeryx is extensively sampled in the late Blancan (late Pliocene) Santa Fe River sites and in the early Irving-

Figure 5. Possible progression of pronghorn evolution, from left to right: (a) Plioceros blicki, late Miocene of New Mexico; (b) Antilocapra (Subantilocapra) garciae, early Pliocene of Florida; (c) Antilocapra (Antilocapra) americana, late Pleistocene and Recent of western North America. These bony cores were sheathed by horns which were shed each year, as in the living pronghorn.

tonian (earliest Pleistocene) Inglis site. These samples are the only ones in Florida that seem to have preserved antilocaprid fossils abundantly, as one might expect of such herd animals. Especially at the Inglis site, a coastal plain sinkhole, the remains of Capromeryx arizonensis are very extensive.

The common cervid in Florida Blancan and Pleistocene sites is Odocoileus, generally indistinguishable from O. virginianus living in Florida today. Occasionally, a very large antler fragment has been considered to represent an elk (Cervus canadensis), but without the corresponding dentitions or nearly complete antlers to show the characteristic branching pattern this interpretation cannot be supported. It is more likely that some Pleistocene white-tailed deer grew very large antlers. A second cervid was named from Sabertooth Cave in Citrus County; it is Blastocerus extraneus, nominally an endemic Florida species. The only living species of Blastocerus is B. dichotomus, the largest South American deer, which favors wetlands and ranges through the Mato Grosso into the Chaco and over major parts of Uruguay, Brazil, and Argentina. Unfortunately, the fossil species from Florida was based on dentitions, whereas the large, multiple-forking antlers would be more distinctive. The fact that no further material has been recognized since its description over 50 years ago is worrisome, but not conclusive one way or the other. The dentition does seem to fall outside of the normal range of variation seen in Odocoileus.

It is interesting to note that cervid samples are rarely very rich in Plio-Pleistocene sites in Florida. Llama-like camelids are usually more abundant than the cervids, and in some other sites Odocoileus is far outnumbered by Capromeryx. Only in the latest Pleistocene and Holocene, during or after the extinction of most of the other large ungulates, do Odocoileus samples become robust, as they would be today if Recent samples were fossilized. A discussion of human butchering of white-tailed deer, as well as several figures of their osteology, are presented in PLASTER JACKET No. 24.

The first record of Bovidae known in Florida appears early in the Pleistocene and consists of a tantalizing partial horncore of a musk ox from Inglis IA. This specimen has been properly referred to the subfamily Ovibovinae, but not with certainty to any particular genus. This unique occurrence represents one of the earliest musk oxen in North America and is also the southernmost record for the group.

The far more familiar Bovidae in Florida belong, of course, to the genus Bison. From the large Sangamonian (last interglacial) species B. latifrons, through the Wisconsinan (last glacial) B. antiquus, to the modern B. bison, the bisons evidently flourished in Florida. Their osteology and distribution are thoroughly reviewed in PLASTER JACKET No. 12.

A remarkable recent discovery relates the latest Pleistocene Bison herds and the earliest Paleoindians in Florida to one another. A partial skull of a female Bison antiquus was donated to the Florida State Museum in 1981 by Roger Alexon, after he, Bill Mathen, and Bob Gingery had collected it in the Wacissa River. The remarkable feature of this skull is the eroded chert projectile point that deeply penetrates its right fronto-parietal area. The point's cross-section closely resembles that of the distal third of a small Suwannee point, although an exact assignment to a projectile point type cannot be made. Two radiocarbon dates from the Bison bone collagen averaged 10,500 years before present, and thus confirm the association between late Pleistocene Bison antiquus and Paleoindians in Florida. This unique association is more fully described in Webb, Milanich, Alexon, and Dunbar (1984).

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