Giant Bison *(Bison latifrons)* Facts

TAXONOMY AND NOMENCLATURE

Describer (Date): C. H. Smith 1827 for *Bison*
R. Harlan 1825 for *Bison latifrons,* Fauna Americana: (Philadelphia: A. Finley). p. 273

Kingdom: Animalia
Phylum: Chordata
Class: Mammalia
Order: Artiodactyla (Even-toed hoofed animals: includes pigs, sheep goats, cattle, deer)
Family: Bovidae (Cattle, water buffalo, bison, antelopes, goats, sheep and more)
Genus: Bison
Species: *Bison priscus* (extinct Steppe Bison)
Species: ***Bison latifrons*** **(extinct Giant Bison)**
Species: *Bison antiquus* (extinct Ancient Bison)
Species: *Bison bison* American Bison
Subspecies: *Bison bison bison* (American Plains Bison)
Subspecies: *Bison bison athabascae* (American Wood Bison)
Species: *Bison bonasus* (European Bison)
Subspecies: *Bison bonasus bonasus* (Lowland Bison)
Subspecies: *Bison bonasus caucasicus* (extinct in 1925)
Subspecies: *Bison bonasus hungarorum* (extinct Hungarian Bison)

Taxonomic History and Nomenclature

- "Latifrons" comes from Latin words referring to a wide forehead
- First fossil bison described in North America was a *Bison latifrons* found in Kentucky (Peale 1803)
- Bison taxonomy underwent a long period of taxonomic splitting that resulted in some 10 fossil species recognized in North America by Skinner and Kaisen in 1947.
  - This taxonomy in great need of revision (McDonald 1981)
- Relationship of modern American bison and European bison is unclear at present, but both are quite similar genetically and can interbreed (Prusak et al 2004)
- Modern North American bison have two recognized subspecies: the American Plains Bison (*B. b. bison)* and the American Wood Bison *(B. b. athabascae*). (McDonald 1981)

Phylogeny

- Even-toed hoofed mammals trace their ancestry back to at least 45 million years ago in Eocene times.
- The *Bison* genus first appeared in southern Asia, around 2 million years ago (McDonald 1981)
- *Bison priscus* was the ancestor of at least some of the North American bison (Prusak 2004)
  - This species flourished in northern Eurasia and Alaska and may have been the dominant hoofed mammal there (Guthrie 1970)
- Bison migrated to North America several times in the Pleistocene during the low sea levels when exposed land connected North America and Asia
- *B. latifrons* appeared less than 200,000 years ago in North America.
- *B. latifrons* became extinct around 20,000 years ago (McDonald 1981)
- All bison nearly became extinct in North America at the end of the Pleistocene when much of the other megafauna did become extinct (McDonald 1981)

Reference: San Diego Zoological Society factsheet on long-horned and ancient bison. http://library.sandiegozoo.org/factsheets/_extinct/bison_extinct/bison_extinct.htm

Discovery of remains of an extinct giant bison (*Bison latifrons*) in Pleistocene (Rancholabrean) fluvial strata in the San Luis Rey River Valley, San Diego County, California, USA

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ABSTRACT

Pleistocene fluvial and lacustrine deposits are preserved in patches along the San Luis Rey River Valley between Interstate 5 and Interstate 15 in northern San Diego County, California, USA. Over the past 20 years, a series of residential, commercial, and public roadway construction projects along the river valley have resulted in the discovery of "Ice Age" vertebrate fossils in these Pleistocene deposits. In April 2013, freeway improvements by Caltrans to the State Route 76—Interstate 15 interchange near Pala Mesa unearthed a partial skeleton of a bison. Recovered fossils include a nearly complete skull and an articulated series of thoracic, lumbar, and sacral vertebrae, as well as both pelvic bones. An isolated right humerus and radius-ulna found 60 meters south of the other bones may be part of the same individual as are a cluster of cervical vertebrae found 52 meters north of the skull. Preliminary analysis of morphometric skull data suggests a taxonomic assignment to the extinct giant bison species, Bison latifrons. *The fossils were found near the base of a 7.6 meter thick sequence of Quaternary fluvial strata in a light yellowish gray, silty, very fine-grained, micaceous sandstone with calcrete nodules. An irregular erosional and bioturbated contact separated the fossiliferous sandstone from an overlying dark yellowish orange to brown, very fine-grained sandstone. The age of the Pleistocene strata has not yet been determined, but the occurrence of* Bison *indicates correlation with the Rancholabrean North American Land Mammal Age and a maximum age of about 220 ka. This discovery represents the first record of extinct giant bison in San Diego County and serves to expand our understanding of the paleobiogeographic range of this charismatic member of the extinct Pleistocene megafauna. Previous records of* Bison *from San Diego County have been based on fragmentary remains that are either not identifiable to species level or have been assigned to the more diminutive species,* Bison antiquus.

INTRODUCTION

Previous paleontological and geological work on the Pleistocene history of western San Diego County has focused on the marine record as preserved on the stair step sequence of emergent marine terraces (abrasion platforms) and adjacent marine and estuarine embayments that characterize the geomorphology of the coastal plain (Kern and Rockwell, 1992). These landforms and their associated sedimentary deposits are in turn the result of both global fluctuations in sea level over the past 2.5 million years, as well more regional episodes of local tectonic uplift. However, an important part of the regional Pleistocene history has been largely overlooked, namely that of the non-marine (fluvial and lacustrine) deposits that accumulated in the coastal river valleys upstream from the Pleistocene bays and estuaries. These

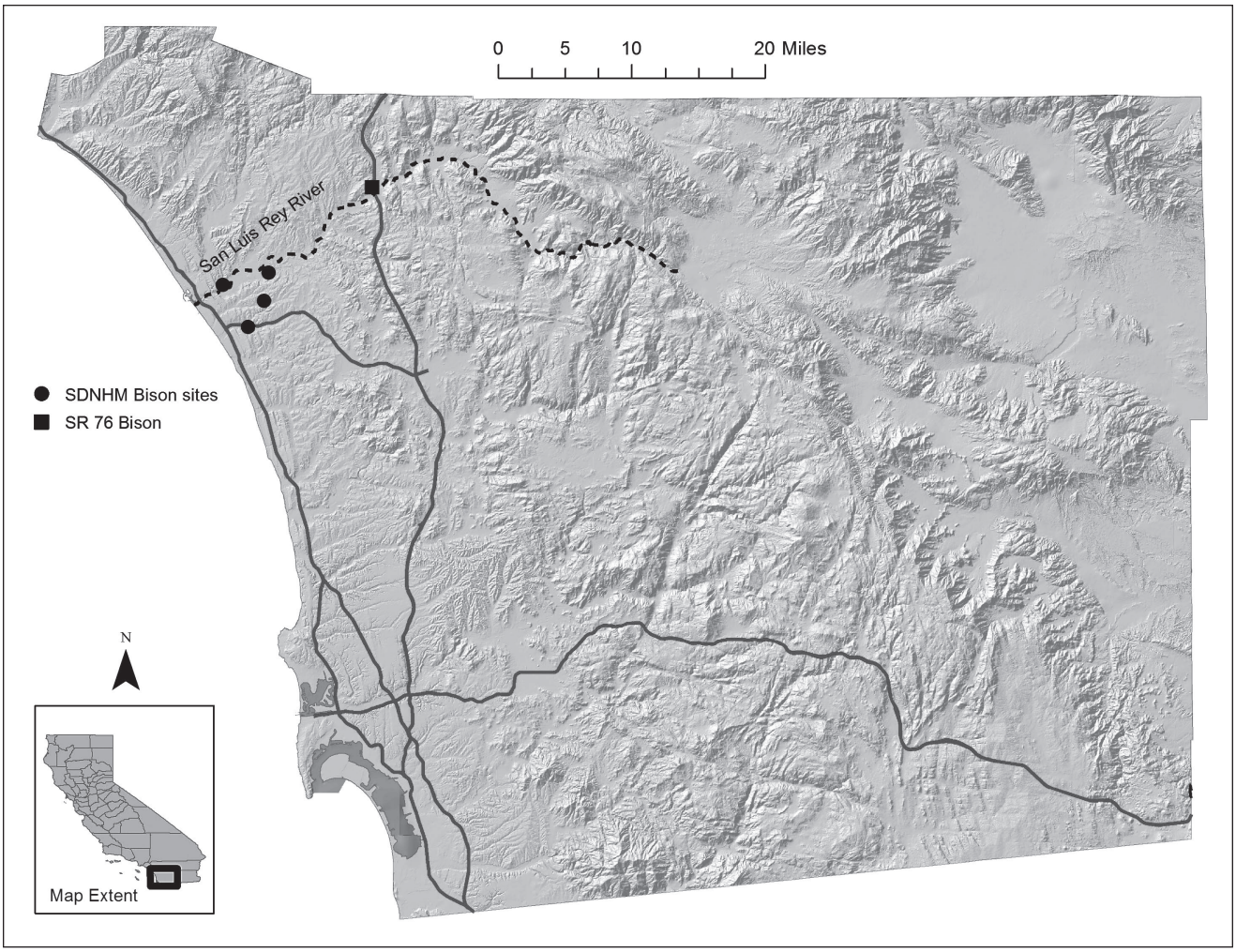

Figure 1. *Index map of San Diego County showing known records of* Bison *fossils in the San Luis Rey River Valley and adjacent coastal drainages.*

deposits are quite extensive, especially in the larger river valleys such as the Sweetwater River Valley in the south county, San Dieguito River Valley in the mid county, and San Luis Rey River Valley in the north county. Majors (1993) described a relatively diverse vertebrate assemblage (Glen Abbey local fauna) from upper Pleistocene (Wisconsin?) deposits preserved in the Sweetwater River Valley and Guthrie (2012) described a large avifauna from upper Pleistocene lacustrine strata in the San Luis Rey River Valley. The fossils described from both sites were discovered as a result of construction-related excavations and were recovered as part of paleontological resource mitigation projects conducted by paleontologists from the San Diego Natural History Museum (SDNHM). Similar mitigation activities carried out in the fall of 2013 during construction improvements to the State Route 76 and Interstate 15 interchange in the eastern part of the San Luis Rey River Valley near Pala Mesa (Figure 1) resulted in the discovery of a nearly complete skull with preserved horn cores and postcanine dentition of a giant bison (*Bison latifrons*). An intact series of sacral, lumbar, and posterior thoracic vertebrae found in articulation with the left and right pelvic bones was associated with the skull. Additional bison postcrania discovered at the site, including portions of the right forelimb and a series of cervical vertebrae, are likely from the same individual. The Pala Mesa discoveries are the most complete *Bison* remains yet found in San Diego County and represent the first record of giant bison in this region. The description and preliminary analysis of these fossils is the subject of this report.

Previous Work

Geology. The State Route 76—Interstate 15 interchange project area lies within the northern portion of the Peninsular Ranges Geomorphic Province, which is primarily composed of Lower Cretaceous (~125 to 90 Ma) plutonic rocks of the Peninsular Ranges Batholith overlain by a westward thickening wedge of Upper Cretaceous and Cenozoic sedimentary deposits (Walawender, 2000).

According to published geologic maps (Tan, 2000), the geologic units underlying the project area include, from oldest to youngest: undivided tonalite (Cretaceous age), granodiorite of Indian Mountain (Cretaceous age; ~120 Ma), tonalite of Couser Canyon (Cretaceous age; ~120 Ma), older alluvial flood plain deposits (Pleistocene age; ~500 to 10 ka), active alluvial flood plain deposits of late Holocene age (<5 ka), and active wash/stream deposits of late Holocene age (<5 ka).

Paleontology. The bovid lineage that includes modern species of the genus *Bison* originally evolved in Europe during the late Pliocene and following an initial radiation in Eurasia, eventually dispersed during the middle to late Pleistocene into North America via the Bering land bridge (McDonald, 1991). Although the taxonomy of the original *Bison* immigrant to North America is somewhat controversial, there is a consensus that once in the New World this lineage radiated to produce at least two endemic taxa, eventually leading to the modern plains bison, *Bison bison*. The extinct North American endemic taxa include the ancient bison, *Bison antiquus* and the giant bison, *Bison latifrons*.

Fossils of *Bison latifrons* and *Bison antiquus* have been reported from numerous late Pleistocene sites in North America. Both species are bi-coastal with fossil occurrences reported from California, Florida and the Eastern Seaboard. *Bison antiquus* sites have dense concentrations in California, Florida, and the central plains and north-central United States. Numerous sites have also been discovered in Mexico and in Canada, with the densest higher latitude concentration in Alberta. *Bison latifrons* fossil sites are mostly restricted to the United States, with concentrations in California, Idaho, Florida, and the Central Plains. Fossils of this species in California cluster in southern California, the San Francisco Bay Area, and the Modoc Plateau (McDonald, 1981).

Fossil remains of *Bison* have been reported from 82 discovery sites in southern California including two localities from Santa Barbara County, one from Ventura County, 45 from Los Angeles County, six from San Bernardino County, 16 from Orange County, five from Riverside County, four from San Diego County, and three from Imperial County (Jefferson, 1991; McDonald, 1981; Miller, 1968; Springer et al., 2009, 2010; Scott and Cox, 2008). Several of these localities have produced multiple bison specimens and in some cases more than one named species. The degree of taxonomic certainty regarding the specific identity of the *Bison* fossil remains also varies, with 16% of reported specimens assigned to *B. antiquus*, 10% assigned to *B. latifrons*, 10% provisionally assigned to *B. antiquus*, 5% provisionally assigned to *B. latifrons*, 57% assigned only to the genus *Bison*, and 2% provisionally assigned to *Bison*. In addition, the documented localities span a range of geologic ages that includes much of the Late Pleistocene (200 ka to 10 ka).

In San Diego County, previous reports of *Bison* are restricted to the northwestern portion of the county, within 20 miles of the coast. Most reported occurrences are from the San Luis Rey River drainage, with isolated occurrences along smaller drainages to the south including Loma Alta Creek and Buena Vista Creek (Figure 1). *Bison* fossils recovered from these northern San Diego County localities were all discovered as a result of paleontological monitoring of construction-related excavation activities. A partial right dentary fragment with a second lower molar (SDSNH 77800) was collected in August 1999 from a Rancho Del Oro residential project site in central Oceanside on the south side of SR-76 and assigned to *Bison antiquus*. In

south-central Oceanside, near the intersection of Oceanside Boulevard and College Boulevard, associated skeletal elements (i.e., vertebrae, pelvic bones, and limb bones) of *Bison antiquus* (SDSNH 83253-83257) were discovered in November 2000 during mass grading of the Ocean Ranch Corporate Centre. In June 2002, a right dentary of a juvenile *Bison antiquus* with deciduous second through fourth premolars (SDSNH 101449) was collected during construction of the Summit at Carlsbad apartment complex in northern Carlsbad, along Marron Road and south of SR-78. In September 2002, construction of the Wanis View Estates residential subdivision on the north side of the San Luis Rey River Valley near the Oceanside Municipal Airport, unearthed a left dentary with deciduous third and fourth premolars, and an erupting first molar, of a juvenile *Bison* sp. (SDSNH 90056). Also collected on this project was the proximal half of a left metatarsal of an adult *Bison* sp. (SDSNH 89548). Until now, no record of giant bison (*B. latifrons*) has been reported from San Diego County.

MATERIALS & METHODS

Field Methods

General. The bison fossil was discovered as a direct result of paleontological field monitoring of earthmoving activities associated with construction of the new freeway interchange. This monitoring involved close examination of active mass grading operations (e.g., grading to construct on ramps, off ramps, and roadways), as well as inspection of deep trenching operations (e.g., trenching to install underground wet and dry utilities). Field observations were focused on the recognition of unearthed fossil remains, but also involved collection of relevant geologic, stratigraphic, and taphonomic contextual data.

Fossil Salvage. Mass grading operations associated with construction of the northbound on ramp to I-15 from eastbound SR-76 in the southeastern portion of the new freeway cloverleaf was actively monitored during the spring of 2013 and on the afternoon of April 10, 2013, SDNHM paleontologist Brad Riney discovered several smears of fossil bone clustered across a three by ten foot area at the surface of the active scraper cut. Grading operations were diverted to other areas of the construction project while the extent of the discovery was evaluated. The first fossil remains to be identified were pelvic elements and associated sacral, lumbar, and thoracic vertebrae. On the following day, additional SDNHM paleontologists (Nicole Anderson, Gino Calvano, and Sarah Siren) joined Brad Riney to begin the recovery process (Figure 2). While the pelvic girdle and associated vertebrae were prepared for plaster jacketing and removal (see below), investigation continued on the other bone smears discovered eight feet northwest of the initial discovery. This investigation revealed first a molar tooth and then a nearly complete skull. Field efforts then shifted back to recovery of the pelvic and vertebral remains. The process began by exploring around the partially exposed fossils with hand tools (e.g., small picks and shovels) to determine the lateral and vertical extent of the remains. Care was taken to leave a three to six

Figure 2. *San Diego Natural History Museum paleontologists (Nicole Anderson, Gino Calvano, and Brad Riney) recovering fossil of* Bison latifrons *from the northbound onramp to Interstate 15. Note continuing mass grading operations in background.*

inch "halo" of intact sedimentary matrix around the fossils to keep them from crumbling. At the same time a consolidant (e.g., Butvar-acetone solution) was applied to the exposed remains to stabilize broken and/or fragile bones. Eventually, the surrounding sedimentary rock was removed until all that remained was an isolated block of sedimentary rock with the enclosed fossil bones. The block was still attached at its base to the underlying stratum by a pedestal of undisturbed sedimentary rock. The pedestal was then slightly undercut to form an overhanging lip. Damp newsprint was then placed on the upper surface of the block. A solution of 20-minute Plaster-of-Paris was then mixed and 5- to 10-inch-wide strips of burlap cloth were soaked in the plaster solution. The strips were laid across the matrix block to dry in various orientations and depending upon the size of the block, one, two, or three layers of plaster-soaked burlap "bandages" were formed on each block. The blocks were then reinforced with wooden splints. Once the plaster hardened, the supporting pedestal was undercut and the block was turned over. Hand digging tools were then used to remove any excess matrix from the bottom of the block. A plaster and burlap cap was then constructed on the inverted bottom of the block, using the same method as described above. When all layers of plaster were dry and hardened, the completed plaster "jacket" was then labeled with a field number and north arrow, and removed from the construction zone.

It should be mentioned that while recovery of the skull, pelvis, and vertebrae was going on, earthwork operations were proceeding in other areas of the construction project. This earthwork required monitoring by SDNHM paleontologists and during the process additional fossils were discovered including an isolated humerus and radius-ulna and a series of five vertebrae. These bones were found in the same stratum that produced the other fossil remains, and were later determined to also represent remains of *Bison*.

Laboratory Methods

Analysis. Skull and postcranial morphologic terminology follows Skinner and Kaisen (1947) and McDonald (1981) and primarily focuses on the morphology of the horn cores and features of the dorsal surface of the skull. Linear and curvilinear measurements were taken of skull and postcranial skeletal elements using metric anthropometers with 0.1 cm increments for larger elements (i.e., >30 cm) and metric calipers with 0.1 mm increments for smaller elements. A series of standard morphometric measurements was taken following the procedures outlined in Skinner and Kaisen (1947) and McDonald (1981) and include the following: Skull Measurement (SM)-1 Spread of horn cores, tip to tip; SM-3 Horn core length, upper curve, tip to burr; SM-5 Horn core straight line distance (chord), dorsal side, tip to burr; SM-14 Least width of frontals, between horn cores and orbits; SM-15 Greatest width of frontals, at orbits; SM-OP Distance, nuchal line to tip of premaxilla; SM-ON Distance, nuchal line to nasal-frontal suture; and SM-21 Angle of divergence of horn cores, forward from sagittal plane. Skull measurements are summarized in Table 1.

In addition to skull measurements, three linear measurements each were taken from the humerus and radius following the standard methodology of McDonald (1981). These include his humeral measurement (hm)-1, approximate rotational (functional) length; hm-2, anteroposterior diameter of diaphysis at transverse minimum; hm-3, transverse minimum at diaphysis; radius measurement (rm)-1, approximate rotational (functional) length; rm-2, anteroposterior diameter of diaphysis at transverse minimum; and rm-3, transverse minimum at diaphysis. These measurements are summarized in the text.

Abbreviations used in this report include the following: SDNHM-San Diego Natural History Museum; SDSNH-San Diego Society of Natural History (the scientific organization that operates SDNHM); ka-kilo annum (1,000 years old); Ma-mega annum (1,000,000 years old).

Table 1. *Skull measurements for SDSNH 135465. Numbers in parentheses correspond to standard measurements in McDonald (1981).*

SKULL: STANDARD MEASUREMENTS	mm
minimum horn core spread (1)	1150
minimum horn core length (3)	490
minimum straight line (5)	460
anteroposterior diameter of horn core base (12)	151
least width of frontals (14)	365
greatest width of frontals (15)	422
Distance, nuchal line to tip of premaxillae (OP)	616
Distance, nuchal line to nasal-frontal suture (ON)	243
rostral width, left doubled (Skinner & Kaisen #16)	114
Width of skull and masserteric (Skinner & Kaisen #16)	182
width of nasal and maxilla contact	91
minimum width of nasal	101
anterior width of nasals	103
posterior width of nasals	120
maximum length of nasals, left	256
length of maxilla-nasal suture, left	50
length of maxilla-nasal suture, right	47
anteroposterior diameter of orbit (right side)	111
angle of divergence of horn core, left	74°
angle of divergence of horn core, right	75°
orbit angle of divergence from midline, left	51°
orbit angle of divergence from midline, right	55°

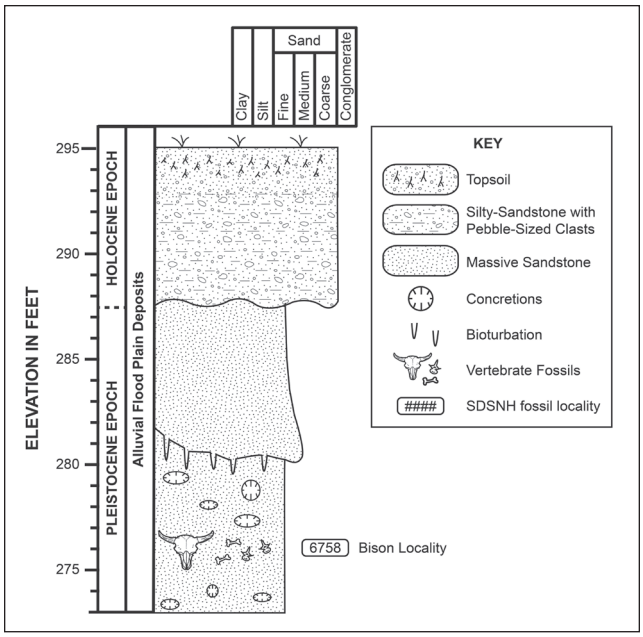

Figure 3. *Quaternary stratigraphic section exposed in the vicinity of the State Route 76-Interstate 15 interchange in northern San Diego County.*

RESULTS

Stratigraphy. The fossils were found near the base of a 25 foot thick sequence of Quaternary sedimentary rocks in a light yellowish gray, silty, very fine-grained, micaceous sandstone with calcrete nodules (Figure 3). An irregular erosional contact separated the fossiliferous sandstone from an overlying dark yellowish orange to brown, very fine-grained sandstone. The erosion surface was faintly bioturbated, with burrows extending into the fossiliferous sandstone. The fine-grained Pleistocene fluvial strata were capped by a yellowish brown, coarse-grained, pebbly sandstone of presumably Holocene age. The depth to crystalline basement at the discovery location is unknown. However, a series of three geotechnical test borings drilled along the SR-76 alignment within 90 meters of the centerline of I-15 penetrated up to 40 meters of interbedded siltstones and silty sandstones with minor beds of claystone and sandstone (Caltrans, District 11 field data). In contrast, geotechnical test borings drilled approximately 455 meters east and west of the centerline of I-15 penetrated only 2 to 3 meters of colluvial sands and residual soils before reaching igneous bedrock.

Taphonomy. The skull was lying upside-down with the snout oriented almost directly west and the horn cores roughly aligned north-south. The posterior axial skeleton and articulated pelvic bones were lying approximately 3 meters east-southeast of the skull and were dorsal side up, with the longitudinal axis of the vertebral column oriented north-south and the anterior-most vertebra positioned to the north. The right humerus and right radius-ulna were found approximately 40 meters southeast of the skull as separate elements about 6 meters apart. The cervical vertebrae and anterior thoracic vertebra were found as a disarticulated group approximately 52 meters north of the skull. Thus, the bison fossils reported here were distributed over an area of approximately 1000 m^2 and over a linear distance of approximately 71 meters. All of these

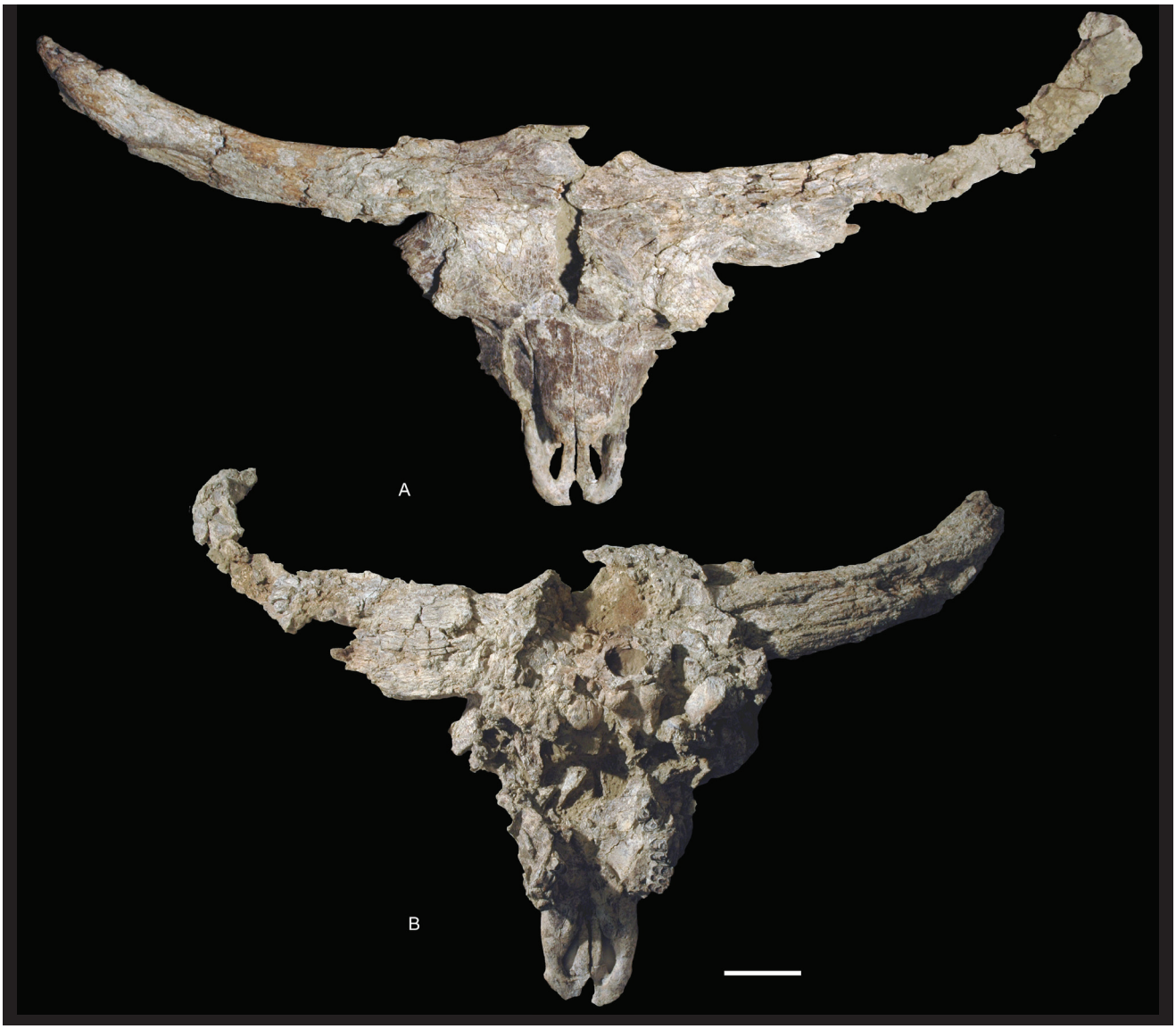

Figure 4. Bison latifrons *skull (SDSNH 135465) in dorsal (A) and ventral (B) views. Scale bar equals 10 cm.*

specimens were found in the same stratum and may be from the same individual. The remainder of the skeleton including the mandible, mid-thoracic vertebrae, ribs, scapulae, left forelimb, and right and left hind limbs were not found.

TAXONOMY & DESCRIPTION

Class Mammalia
Order Artiodactyla
Family Bovidae
Genus *Bison*
Bison latifrons (Harlan, 1825)
Figures 4, 5, 6

Referred specimens: SDSNH 135465; skull and associated postcrania (three posterior thoracic, five lumbar, and five sacral vertebrae plus right and left innominates). SDSNH 135466; associated right humerus and radius-ulna. SDSNH 135958, associated cervical (C-2, C-3?, C-4?, and C-5?) and thoracic (T-1?) vertebrae. All presumably from the same mature adult animal. Collected by SDNHM field crew, April 10-12, 2013 from SDSNH Locality 6685; SR-76/I-15 interchange, San Diego County, California, USA.

DESCRIPTION

Skull, General. The skull of SDSNH 135465 is nearly complete (Figure 4) and preserves an intact right horn core and partial left horn core (the ventral portion of the horn core was scraped away by heavy equipment). The dorsal surface of the

skull is essentially complete with all major bones preserved including the premaxilla, maxilla, nasals, lacrimals, and frontals. The skull roof is deformed, with portions of the left frontal separated from the right frontal at the midline. Portions of the left frontal have been broken and offset as small, but distinct fragments. The orbital portion of the left frontal is relatively undeformed, while the right orbital portion of the frontal has been pushed medially beneath the adjacent dorsal surface of the frontal. The horn cores appear to have been posteriorly rotated, such that the horn tips and axis of curvature are directed posteriorly rather than posterodorsally. The ventral surface of the skull has been broken transversely such that the basicranium is crushed up against the region of the internal nares and rotated to the right. Related to this deformation, the ventral margin of the occipital shield has been pushed forward causing some backward rotation of at least the right horn core. The articular portions of the occipital condyles have been scraped away, leaving only a roughly circular opening (foramen magnum) into the braincase.

Premaxilla. The left and right premaxillae are undeformed and tightly articulated with the adjacent maxillae. The ascending process of the premaxilla extends as a slender bone along the anterior 60% of the lateral margin of the narial fossa, but does not contact the anterolateral corner of the nasals. This is also the condition in *Bison bison*, while in *Bos taurus*, the ascending process of the premaxilla forms the entire lateral margin of the narial fossa and extends posterodorsally to contact the nasals. The premaxillae on the palate is marked by large, right and left incisive foramina, each with a roughly spatulate outline.

Maxilla. The left maxilla is relatively undeformed, with its lateral surface primarily oriented in the vertical plane. This contrasts with the condition in most bovids where the lateral surface of the maxilla has a distinct ventrolateral slope from the nasals to the alveolar margin. The right maxilla is broken into a series of small plates of bone that ventrally become more and more displaced from each other. Like the left side, the overall slope of the lateral surface of the right maxilla is vertical and not ventrolateral. A prominent infraorbital foramen measuring 13.9 mm in diameter is positioned at the level of P3 on the left maxilla. Posteroventral to this foramen the area of the maxillary tuberosity has been broken along a longitudinal fracture line. The right maxillary tuberosity is better preserved, but also has some distortion. Although broken with varying degrees of offset, the maxilla on the palate retains a useful amount of morphology. Between the tooth rows the maxilla is as wide as it is long. The right toothrow consists of P4 through M3, while the left toothrow consists of only P2-3 (Figure 5). The molars are short anteroposteriorly relative to their transverse width and when compared with teeth of *B. bison* are less selenodont.

Lacrimal. The left lacrimal is still in articulation with the adjacent maxilla and nasal anteriorly, while posteriorly it is separated from the frontal and broken deflected laterally in the transverse plane. The right lacrimal is better preserved and remains in articulation with all adjacent bones. It measures ~141 mm in length and has the overall shape of an elongate parallelogram The nasal-lacrimal suture measures ~60 mm long. It appears not to invade between the nasal and the maxilla nearly as far anteriorly as in *Bos taurus*.

Frontal. The right frontal is largely undeformed, while the medial portion of the left frontal has been broken into several large plates of bone along roughly transverse hinge fracture lines. Individual plates are positioned at various angles from horizontal to steeply inclined. The overall deformation of the left frontal has been one of anteroposterior compression, such that the orbital portion of the frontal has been telescoped forward to override the orbital regions of the lacrimal and jugal. The midline suture between the right and left frontals is open and appears to be unfused, a condition

Figure 5. *Partial right upper dentition (P4-M3) of* Bison latifrons *(SDSNH 135465). Anterior is to the right. Scale bar equals 2 cm.*

thought to be related to ontogenetic immaturity (McDonald, 1981). The skull roof formed by the right frontal preserves a relatively flattened transverse profile, a feature reported as characteristic of specimens of *Bison latifrons* (McDonald, 1981). This contrasts with the condition in short-horned bison like *B. bison bison*, wherein the medial portion of the frontal is slightly to distinctly domed (McDonald, 1981). The orbital regions of both frontals are relatively intact and preserve features related to orbital protrusion and orbital orientation. Orbital protrusion (OP) as defined by McDonald (1981) is quantified using two metrics, absolute OP which is the maximum distance the posterior orbit margin extends lateral to the posterolateral margin of the frontal and relative OP which is expressed as a percentage of minimal frontal width (SM-14) to maximum frontal width (SM-15). In SDSNH 135465 these values are 28 mm and 86%, respectively, and fall within the range of published values for *B. latifrons* (McDonald, 1981).

Horn cores. The right horn core is largely intact, while the ventral 80% of the left horn core was scraped away by grading equipment during construction. The base of the right horn core has been displaced anteriorly such that the ventral portion of its anterior margin now aligns with the posterior rim of the orbit. More distally, the right horn core displays a distinctly concave posterior margin as viewed dorsally. The distal tip is intact and terminates at a point posterior to the nuchal crest and slightly elevated above the level of the frontals forming the skull roof. Vascular grooves on the horn core suggest straight growth rather than spiral growth along the longitudinal axis. There is no obvious bony ridge or burr at the base of either horn core, a condition generally associated with female or immature male bison (McDonald, 1981). The absence, however, of these structures may be a preservational artifact rather than an actual developmental feature of the specimen. Overall, the intact right horn core does not display

the level of distal tapering preserved in published specimens of adult *B. latifrons*. Instead, the horn core remains relatively robust nearly to its distal termination (Figure 4A).

Jugal. The right jugal is relatively short anteroposteriorly in dorsal aspect and deep dorsoventrally when compared with the more gracile jugal of *Bos taurus* and *Bison bison.* In ventral aspect the right jugal is well exposed and expanded laterally, with a sharply defined lateral margin marking the lateral extent of the origin of the masseter muscle. The temporal process of the jugal is also transversely broad where it forms the ventral margin of the laterally protruding orbit.

Nasals. The nasals are undeformed for most of their length and transversely very broad, measuring 103.6 mm across at the level of the narial incision. Anteriorly, they are bluntly triangular and overhang the external nares to form a distinct narial incision with the adjacent premaxilla. Unlike the condition in most species of long horned bison, the dorsal surface formed by the right and left nasals is low and relatively flattened. The suture with the adjacent maxilla is horizontal and lies essentially at the lateral edge of the snout rather than being medially retracted. This configuration correlates with the steeper slope of the lateral surface of the maxilla.

Palatine. The right and left palatines are broken and deformed especially posteriorly where the internal narial passage has been obscured by matrix and displaced bony elements. The medial portion of the right palatine is better preserved than the left and is marked by a large diameter medial palatine foramen positioned immediately posterior to the damaged maxilla-palatine suture.

Squamosal. Portions of the left squamosal were exposed and include a partial glenoid fossa and the finger-like zygomatic process. These elements have been displaced anteriorly as part of the deformation of the occipital and basicranial region. The right squamosal has been obscured by crushing of the right paroccipital process.

Table 2. *Measurements of upper dentition for SDSNH 135465. AP= maximum anteroposterior crown diameter; TR= maximum transverse crown diameter*

Tooth position	AP (mm)	TR (mm)
LP3		20.0
LP4	18.9	22
RP4	19.7	22.3
RM1	31.1	26.7
RM2	33.3	27.3
RM3	34.1	25.4

Basicranium. The basioccipital has been rotated anterodorsally and displaced to the right. This distortion has obscured the region of the internal narial opening, as well as the right glenoid fossa and much of the left glenoid fossa. The basioccipital crests are relatively robust and protrude ventrolaterally. The left auditory bulla was exposed after removal of the displaced left postglenoid process of the squamosal and closely approaches the general bulbous shape of other bovid bullae.

Dentition. Measurements of the upper dentition are summarized in Table 2. The left P3-4 and right P4 are preserved in their respective maxillae (Figure 5). The left P3 has been rotated posteriorly such that the surface of the occlusal surface of the crown is lying against the anterior margin of the P4 crown. In this configuration the crown morphology of P3 is not visible. The crowns of the other premolars, however, are well exposed and reflect a degree of crown wear consistent with a mature adult individual. The right M1-3 series is preserved in the right maxilla, which is distorted to the point that the M3 has been dorsally displaced relative to M1-2. Like the premolars the degree of crown wear is consistent with a mature adult individual. Overall, the premolars and molars of SDSNH 135465 are relatively small, a condition noted earlier by Vanderhoof (1942) who commented that in spite of its large body size the cheek teeth of *B. latifrons* are about the same size as those of modern *B. bison*. McDonald (1981) utilized only two dental morphometric characters:

M1-3 labial length, and M3 anterior cups transverse width. For both measurements, the teeth of SDSNH 135465 are about 15% smaller than published records of male and female *B. latifrons*.

Postcrania. Recovered postcranial elements include an isolated axis vertebra, an associated series of three posterior cervical vertebrae and one anterior thoracic vertebra, a semi-articulated series of three posterior thoracic and five lumbar vertebrae, a fused series of five sacral vertebrae, the right and left innominates, a right humerus, and a fused right radius-ulna. The cervical vertebrae were found in close proximity and are presumably from the same individual. Because they were collected approximately 52 meters from the skull, they have been catalogued separately as SDSNH 135958. Both transverse processes are preserved on L2-L5, while L1 has only the left transverse process. The neural spines and neural arches were scraped away from all lumbar and thoracic vertebrae. The sacral vertebrae are tightly ankylosed into a single sacral element measuring 244 mm in anteroposterior length. The sacrum, in turn, is partially articulated with the right and left innominates. The sacroiliac joint is open and the sacral vertebrae have shifted ventrally relative to the pelvic bones. The innominates are complete and strongly fused at the pubic symphysis. Internally, the three bones making up each innominate (ilium, ischium, and pubis) are also strongly fused, suggesting that the individual was a mature individual. The right humerus (Figure 6A, B) has a functional length (humeral head to distal condyle) of 355 mm, an anteroposterior diaphysis minimum diameter of 71 mm, and a transverse minimum diphysis diameter of 66 mm. Except for some equipment damage to the lateral epicondyle, the humerus is complete. The medial portion of the robust lateral tuberosity only slightly overhangs the bicippital groove, a feature characteristic of *Bison* and distinct from the broadly overhanging lateral tuberosity in species of *Bos*. The deltoid tuberosity on the lateral border of the diaphysis is developed as an elongate raised process as in *Bison*. The right radius and ulna (Figure 6C, D) are tightly fused together along the radial diaphysis.

Figure 6. Bison latifrons *(SDSNH135466) forelimb bones. A, right humerus (caudal view); B, right humerus (cranial view); C, right radius-ulna (medial view); D, right radius-ulna (lateral view). Scale bar equals 10 cm.*

Both are complete except for equipment damage to the radial tuberosity. The radius has a functional length (capitular fossa to distal condyle) of 356 mm, while the total length of the ulna (olecranon process to distal styloid process) measures 459 mm. The transverse minimum diaphysis diameter of the radius is 62.5 mm. The humerus and radius-ulna were found in close proximity and are presumably from the same individual. Because they were collected approximately 40 meters from the skull, they have been catalogued separately as SDSNH 135466.

DISCUSSION

Taxonomic identifications of species of North American *Bison* have been primarily based on morphometric features of the horn cores. This is a bit surprising given the obvious social display function of such structures and the apparent morphological complexity of other parts of the skull, dentition, and postcrania. However, numerous authors have pointed out the phylogenetically conservative aspects of bovid cranial and postcranial anatomy and the difficulty presented by the generalized nature of many anatomical features (McDonald, 1981 and references therein). Having said this, certain morphometric features of the Pala Mesa bison fossils can be used to assign these specimens to the extinct giant bison, *Bison latifrons*. These features include the large size of the horn cores, the lack of longitudinal spiraling of the distal portion of the horn cores, the lack of doming of the frontals, the high degree of relative orbital protrusion, and the overall large size of all recovered skeletal elements. A review of the morphometric conclusions of McDonald (1981) concerning sexually dimorphic features of the skull of *B. latifrons*, suggests that the Pala Mesa bison likely is a female individual. These features include the relatively shorter length of the horn cores, the presence of a slight dorsal burr at the base of the horn cores, and the relatively short skull length between the nuchal crest and the tip of the premaxillae. Although some of these features have also been reported in immature male specimens of *B. latifrons*, the fused condition of most cranial sutures and the degree of wear on the occlusal surfaces of cheek tooth crowns suggests that SDSNH 135465 was a mature adult individual. Thus, it appears that the Pala Mesa bison represents an adult female specimen of *Bison latifrons*.

The earliest occurrence of *Bison* in North America represents an important biochronological datum that marks the initial dispersal of this lineage from Eurasia over the Bering land bridge and into the New World. This datum has been employed by vertebrate paleontologists to mark the beginning of the Rancholabrean North American Land Mammal Age, which is roughly calibrated at between 210± 60 ka and about 160 ka (Bell et al., 2004; Scott and Cox, 2008). This date represents a maximum age for the Pleistocene strata exposed at the State Route 76–Interstate 15 interchange. McDonald (1981) further proposed that the maximum population numbers and geographic distribution of *Bison latifrons* was during the Sangamon interglacial approximately 120 ka and that extinction of this species occurred during the late Wisconsin glaciation between approximately 20–30 ka. Future geochronologic studies of SDSNH 135465 will focus on obtaining accurate radiometric dates for this site.

SUMMARY

Paleontological mitigation work during construction of the State Route 76—Interstate 15 interchange in the San Luis Rey River Valley near Pala Mesa resulted in the discovery of well-preserved fossil remains of *Bison*. Morphometric analysis of these fossil remains, especially a nearly complete skull (SDSNH 135465), suggest that the fossils belong to the extinct giant bison, *Bison latifrons*. Cranial suture fusion, occlusal wear of cheek teeth, and sexual dimorphic features suggest the specimens may represent a mature, female individual. The Pala Mesa specimen of *Bison latifrons* represents the first record of this species in the Pleistocene of San Diego County.

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