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THE FIRST MID-BLANCAN OCCURRENCE OF *AGRIOTHERIUM* (URSIDAE) IN NORTH AMERICA: A RECORD FROM HAGERMAN FOSSIL BEDS NATIONAL MONUMENT, IDAHO

JOSHUA X. SAMUELS,[1] JULIE A. MEACHEN-SAMUELS,[1] AND PHILIP A. GENSLER[2]
[1]Ecology and Evolutionary Biology, University of California, Los Angeles, 90095, USA, <jsamuels@ucla.edu>, <jmeachen@ucla.edu>; and
[2]Hagerman Fossil Beds National Monument, Hagerman, Idaho 83332, USA, <Phil_Gensler@nps.gov>

MEMBERS OF the subfamily Ursinae dispersed into North America from Africa and Asia during the Miocene, with the appearance of *Ursavus* (Schlosser, 1899), *Indarctos* (Pilgrim, 1913), and *Agriotherium* (Wagner, 1837) (Dalquest, 1986; Miller and Carranza-Castañeda, 1996; Hunt, 1998). However, none of these genera were thought to have survived past the Hemphillian Land Mammal Age in North America. It is thought that these genera were replaced, and possibly outcompeted, by members of the extant genus *Ursus* (Linnaeus, 1758), or *Plionarctos* (Frick, 1926), as suggested by several sources (Bjork, 1970; Dalquest, 1986; Bell et al., 2004). It has also been suggested that the Ursavini (*Agriotherium* and *Indarctos*) may have given rise to the extant ursids and the Tremarctinae (Harrison, 1983; Miller and Carranza-Castañeda, 1996). Of the Ursavini, *Agriotherium* is consistently found in the Hemphillian Land Mammal Age, and so is used as an index fossil in that its absence is assumed to indicate that a site is Blancan rather than Hemphillian (Lundelius et al., 1987; Bell et al., 2004; Hunt, 2004).

Agriotherium is the most widely distributed member of the Ursidae, and its fossils are known from approximately 20 localities in North America, including fossil sites in Arizona, California, Florida, Kansas, Oklahoma, Nevada, Nebraska, Texas, and Mexico. These sites range from approximately 6.0 to 4.6 Ma in age and all are considered mid-late Hemphillian (Tedford et al., 2004). The latest recorded occurrence of *Agriotherium* from North America was ~4.8 to 4.6 million years ago from the Yepomera Fauna, Chihuahua, Mexico (Lindsay et al., 1984; Bell et al., 2004). However, middle to late Pliocene and Pleistocene specimens are known from Poland, China, Ukraine, and South Africa. The dentary of *Agriotherium* described in this paper from the Hagerman Fossil Beds National Monument in Idaho is the first specimen of *Agriotherium* from Idaho, and the most northern occurrence of the genus to date in North America. Its occurrence in the Blancan is also the latest known record of the genus in North America.

METHODS

Measurements were made with Mitutoyo Absolute digital calipers to the nearest 0.01 mm. All measurements follow Van Valkenburgh and Koepfli (1993). Comparisons were made with known specimens of *Agriotherium* from the National Museum of Natural History (holotype specimen of *A. schneideri*), Field Museum of Natural History, and Texas Memorial Museum, as well as photographs and measurements in several publications (including Hendey, 1980; Dalquest, 1986; Miller and Carranza-Castañeda, 1996; Sorkin, 2005). Comparisons were also made to several *Arctodus simus* specimens housed at the George C. Page Museum.

Specimen repositories.—HAFO-Hagerman Fossil Beds National Monument, Hagerman, Idaho; USNM-United States National Museum of Natural History, Washington D.C.; TMM-Texas Memorial Museum, University of Texas, Austin; MWSU-Midwestern State University Collection of Fossil Vertebrates; IGM-Instituto de Geología de México.

GEOLOGIC SETTING

The Hagerman Fossil Beds National Monument (HAFO) in southcentral Idaho includes hundreds of fossil localities from the Blancan Land Mammal Age, and the associated Hagerman Local Fauna is one of the richest known assemblages from this age, including more than 150 species of vertebrates and invertebrates (McDonald et al., 1996). Faunal studies (Gazin, 1933a, 1933b, 1935, 1938; Bjork, 1970; McDonald et al., 1996; Bell et al., 2004) confirm a Blancan age for the fauna (following Bell et al., 2004), an assignment with which the authors agree.

The Glenns Ferry Formation at HAFO includes several Ar^{39}-Ar^{40} dated volcanic ash layers, ranging from 4.0–3.2 Ma (Hart et al., 1999). The general nature of the geology at HAFO (Fig. 1) consists of relatively thin, non-laterally extensive units of fine sands, silts, and clays with some minor components of coarser sands. Nearly all of the exposed stratigraphy at HAFO is interpreted as a deltaic system. Exposures of the Glenns Ferry Formation west of Hagerman are mostly thicker

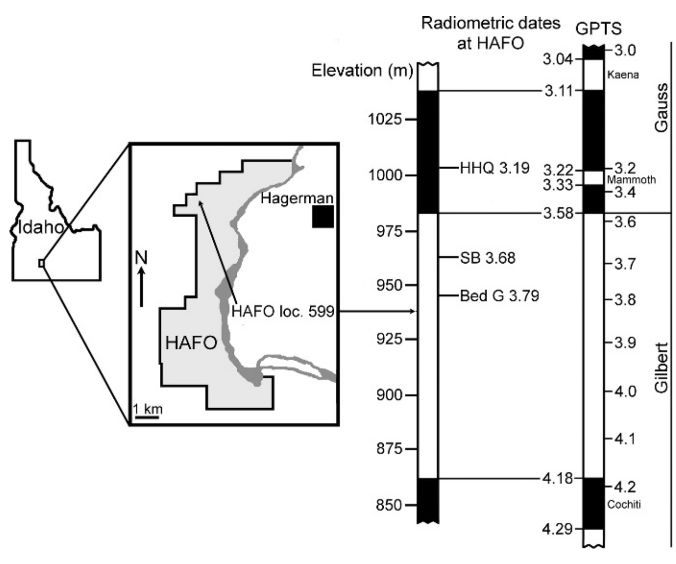

FIGURE 1—Map showing the location of HAFO loc. 599 and the stratigraphy of the Glenns Ferry Formation at Hagerman Fossil Beds National Monument, Twin Falls County, Idaho. Abbreviations: GPTS, geomagnetic polarity time scale; HAFO, Hagerman Fossil Beds National Monument; HHQ, Hagerman Horse Quarry; SB, Shoestring basalt. GPTS dates follow Berggren et al. (1995) and are given in Ma. Paleomagnetic stratigraphy for the Glenns Ferry Formation follows Neville et al. (1979). Dates for Bed G and SB are Ar-Ar analyses from Hart and Brueseke (1999). The HHQ date is based on a combination of evidence (Hart and Brueseke, 1999). Figure modified from Ruez and Gensler, 2008.

lacustrine deposits with some lake margin deposits. These lacustrine deposits represent the remains of the now extinct Lake Idaho which extended from just west of Hagerman into southeastern Oregon. The western portion of the Glenns Ferry Formation, approximately 40 mi west-northwest of the HAFO locality, is underlain with the late Miocene-aged Chalk Hills Formation and represents the early development of Lake Idaho. In the Hagerman area there are no known sedimentary deposits that are older than the Pliocene-aged Glenns Ferry Formation, though there are several known Pleistocene-aged deposits.

The dentary was found in situ in a unit of unconsolidated cross-bedded sandstone with its posterior end exposed. The cross-bedded sands which constitute this unit were fluvially deposited and are interbedded with thin layers of silts and "clay balls" deposited from bank erosion. Abundant fresh-water mollusks are found throughout the exposure, with larger sized (~8 cm wide) pelecypods eroding from the thin silt lenses. The full lateral extent of this river deposit is at least 150 m in length. Though the base of this unit is not fully exposed, making the determination of thickness difficult, the exposed portion is ~5 m vertically. The unit in which the referred specimen was recovered represents one of the thicker stratigraphic units exposed at HAFO.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowditch, 1821
Family URSIDAE Gray, 1825
Genus AGRIOTHERIUM Wagner 1837
AGRIOTHERIUM cf. A. SCHNEIDERI (Sellards, 1916)
(Figs. 2–4)

Material.—HAFO 17884: Partial left dentary, nearly complete left p4, partial left m1, partial left m2, approximately 10 tooth fragments. All recognizable teeth fit into the dentary with the exception of the m2; the coloration and thickness of the enamel in the tooth fragments match the teeth associated with the dentary and are thus assumed to be from the same individual. All specimens were collected by J. Samuels and J. Meachen-Samuels on 7 July 2006. Since Miller and Carranza-Castañeda (1996) synonymized all North American *Agriotherium* species to *Agriotherium schneideri*, the HAFO specimen is referred to as *Agriotherium* cf. *A. schneideri*. We designate this specimen as *Agriotherium* cf. *A. schneideri* due to the relative incompleteness of the specimen and the possibility it may represent a new species.

Locality.—HAFO loc. 599, Glenns Ferry Formation, west of Hagerman (NW 1/4, sec. 17, T7S, R13E), Twin Falls County, Idaho; approximate elevation 937 m above mean sea

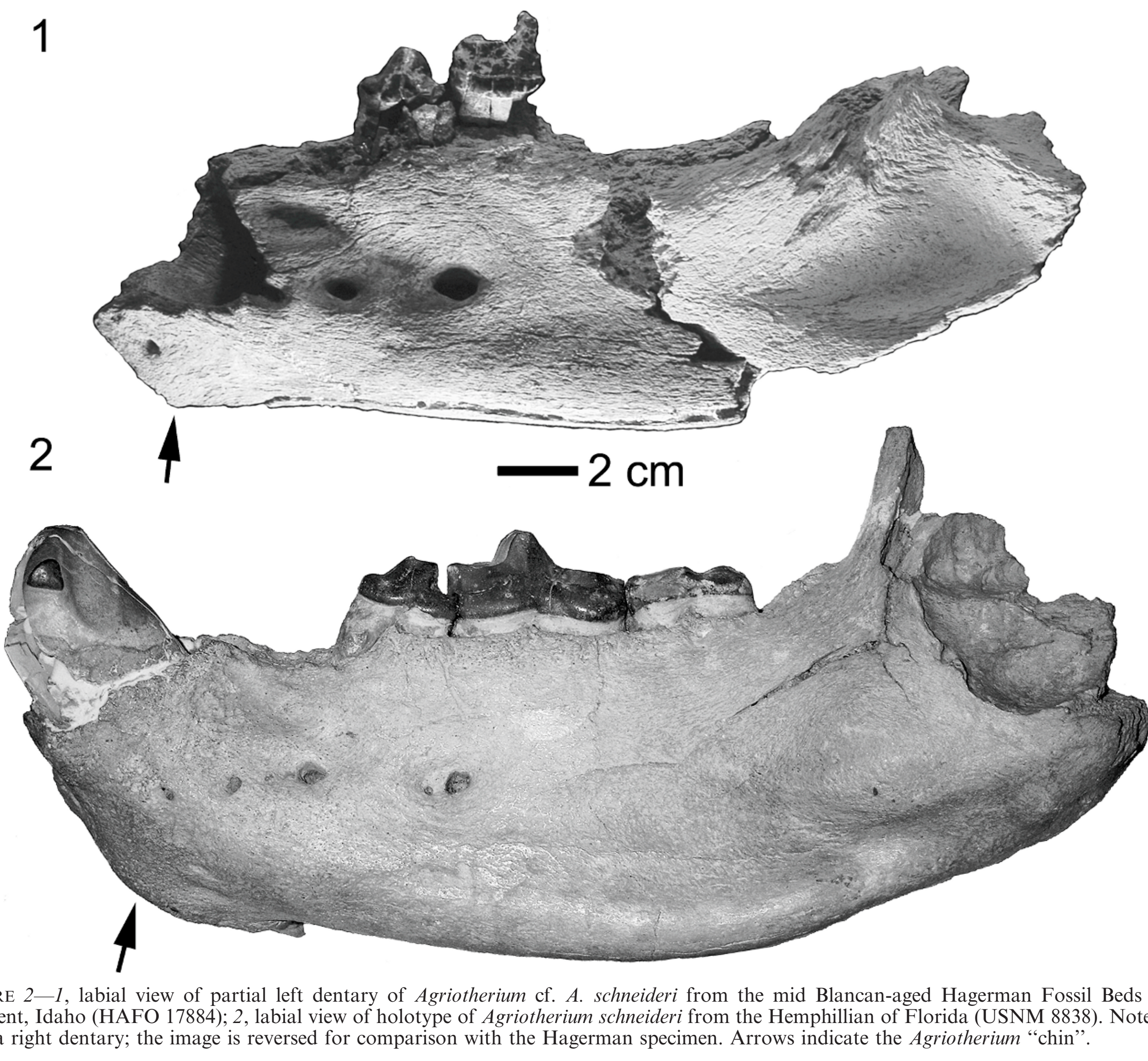

FIGURE 2—*1*, labial view of partial left dentary of *Agriotherium* cf. *A. schneideri* from the mid Blancan-aged Hagerman Fossil Beds National Monument, Idaho (HAFO 17884); *2*, labial view of holotype of *Agriotherium schneideri* from the Hemphillian of Florida (USNM 8838). Note: USNM 8838 is a right dentary; the image is reversed for comparison with the Hagerman specimen. Arrows indicate the *Agriotherium* "chin".

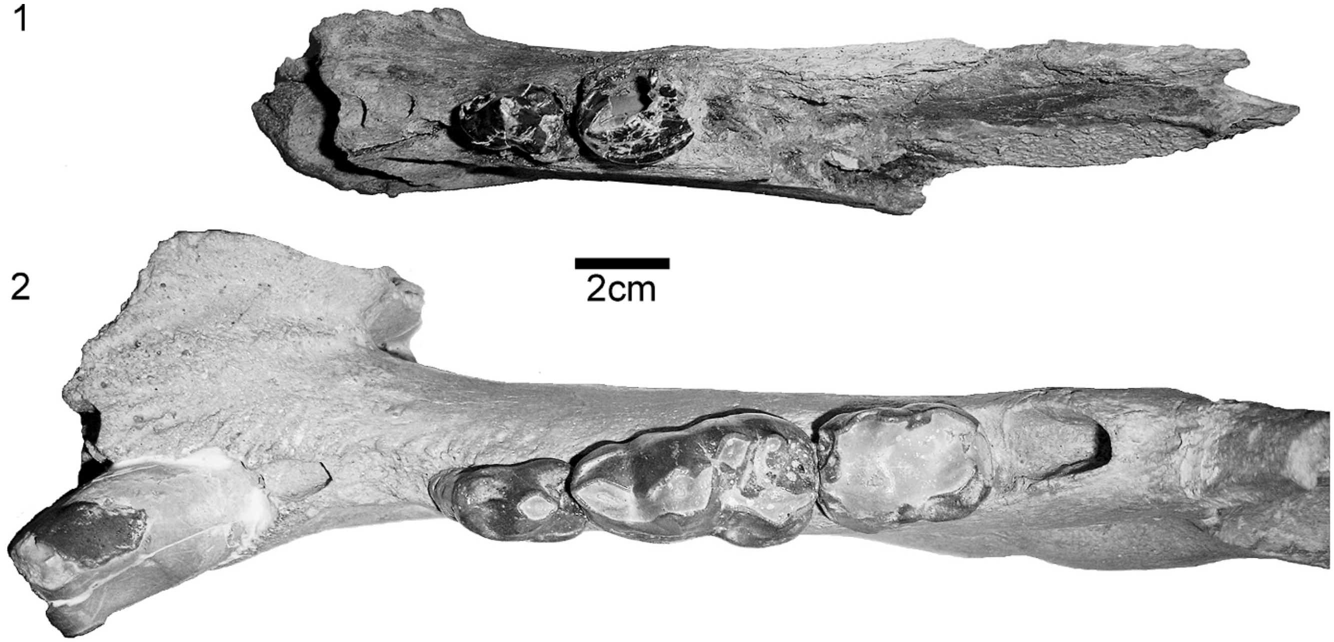

FIGURE 3—*1*, Occlusal views of partial left dentary of *Agriotherium* cf. *A. schneideri* from the mid Blancan-aged Hagerman Fossil Beds National Monument, Idaho (HAFO 17884); *2*, Occlusal view of holotype of *Agriotherium schneideri* from the Hemphillian of Florida (USNM 8838). Note: USNM 8838 is a right dentary; the image is reversed for comparison with the Hagerman specimen.

level. More precise locality information, including GPS data, is on file at HAFO.

Specimen Description.—This specimen was found in an area where erosion occurs rapidly, and as a result, some of the teeth and part of the dentary were eroded away. However, what remains of the specimen has fairly good preservation (Figs. 2–4). This specimen consists of most of the horizontal ramus and a partial angle of the dentary, including a complete premasseteric fossa and the initial depression of the masseteric fossa. These fossae have poorly defined edges and are separated by a small ridge of bone. The canine is missing, but the large canine alveolus is present. The symphyseal region of the dentary extends anteroventrally past the canine alveolus, producing a ‘‘chin'' effect (indicated by arrows in Fig. 2). Four mental foramina are present on the lateral side of the jaw, one small and anterior to the canine alveolus and three rather large foramina posterior to the canine alveolus, the last one being ventral and just posterior to the p4. As is typical of fossil bears, the reduced anterior premolars are lost and only alveoli remain (Dalquest, 1986). Three shallow dorsal alveoli located between the canine alveolus and the p4 indicate that there may have been single-rooted p1–p3 present. A pronounced depression is present ventral to the alveoli of p1 and p2 and shallowly continues posteriorly, ending in the largest, most posterior mental foramen.

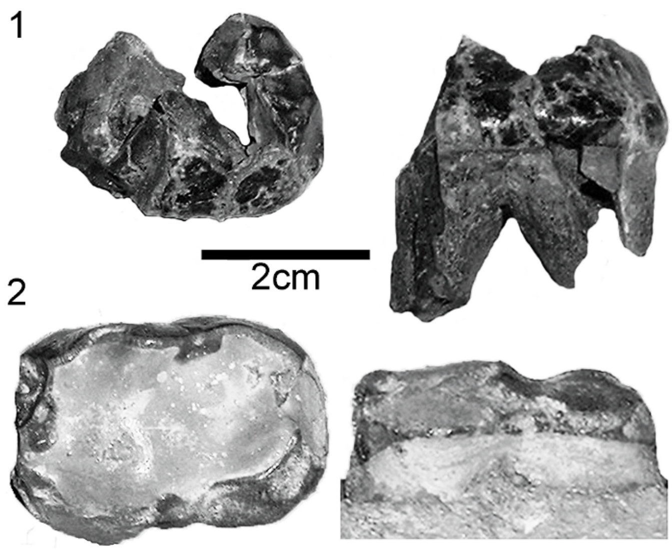

FIGURE 4—Occlusal and labial views of *1*, partial left m2 of *Agriotherium* cf. *A. schneideri* from the mid Blancan-aged Hagerman Fossil Beds National Monument, Idaho (HAFO 17884), and *2*, m2 of holotype *Agriotherium schneideri* from the Hemphillian of Florida (USNM 8838). Note: USNM 8838 is a right dentary; the image is reversed for comparison with the Hagerman specimen.

Measurements of the teeth of HAFO 17884 are smaller than the holotype (USNM 8838) but are within the range of other *Agriotherium* specimens reported in the literature from North America (Table 1). *Agriotherium*, like most ursids, also shows pronounced sexual dimorphism (Kurtén, 1966, 1967; Hendey, 1977; Hunt, 1998) and this individual may be a female, while the holotype specimen may be a male. The p4 is the most nearly complete tooth; it is slightly worn, and the enamel is chipped at its most posterior edge. It is dominated by a single main cuspid, with a wide cingulum at the base of the tooth that is most pronounced anteriorly and posteriorly. This tooth is wide posteriorly, tapers anteriorly, and has two large roots, with the posterior root larger. Only the anteriolateral portion of the m1 was recovered. The m1 trigonid is trenchant, and it is evident that the m1 is modified into a carnassial shearing blade. The anterior portion of the m1 that is present is moderately worn. The anterior root of the m1 is embedded in the dentary, while the large posterior root is broken off of the crown and is free from the dentary. For the m2, only the posterior portion is present, the anterior portion is completely broken off, and a portion of the talonid basin is also missing (Fig. 4). The portion of the m2 available is wide mediolaterally and has multiple bunodont cusps. One root of the m2 was also recovered.

TABLE 1—Measurements (in mm) of the dentary and lower dentition in *Agriotherium*. Specimens included are from Hagerman Fossil Beds National Monument, Idaho, the holotype of *Agriotherium schneideri* from Florida, and measurements for *A. schneideri* reported elsewhere in the literature.

Character	Hagerman, Idaho HAFO 17884	Brewster, Florida USNM[1] 8838	Coffee Ranch, Texas TMM 41261	Coffee Ranch, Texas[2] MWSU 12147	Rancho Viejo, Mexico[3] IGM 6413
Anteroposterior diameter of canine (alveolus)	32.4	33.3	33.1	—	—
Transverse diameter of canine (alveolus)	26.5	27.7	25.1	—	—
Anteroposterior length of p4	22.8	23.5	25.5	23.9	21.3
Transverse breadth of p4	14.3	14.4	14.5	13.2	12.7
Anteroposterior length of m1	—	41.5	43.1	40.1	37.1
Transverse breadth of m1	—	22.8	24.2	21.3	19.2
Anteroposterior length of m2	—	29.0	31.1	30.2	25.0
Transverse breadth of m2	20.4	20.6	20.7	21.9	19.8
Dorsoventral depth of the dentary between the p3 and p4	61.3	70.5	57.5	—	—
Dorsoventral breadth of the dentary between the p3 and p4	25.8	24.4	25.5	—	—
Dorsoventral depth of the dentary between the p4 and m1	66.9	73.6	57.6	—	—
Dorsoventral breadth of the dentary between the p4 and m1	24.6	25.8	24.1	—	—

[1] Holotype of *Agriotherium schneideri*.
[2] From Dalquest, 1986.
[3] From Miller and Carranza-Castañeda, 1996.

DISCUSSION

On the assignment to Agriotherium.—This specimen is assigned to the genus *Agriotherium* for several reasons. It is more similar in size and shape to known specimens of *Agriotherium*, than any other bear species. The Hagerman specimen possesses a premasseteric fossa, which is anteroposteriorly elongate and extends anteriorly to terminate below the m2 like other specimens of *Agriotherium* (Hendey, 1980). This specimen also has the symphyseal region of the mandible protruding as a "chin" (Fig. 2), which is a characteristic of the genus *Agriotherium* (Hendey, 1977, 1980). The position of the mental foramina is also consistent with other specimens of *Agriotherium schneideri*. The shape of the robust p4 is distinct in *Agriotherium*, with a prominent parastylar cusp and protocone shelf (Hunt, 1998) and the m1 has a well-defined carnassial blade. Although the m1 is incomplete in this specimen, the p4 and the remaining m1 possess the correct size and shape for *Agriotherium*.

As large bears have been described at Hagerman and other Blancan localities, it is important to determine that this specimen is not from another ursid species. The presence of the premasseteric fossa precludes this specimen from belonging to *Indarctos* or *Ursus* (Hunt, 1998). Though the premasseteric fossa is also present in some tremarctine bears (Merriam and Stock, 1925), the structure of the fossa in the HAFO specimen lacks the depth, circular shape, and prominent ridge separating the premasseteric and masseteric fossae characteristic of the Tremarctinae (Kurtén, 1966; Hendey, 1980).

This specimen also falls outside of the average size range for *Tremarctos* and *Plionarctos*, with the measurements of its teeth being almost twice as large as average *Tremarctos* and *Plionarctos* specimens (Kurtén, 1966). Additionally, size and dental morphology also exclude this specimen from the genus *Ursus* (Hunt, 1998).

The "chin" (Fig. 2) that extends anteriorly beyond the canine is diagnostic of the genus *Agriotherium*, and is not present in *Tremarctos* or any other tremarctine bear, including *Arctodus*. Nor is this "chin" found in the genus *Ursus*. Though similar in size to *Arctodus simus* (Cope, 1879), the dental morphology of this specimen is very different from that of *Arctodus*, especially with regards to the p4. The p4 of *Agriotherium* is much more robust than that of *Arctodus* and is slanted posteriorly in *Agriotherium* to expose the anterior root, as is found in this specimen.

Age of Agriotherium *from HAFO.*—Since *Agriotherium* has been considered an important species for biochronology and the definition of the Hemphillian Land Mammal Age (Hunt, 2004; Tedford et al., 2004), it is important to discuss the age of the specimen found at Hagerman. The well-documented age of the entire HAFO locality, the position of this specific site, HAFO loc. 599, relative to dated ash layers and magnetostratigraphy, and the presence of multiple species restricted to the Blancan at that site support the contention that this specimen is of Blancan age.

Precise stratigraphy of the entire Hagerman area has not been firmly established, but the relative age of this HAFO specimen of *Agriotherium* can be inferred from its position relative to a series of radiometrically dated volcanic ash layers and magnetostratigraphy, as well as the presence of other chronologically important species at the locality. HAFO loc. 599 lies approximately 937 m above sea level, and is approximately 23 m below a basalt flow dated at 3.68 $\pm$Ma and about 9 m below a basaltic ash dated at 3.79 $\pm$ 0.03 Ma (Hart and Brueseke, 1999; Hart et al., 1999) (Fig. 1). Though these dated ash beds are not exposed in the drainage where this specimen of *Agriotherium* was recovered, the horizontal nature of the Glenns Ferry Formation at HAFO allows for lateral interpretation of age based on the elevation of a given locality. Hart and Brueseke (1999) coupled their radiometric dates to paleomagnetic data from Neville et al. (1979), allowing them to create a composite chronostratigraphy and interpolate ages throughout the Glenns Ferry Formation at HAFO between 3.2 and 4.0 Ma. The stratigraphic relationships illustrated in Fig. 1 are modified from those presented in Hart and Brueseke (1999) and Ruez and Gensler (2008).

The Hagerman fauna is quite diverse and has been extensively studied (see McDonald et al., 1996 for a faunal list). Fossils from this specific site, HAFO loc. 599, include at least 27 invertebrate and vertebrate species, consisting of some taxa that originated prior to the Blancan and some species known only from the Blancan. The Glenns Ferry Formation includes many species that first occurred in the Hemphillian and persisted into the Blancan, including an unidentified gomphothere, a horse, a beaver, and several rabbits. *Castor californicus* (Kellogg, 1911), like *Agriotherium*, immigrated to North America from Asia in the Hemphillian and is one of the most abundant species in the Hagerman fauna (Zakrzewski, 1969; Tedford et al., 2004). A maxilla and several teeth of the jackrabbit-like *Alilepus vagus* (Hibbard, 1969) and teeth of *Hypolagus vetus* (Hibbard, 1969) were found at HAFO loc. 599; both rabbits are commonly found throughout the Hagerman section. The persistence of these taxa into the Blancan suggests that the presence of other taxa known primarily from the Hemphillian at this site should not be surprising.

Distinctive Blancan taxa include several species of biostratigraphically important rodents and some taxa known only from the Glenns Ferry Formation. The specimens found at HAFO loc. 599 included one dentary with the m2 and m3 and another isolated tooth of the ancestral muskrat, *Pliopotamys minor* (Wilson, 1933). *Pliopotamys minor* is one of the species used to define the Blancan Land Mammal Age, and given its small size and the rapid evolutionary changes typical of rodents, it is considered a good biostratigraphic indicator species (Bell et al., 2004). Other typically Blancan arvicoline rodents found at HAFO loc. 599 were the voles *Cosomys primus* (Wilson, 1932) and *Ophiomys taylori* (Hibbard, 1959). Most of the 14 specimens of *Cosomys primus* and five specimens of *Ophiomys taylori* at HAFO loc. 599 were isolated teeth, though one complete dentary and one dentary with the m1 of *C. primus* were found as well. A dentary with the i1–m2 from the extinct shrew, *Paracryptotis gidleyi* (Gazin, 1933a), was also found at this site. *Pliopotamys minor*, *Cosomys primus*, *Ophiomys taylori*, and *Paracryptotis gidleyi* are all species confined exclusively to the Blancan Land Mammal Age (4.9 to 1.5 Ma, Bell et al., 2004) and are abundant at many localities from Hagerman (Zakrzewski, 1969). Based on the occurrence of these taxa throughout HAFO, the entire Glenns Ferry Formation at HAFO is ascribed to the Blancan Land Mammal Age (Bell et al., 2004).

Though incomplete and fragmented, the dentary and teeth of this HAFO specimen of *Agriotherium* are relatively well preserved, particularly the portion found in situ. If the specimen was reworked and deposited from older Hemphillian aged sediments, approximately 40 mi away, then we would expect the teeth to show signs of abrasion by the coarse sands in which they were found, but they do not. Also, the dentary and teeth of *Agriotherium* display the same preservation as seen in specimens of other species from HAFO loc. 599, as well as most of the other Glenns Ferry Formation sites at HAFO. The circumstances under which this specimen of *Agriotherium* was found assure that it is definitively of Blancan age. This find extends the geographic and temporal range of *Agriotherium* in North America, a range which was likely much larger than indicated by the current fossil record.

Ecological context.—Nearly 20 carnivoran species are represented in the Hagerman Local Fauna (Bjork, 1970). In addition to *Agriotherium*, the ursine bear *Ursus abstrusus* (Bjork, 1970) is present. Felids are represented by four species: *Homotherium* sp. (Fabrini, 1890), *Megantereon hesperus* (Gazin, 1933b), *Felis lacustris* (Gazin, 1933b), and *Lynx rexroadensis* (Stevens, 1959). Canids include *Canis lepophagus* (Johnston, 1938) and *Borophagus hilli* (Johnston, 1939). About a dozen mustelids and mephitids are found at Hagerman, most notably the very large, wolverine-like *Ferinestrix vorax* (Bjork, 1970), the badger *Taxidea* (Waterhouse, 1839), the river otter *Satherium piscinaria* (Leidy, 1873), and three species of grisons (Bjork, 1970; McDonald et al., 1996).

The carnivores of Hagerman were supported by a diverse and abundant array of potential prey species. The fauna includes one or more proboscideans, possibly a gomphothere (*Stegomastodon* (Pohlig, 1912) or *Rhynchotherium* (Falconer, 1868)) and *Mammut americanum* (Blumenbach, 1799). Proboscidean carcasses and their young may have provided food for large bears. Ungulates include a horse (*Equus simplicidens* (Gidley, 1930)), 3–4 species of camels and llamas (*Camelops traviswhitei* (Mooser and Dalquest, 1975), *Hemiauchenia gracilis* (Meachen, 2005), *Hemiauchenia macrocephala* (Cope, 1893) and possibly another llama), a peccary (*Platygonus pearcei* (Gazin, 1938)), a pronghorn (*Ceratomeryx prenticei* (Gazin, 1935)), and at least two cervids. Beavers, ground squirrels, and the giant marmot (*Paenemarmota barbouri* (Hibbard and Schultz, 1948)) may all have been potential prey as well. Rodents are not often considered prey for bears, but brown bears and black bears often depend on ground squirrels for parts of the year and occasionally they will include beavers in their diet (Carl, 1971; Banfield, 1974; Müller-Schwarze and Sun, 2003). Abundant beaver fossils are present at the *Agriotherium* locality, as was one specimen of *Spermophilus* (Cuvier, 1825). Fish fossils are abundant at Hagerman, including several salmonid specimens found at HAFO loc. 599. The importance of living salmon to brown bears is well known, and given the historic migratory path of salmon up the Snake River and the large size of Lake Idaho, prehistoric salmon may have also spawned in the Hagerman area.

In the past, the extinction of *Agriotherium* in North America was attributed to replacement by the emigration of *Ursus* to North America from Asia in the earliest Blancan (Kurtén and Anderson, 1980; Miller and Carranza-Castañeda, 1996), but this may not have been the case if they filled different niches. Whether *Agriotherium* was an active hunter or scavenger (see Miller and Carranza-Castañeda, 1996; Sorkin, 2005), its dental morphology suggests it had a more carnivorous than omnivorous diet. The short face and robust p4 and carnassials of *Agriotherium* have led some to suggest it occupied a bone-cracking niche, similar to living hyaenas (Sorkin, 2005). In contrast, *Ursus abstrusus* from Hagerman is most similar to and likely filled a similar ecological role to the living black bear, *Ursus americanus*, which is a relatively small omnivorous bear (Bjork, 1970; Nowak, 1999). Given these differences, it is unlikely that these two bears competed. If *Agriotherium* competed with any other carnivorans at Hagerman, it is more likely to have competed with the bone-cracking dog, *Borophagus hilli*, or the large wolverine-like mustelid, *Ferinestrix vorax*.

Biostratigraphic implications.—In several instances, well-known Hemphillian indicator species have persisted longer than previously believed and have been found at other definitively Blancan sites. The Hemphillian rhino, *Aphelops* (Owen, 1845), had been previously used as a Hemphillian indicator, because rhinos were thought to be extinct by the end of this land mammal age (Wood et al., 1941). However, a specimen of this rhino was found in the Blancan age, Beck Ranch local fauna in Texas (Madden and Dalquest, 1990). *Machairodus* (Kaup, 1833) is another species that is normally found in Hemphillian-aged sediments but has also been found in Blancan-aged sediments from the Rancho Viejo fossil site in Mexico. Rancho Viejo has both Hemphillian- and Blancan-aged sediments, and *Machairodus* was found in sediments from both ages (Carranza-Casteñeda and Miller, 2001). It is also notable that *Agriotherium schneideri* was found in the

Hemphillian deposits at this locality as well. The faunal list from Hemphillian-aged sediments at Rancho Viejo is composed mainly of large mammals (Carranza-Casteñeda and Miller, 2001) and may warrant reconsideration of its age.

Like living large carnivores, *Agriotherium* most likely occurred at very low population densities. The other two Hemphillian holdovers, *Aphelops* and *Machairodus*, mentioned above, are also large-bodied creatures with relatively long generation times and most likely, small population sizes. Using large carnivore species to determine biostratigraphic land mammal ages may be problematic for several reasons. The first and last appearance data of rare taxa are probably not as reliable as more common species, because their rarity may result in a lower chance of fossilization and subsequent discovery (Kidwell and Flessa, 1996). Given the general scarcity of extant large carnivores in most areas, their extinct relatives probably do not make good index fossils for any land mammal age. There are, of course, exceptions to this generality in unusual circumstances, such as the fauna at Rancho La Brea and other natural traps. We recommend *Agriotherum* should not be used as a biostratigraphic indicator species for the Hemphillian Land Mammal Age, and that more common species would be more suitable biostratigraphic indicator species.

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