RESEARCH ARTICLE

Osteopathology in Rhinocerotidae from 50 Million Years to the Present

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Abstract

Individual elements of many extinct and extant North American rhinocerotids display osteopathologies, particularly exostoses, abnormal textures, and joint margin porosity, that are commonly associated with localized bone trauma. When we evaluated six extinct rhinocerotid species spanning 50 million years (Ma), we found the incidence of osteopathy increases from 28% of all elements of Eocene Hyracotherium eximius to 65–80% of all elements in more derived species. The only extant species in this study, Diceros bicornis, displayed less osteopathologies (50%) than the more derived extinct taxa. To get a finer-grained picture, we scored each fossil for seven pathological indicators on a scale of 1–4. We estimated the average mass of each taxon using M1-3 length and compared mass to average pathological score for each category. We found that with increasing mass, osteopathy also significantly increases. We then ran a phylogenetically-controlled regression analysis using a time-calibrated phylogeny of our study taxa. Mass estimates were found to significantly covary with abnormal foramen shape and abnormal bone textures. This pattern in osteopathological expression may reflect a part of the complex system of adaptations in the Rhinocerotidae over millions of years, where increased mass, cursoriality, and/or increased life span are selected for, to the detriment of long-term bone health. This work has important implications for the future health of hoofed animals and humans alike.

Introduction

Rhinos diverged from their closest living relative, the tapir, about 50.3 million years ago (Ma) [1,2,3] and quickly increased in abundance and species richness through the mid-Cenozoic. The rhinocerotid lineage is hypothesized to have diversified into four major clades in North America and Eurasia: the Diceratheriinae in the Oligocene, and the Aceratheriinae, Teleoceratinae, and Rhinocerotinae in the Miocene [4, 5]. Cursoriality, or the habit of running, has been hypothesized to have been maintained through the majority of these lineages [5,6]. These grazing and browsing lineages were some of the most numerous and widespread large mammals in
the mid-Cenozoic, with frequent periods of migration between North America, Eurasia, and Africa [7, 8, 9]. About five million years ago the last North American genus, *Teleoceras*, disappeared from the fossil record [5]. North American rhino populations are estimated to have been smaller in size and weight than their Eurasian relatives [10], but both continents record taxa with increasingly robust and graviportal skeletons over time [5,11].

There are five extant species of rhino, all within the Rhinocerotinae. Two species are in Africa and three in Asia. As with many Animalia, a certain percentage of extinct and extant taxa show evidence of bony and soft-tissue pathologies [12, 13,14], with a recent increase in studies of pathologies in captive modern populations and individuals as wild numbers decline. For Rhinocerotidae, the great majority of studies are reports on captive rhinos with foot disorders [4,12,15,16], discovered during surgery or necropsy. For example, a recent study examined 27 modern captive individuals and a subset were scanned using computed tomography [13]. They found the majority displayed osteoarthritis and/or enthesopathy, particularly in the feet, and hypothesized that increased stress or strain, nutritional imbalance, habitat, and/or ascending infection could contribute the observed pathologies. A similar study [14] noted a wide range of osteopathologies in *Ceratotherium simum* and *Rhinoceros unicornis* using computed tomography and hypothesized that care, the weight of the animal, nutrition, or age could all contribute to pathological expression [14]. Extinct taxa have also displayed arthritis-like features, the most prominent being an increase in the frequency of spondylarthropathy (inflammatory arthritis, indicated by abnormal joint erosion or bone fusion) from around 10% in Oligocene Equidae and Rhinocerotidae to around 30% in the Holocene [17]. The common thread from these studies is the type of pathology recorded. These pathologies could all be grouped not as sudden traumatic events but, like runner’s knee or tennis elbow, growth or destruction of bone in response to increased physical stress over the lifetime of an individual.

Bone growth in mammals is promoted by a combination of mechanical (low level stress) and hormone stimulation [18]. After primary growth and development of a mammal is complete, bone repair and remodeling responds primarily to local stimulation [16,18,19] caused by mechanical load. Local osteocytes (bone cells) respond to bone damage and wear with cell hyperplasia (increased cell growth or proliferation). Extensive cellular damage, localized biomechanics (e.g. joint loading, genetic predisposition, and the environment are all potential causal factors of bone degeneration, inflammation and infection in the bone or surrounding tissue [12, 16, 20]. Thus, continuous remodeling of bone can result in bone morphologies and pathologies that reflect what happened to the bone when it was part of a living organism.

Increased mechanical load increases the likelihood of arthropathies such as proliferative joint diseases, erosive joint diseases, synovitis, and traumatic injury [16]. We will briefly examine the major arthropathies, but emphasize that the goal of this paper is not to diagnose the Rhinocerotidae lineage with a specific disease, but record and examine the osteopathologies that are possibly the result of these or related diseases. Four indicators of osteoarthritis (i.e. proliferative joint disease) commonly used in anthropologic studies are: eburnation, a wearing away of the bony articular surface, marginal osteophytes (known as lipping), sclerotic lesions or pitting on the articular surfaces, and alteration in the shape of the joint [21,22]. There are many other erosive arthropathies, but the most characteristic is rheumatoid arthritis (RA). RA includes symmetrical erosions of the hands and feet, minimal new bone formation, erosions, and osteoporosis [16]. Synovitis includes cortical erosion and irregular cysting [16]. Cysting, and ankyloses, or the fusion of a joint [16, 22] may also result from increased mechanical load. Other pathologies related to mechanical stress include inflammation of the peristium, which can form exostoses. Traumatic breaking and healing of the bone may occur, in conjunction with chronic arthropathies.
We initially expected to see a correlation between the severity of pathological expression and an increase in rhino mass and cursorial habits, because of the known correlation between osteopathology and mechanical stress [16, 18, 20, 21, 22], as well as previous observations of pathologies in rhinos [4, 13, 14, 15]. We reasoned that an increase in mass would put greater stress on bones and joints, increasing the likelihood that arthritis-like pathologies, such as osteophyte formation and articular surface degradation, would occur. If this were the case, the tendency to develop stress-related osteopathologies would be trackable and predictable. We asked two overarching questions in this study: (1) Do these osteopathologic features exhibit a trend over time? And (2) what is the relationship between mass and osteopathy?

**Materials and Methods**

To determine the relationship between mass and osteopathy through time, we collected data on osteopathologies from a number of extinct and extant taxa in the family Rhinocerotidae, Table 1, and an outgroup, *Hyrachyus eximius*, a perissodactyl sister group to the Rhinocerotidae [8, 23]. We collected data from localities with a large number of rhino skeletal elements to avoid individual preservation bias as much as possible, forming a series of species-level “snapshots” of the rhino lineage. Fossil species were chosen to span the temporal range of rhinocerotids and for the presence of adequate samples of identified elements, Table 2. Data resolution is not on the order of populations, but species in formations; this lumping of occurrences allows us to achieve a statistically adequate sample. For example, there are 15 different localities that comprise the *Hyrachyus eximius* sample, but they are all part of the Bridger Formation within Uinta County, Wyoming. No permits were required for the described study, which complied with all relevant regulations.

Phylogenetic Data, R scripts and digital photographs associated with this study are available at Morphobank (project ID: 1238) [27] with permission from The American Museum of Natural History, The University of Washington Burke Museum, The University of Oregon Museum of Natural and Cultural History, and The University of Texas Jackson School of Geosciences Vertebrate Paleontology Laboratory. Digital photographs of fossils from the UCMP are also available through the Calphotos archive (http://calphotos.berkeley.edu/). S1 File of raw pathology scores available online through PLoS One.

**Study Species**

*Hyrachyus eximius*, (50.5–45.4 Ma) (Fig 1) is a sister lineage of both the tapir and rhinos. This species is estimated to have weighed around 36.3 kg (equivalent in mass to a large dog), lacked
| Prefix | Specimen Num. | Genus | Species | element | NISP | Locality Name | Formation | Age |
|--------|--------------|-------|---------|---------|------|---------------|-----------|-----|
| AMNH   | 1645         | Hyracryus | eximius | pelvis  | 1    | Twin Buttes   | Bridger   | Bridgerian |
| AMNH   | 11652        | Hyracryus | eximius | pelvis  | 3    | Little Dry Crk | Bridger   | Bridgerian |
| AMNH   | 12364        | Hyracryus | eximius | pelvis  | 2    | 30 ft. above upper white stratus | Bridger   | Bridgerian |
| AMNH   | 1621         | Hyracryus | eximius | femur   | 1    | Bridger Basin | Bridger   | Bridgerian |
| AMNH   | 1621         | Hyracryus | eximius | tibia   | 1    | Bridger Basin | Bridger   | Bridgerian |
| AMNH   | 1623         | Hyracryus | eximius | radius  | 1    | Bridger Basin | Bridger   | Bridgerian |
| AMNH   | 1638         | Hyracryus | eximius | radius  | 1    | Cottonwood Corral | Bridger   | Bridgerian |
| AMNH   | 1638         | Hyracryus | eximius | ulna    | 1    | Cottonwood Corral | Bridger   | Bridgerian |
| AMNH   | 1640         | Hyracryus | eximius | femur   | 1    | Bridger Basin | Bridger   | Bridgerian |
| AMNH   | 1640         | Hyracryus | eximius | radius  | 1    | Bridger Basin | Bridger   | Bridgerian |
| AMNH   | 1641         | Hyracryus | eximius | femur   | 1    | Bridger Basin | Bridger   | Bridgerian |
| AMNH   | 1644         | Hyracryus | eximius | tibia   | 1    | Bridger Basin | Bridger   | Bridgerian |
| AMNH   | 1645         | Hyracryus | eximius | tibia   | 1    | Twin Buttes   | Bridger   | Bridgerian |
| AMNH   | 1646         | Hyracryus | eximius | humerus | 1    | Twin Buttes   | Bridger   | Bridgerian |
| AMNH   | 1646         | Hyracryus | eximius | radius (juvenile) | 1 | Twin Buttes | Bridger   | Bridgerian |
| AMNH   | 1646         | Hyracryus | eximius | tibia   | 1    | Twin Buttes   | Bridger   | Bridgerian |
| AMNH   | 1646         | Hyracryus | eximius | ulna    | 1    | Twin Buttes   | Bridger   | Bridgerian |
| AMNH   | 1903         | Hyracryus | eximius | ulna    | 1    | Henry's Fork LT | Bridger   | Bridgerian |
| AMNH   | 11693        | Hyracryus | eximius | femur head | 1 | Bridger | Bridger   | Bridgerian |
| AMNH   | 11693        | Hyracryus | eximius | radius—broken into two parts | 1 | Bridger | Bridger   | Bridgerian |
| AMNH   | 11693        | Hyracryus | eximius | tibia   | 1    | Bridger | Bridger   | Bridgerian |
| AMNH   | 11707        | Hyracryus | eximius | femur   | 1    | Henry's Fork LT | Bridger   | Bridgerian |
| AMNH   | 11712        | Hyracryus | eximius | femur   | 1    | Cat-tail Spring | Bridger   | Bridgerian |
| AMNH   | 11712        | Hyracryus | eximius | tibia   | 1    | Church Buttes | Bridger   | Bridgerian |
| AMNH   | 12179        | Hyracryus | eximius | femur   | 1    | Bridger | Bridger   | Bridgerian |
| AMNH   | 12179        | Hyracryus | eximius | tibia- lower | 1 | Bridger | Bridger   | Bridgerian |
| AMNH   | 12179        | Hyracryus | eximius | tibia- upper | 1 | Bridger | Bridger   | Bridgerian |
| AMNH   | 12225        | Hyracryus | eximius | humerus | 1    | Summer's Dry Crk | Bridger | Bridgerian |
| AMNH   | 12225        | Hyracryus | eximius | radius  | 1    | Summer's Dry Crk | Bridger | Bridgerian |
| AMNH   | 12255        | Hyracryus | eximius | ulna    | 1    | Summer's Dry Crk | Bridger | Bridgerian |
| AMNH   | 12356        | Hyracryus | eximius | radius, ulna, distal humerus (articulated) | 1 | Mouth of Summer's Dry Creek | Bridger | Bridgerian |

(Continued)
Table 2. (Continued)

| Prefix | Specimen Num. | Genus    | Species | element | NISP | Locality Name                          | Formation | Age            |
|--------|---------------|----------|---------|---------|------|----------------------------------------|-----------|----------------|
| AMNH   | 12675         | Hyrachyus | † eximius† | tibia   | 1    | Black's Fork above Millersville        | Bridger   | Bridgerian     |
| AMNH   | 93050         | Hyrachyus | † eximius† | femur   | 1    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 93050         | Hyrachyus | † eximius† | radius  | 1    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 93050         | Hyrachyus | † eximius† | ulna    | 1    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 93052         | Hyrachyus | † eximius† | femur   | 1    | Grizzly Buttes                         | Bridger   | Bridgerian     |
| AMNH   | 93058         | Hyrachyus | † eximius† | tibia   | 1    | Grizzly Buttes                         | Bridger   | Bridgerian     |
| AMNH   | 93059         | Hyrachyus | † eximius† | tibia   | 1    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 93060         | Hyrachyus | † eximius† | femur   | 1    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 93064         | Hyrachyus | † eximius† | femur   | 1    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 93065         | Hyrachyus | † eximius† | tibia   | 1    | Grizzly Buttes                         | Bridger   | Bridgerian     |
| AMNH   | 93066         | Hyrachyus | † eximius† | tibia   | 1    | Bridger                                | Bridger   | Bridgerian     |
| AMNH   | 1644-A        | Hyrachyus | † eximius† | femur   | 1    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 5065-A        | Hyrachyus | † eximius† | humerus | 1    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 5065-A        | Hyrachyus | † eximius† | ulna    | 1    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 1602          | Hyrachyus | † eximius† | metapodial | 8   | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 1607          | Hyrachyus | † eximius† | metapodial | 1   | Bridger                                | Bridger   | Bridgerian     |
| AMNH   | 1615          | Hyrachyus | † eximius† | metapodal | 1    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 1621          | Hyrachyus | † eximius† | metapodal | 1    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 1629          | Hyrachyus | † eximius† | metapodal | 5    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 1645          | Hyrachyus | † eximius† | metapodal | 3    | Twin Buttes                            | Bridger   | Bridgerian     |
| AMNH   | 5181          | Hyrachyus | † eximius† | metapodal | 3    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 11693         | Hyrachyus | † eximius† | metapodal | 8    | Bridger                                | Bridger   | Bridgerian     |
| AMNH   | 12353         | Hyrachyus | † eximius† | metapodal | 3    | Cat-tail Spring                        | Bridger   | Bridgerian     |
| AMNH   | 12368         | Hyrachyus | † eximius† | metapodal | 3    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 12665         | Hyrachyus | † eximius† | metapodal | 3    | Grizzly Buttes                         | Bridger   | Bridgerian     |
| AMNH   | 12673         | Hyrachyus | † eximius† | metapodal | 5    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 12674         | Hyrachyus | † eximius† | metapodal | 2    | Bridger                                | Bridger   | Bridgerian     |
| AMNH   | 12675         | Hyrachyus | † eximius† | metapodal | 5    | Kinney Ranch                           | Bridger   | Bridgerian     |
| AMNH   | 12765         | Hyrachyus | † eximius† | metapodal | 3    | Black's Fork above Millersville        | Bridger   | Bridgerian     |
| AMNH   | 93050         | Hyrachyus | † eximius† | metapodal | 1    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 93060         | Hyrachyus | † eximius† | metapodal | 1    | Bridger                                | Bridger   | Bridgerian     |
| AMNH   | 93061         | Hyrachyus | † eximius† | metapodal | 4    | Grizzly Buttes                         | Bridger   | Bridgerian     |
| AMNH   | 93064         | Hyrachyus | † eximius† | metapodal | 1    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 105435        | Hyrachyus | † eximius† | metapodal | 1    | Tabernacle Butte                       | Bridger   | Bridgerian     |
| AMNH   | 1644-A        | Hyrachyus | † eximius† | metapodal | 2    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 1602          | Hyrachyus | † eximius† | phalanx  | 3    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 1626          | Hyrachyus | † eximius† | phalanx  | 1    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 1635          | Hyrachyus | † eximius† | phalanx  | 1    | Bridger Basin                          | Bridger   | Bridgerian     |
| AMNH   | 11693         | Hyrachyus | † eximius† | phalanx  | 11   | Bridger                                | Bridger   | Bridgerian     |
| AMNH   | 12353         | Hyrachyus | † eximius† | phalanx  | 4    | Cat-tail Spring                        | Bridger   | Bridgerian     |
| AMNH   | 12673         | Hyrachyus | † eximius† | phalanx  | 6    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 12675         | Hyrachyus | † eximius† | phalanx  | 1    | Black's Fork above Millersville        | Bridger   | Bridgerian     |
| AMNH   | 93064         | Hyrachyus | † eximius† | phalanx  | 4    | Henry's Fork LT                        | Bridger   | Bridgerian     |
| AMNH   | 1644-A        | Hyrachyus | † eximius† | phalanx  | 4    | Bridger Basin                          | Bridger   | Bridgerian     |

(Osteropathology in Rhinocerotidae from 50 Million Years to the Present)
| Prefix | Specimen Num. | Genus | Species | element | NISP | Locality Name | Formation | Age |
|--------|---------------|-------|---------|---------|------|---------------|-----------|-----|
| AMNH 1602 | Hyracychus† | eximius† | astragalus | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1607 | Hyracychus† | eximius† | astragalus | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1607 | Hyracychus† | eximius† | podial | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1615 | Hyracychus† | eximius† | astragalus | 2 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1615 | Hyracychus† | eximius† | calcaneum | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1615 | Hyracychus† | eximius† | podial | 2 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1612 | Hyracychus† | eximius† | calcaneum | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1626 | Hyracychus† | eximius† | podial | 2 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1629 | Hyracychus† | eximius† | podial | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1635 | Hyracychus† | eximius† | astragalus | 2 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1644 | Hyracychus† | eximius† | calcaneum | 2 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1644 | Hyracychus† | eximius† | podial | 2 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1645 | Hyracychus† | eximius† | astragalus | 1 | Twin Buttes | Bridger | Bridgerian |
| AMNH 1645 | Hyracychus† | eximius† | calcaneum | 1 | Twin Buttes | Bridger | Bridgerian |
| AMNH 1645 | Hyracychus† | eximius† | podial | 2 | Twin Buttes | Bridger | Bridgerian |
| AMNH 5056 | Hyracychus† | eximius† | astragalus | 1 | Grizzly Buttes | Bridger | Bridgerian |
| AMNH 5056 | Hyracychus† | eximius† | calcaneum | 1 | Grizzly Buttes | Bridger | Bridgerian |
| AMNH 5056 | Hyracychus† | eximius† | navicular | 1 | Grizzly Buttes | Bridger | Bridgerian |
| AMNH 5056 | Hyracychus† | eximius† | podial | 3 | Grizzly Buttes | Bridger | Bridgerian |
| AMNH 5181 | Hyracychus† | eximius† | magnum | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 5196 | Hyracychus† | eximius† | astragalus | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 5196 | Hyracychus† | eximius† | calcaneum | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 11693 | Hyracychus† | eximius† | podial | 9 | Bridger | Bridger | Bridgerian |
| AMNH 11712 | Hyracychus† | eximius† | astragalus | 2 | Church Buttes | Bridger | Bridgerian |
| AMNH 11712 | Hyracychus† | eximius† | calcaneum | 1 | Church Buttes | Bridger | Bridgerian |
| AMNH 12179 | Hyracychus† | eximius† | astragalus | 1 | Mid. Cottonwood Cr. | Bridger | Bridgerian |
| AMNH 12179 | Hyracychus† | eximius† | calcaneum | 1 | Mid. Cottonwood Cr. | Bridger | Bridgerian |
| AMNH 12225 | Hyracychus† | eximius† | podial | 1 | Summer's Dry Cr'k | Bridger | Bridgerian |
| AMNH 12353 | Hyracychus† | eximius† | calcaneum | 1 | Cat-tail Spring | Bridger | Bridgerian |
| AMNH 12353 | Hyracychus† | eximius† | podial | 6 | Cat-tail Spring | Bridger | Bridgerian |
| AMNH 12353 | Hyracychus† | eximius† | sesimoid | 3 | Cat-tail Spring | Bridger | Bridgerian |
| AMNH 12368 | Hyracychus† | eximius† | podial | 11 | Henry's Fork LT | Bridger | Bridgerian |
| AMNH 12665 | Hyracychus† | eximius† | astragalus | 2 | Grizzly Buttes | Bridger | Bridgerian |
| AMNH 12665 | Hyracychus† | eximius† | calcaneum | 1 | Grizzly Buttes | Bridger | Bridgerian |
| AMNH 12665 | Hyracychus† | eximius† | podial | 6 | Grizzly Buttes | Bridger | Bridgerian |
| AMNH 12673 | Hyracychus† | eximius† | calcaneum | 1 | Henry's Fork LT | Bridger | Bridgerian |
| AMNH 12673 | Hyracychus† | eximius† | podial | 10 | Henry's Fork LT | Bridger | Bridgerian |
| AMNH 12674 | Hyracychus† | eximius† | astragalus | 1 | Bridger | Bridger | Bridgerian |
| AMNH 12674 | Hyracychus† | eximius† | calcaneum | 1 | Bridger | Bridger | Bridgerian |
| AMNH 12674 | Hyracychus† | eximius† | podial | 6 | Bridger | Bridger | Bridgerian |
| AMNH 12675 | Hyracychus† | eximius† | calcaneum | 1 | Kinney Ranch | Bridger | Bridgerian |
| AMNH 12675 | Hyracychus† | eximius† | podial | 1 | Henry's Fork LT | Bridger | Bridgerian |
| AMNH 12675 | Hyracychus† | eximius† | calcaneum | 1 | Grizzly Buttes East | Bridger | Bridgerian |
| AMNH 12675 | Hyracychus† | eximius† | calcaneum partial | 1 | Grizzly Buttes East | Bridger | Bridgerian |
| AMNH 12675 | Hyracychus† | eximius† | cuboid | 1 | Grizzly Buttes East | Bridger | Bridgerian |

(Continued)
| Prefix | Specimen Num. | Genus | Species | element | NISP | Locality Name | Formation | Age |
|--------|---------------|-------|---------|---------|------|---------------|-----------|-----|
| AMNH 93064 | Hyrachyus † | eximius † | astragalus, calcaneum, and podial (articulated) | 1 | Henry's Fork LT | Bridger | Bridgerian |
| AMNH 93064 | Hyrachyus † | eximius † | podial | 1 | Henry's Fork LT | Bridger | Bridgerian |
| AMNH 98726 | Hyrachyus † | eximius † | pisiform | 1 | S. Hyopsodus Hill, Tabernacle Butte | Bridger | Bridgerian |
| AMNH 105435 | Hyrachyus † | eximius † | astragalus | 1 | Tabernacle Butte | Bridger | Bridgerian |
| AMNH 12665-A | Hyrachyus † | eximius † | astragal | 1 | Grizzly Buttes | Bridger | Bridgerian |
| AMNH 12665-A | Hyrachyus † | eximius † | calcaneum | 1 | Grizzly Buttes | Bridger | Bridgerian |
| AMNH 1536-A | Hyrachyus † | eximius † | astragalus | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1592-A | Hyrachyus † | eximius † | astragalus | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1596-A | Hyrachyus † | eximius † | astragalus | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1644-A | Hyrachyus † | eximius † | calcaneum | 1 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1644-A | Hyrachyus † | eximius † | podial | 4 | Bridger Basin | Bridger | Bridgerian |
| AMNH 5065-B | Hyrachyus † | eximius † | calcaneum | 3 | Bridger Basin | Bridger | Bridgerian |
| AMNH 1602 | Hyrachyus † | eximius † | axis | 1 | Bridger Basin | Bridger | Bridgerian |
| UCMP 32011 | Trigonias † | osborn † | left femur | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | humerus | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | left humerus | 2 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | left radius | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32012 | Trigonias † | osborn † | left ulna | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | left scapula | 2 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | left tibia | 2 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | left fibula | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32012 | Trigonias † | osborn † | left tibia | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | patella | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | right tibiufibula | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | right ulna | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32012 | Trigonias † | osborn † | right radius | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | right ulna | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | left femur | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | patellae | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | left humerus | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | right humerus | 2 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | metatarsal | 23 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | metatarsal | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | left metatarsal | 2 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | metatarsal | 4 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | metatarsal | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | phalanx | 33 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | phalanx 3 | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | astragalus | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | calcaneum | 2 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | cuneiform | 8 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | left podial | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | carpal | 1 | Figgins Quarry | White River | Chadronian |
| UCMP 32011 | Trigonias † | osborn † | podial | 1 | Figgins Quarry | White River | Chadronian |

(Continued)
Table 2. (Continued)

| Prefix | Specimen Num. | Genus  | Species | element | NISP | Locality Name | Formation | Age   |
|--------|---------------|--------|---------|---------|------|---------------|-----------|-------|
| UCMP   | 32011         | Trigonias† | osborni† | pisiform | 4    | Figgins Quarry | White River | Chadronian |
| UCMP   | 32011         | Trigonias† | osborni† | podial   | 2    | Figgins Quarry | White River | Chadronian |
| UCMP   | 32011         | Trigonias† | osborni† | navicular| 3    | Figgins Quarry | White River | Chadronian |
| UCMP   | 32011         | Trigonias† | osborni† | left pisiform | 1 | Figgins Quarry | White River | Chadronian |
| UCMP   | 32011         | Trigonias† | osborni† | right pisiform | 1 | Figgins Quarry | White River | Chadronian |
| AMNH   | 144571        | Menoceras† | arikarense† | scapula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144572        | Menoceras† | arikarense† | scapula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144573        | Menoceras† | arikarense† | scapula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144574        | Menoceras† | arikarense† | scapula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144575        | Menoceras† | arikarense† | scapula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144576        | Menoceras† | arikarense† | scapula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144577        | Menoceras† | arikarense† | scapula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144578        | Menoceras† | arikarense† | scapula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144579        | Menoceras† | arikarense† | scapula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 14213         | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 14213         | Menoceras† | arikarense† | radius-ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 14214         | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 14214         | Menoceras† | arikarense† | proximal tibia | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 22486         | Menoceras† | arikarense† | femur | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 22486         | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 22487         | Menoceras† | arikarense† | radius | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 22487         | Menoceras† | arikarense† | fibula | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 22487         | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 22487         | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144597        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144598        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144599        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144600        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144602        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144603        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144604        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144605        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144606        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144607        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144608        | Menoceras† | arikarense† | ulna | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144580        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144581        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144582        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144583        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144585        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144586        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144587        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144588        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144589        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144590        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144591        | Menoceras† | arikarense† | humerus | 1 | Agate Spring Quarry | Harrison | Arikareean |

(Continued)
Table 2. (Continued)

| Prefix | Specimen Num. | Genus | Species | element | NISP | Locality Name | Formation | Age |
|--------|---------------|-------|---------|---------|------|---------------|-----------|-----|
| AMNH   | 144592        | Menoceras | arikarense | humerus | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144593        | Menoceras | arikarense | humerus | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144594        | Menoceras | arikarense | humerus | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144595        | Menoceras | arikarense | humerus | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144596        | Menoceras | arikarense | humerus | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144609        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144610        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144611        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144612        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144616        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144613        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144614        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144615        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144617        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144618        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144619        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144622        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144621        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144620        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144623        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144625        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144624        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144627        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144628        | Menoceras | arikarense | radius  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144636        | Menoceras | arikarense | fibula  | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144584        | Menoceras | arikarense | humerus | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 86090         | Menoceras | arikarense | partial metapodials | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144626        | Menoceras | arikarense | metapodial | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144627        | Menoceras | arikarense | metapodial | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144628        | Menoceras | arikarense | metapodial | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 86090         | Menoceras | arikarense | left phalanx | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 86091         | Menoceras | arikarense | right phalanx | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 86092         | Menoceras | arikarense | phalanx | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144629        | Menoceras | arikarense | phalanx | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144632        | Menoceras | arikarense | phalanx | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144630        | Menoceras | arikarense | phalanx | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 144631        | Menoceras | arikarense | phalanx | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 86090         | Menoceras | arikarense | astragalus | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 86090         | Menoceras | arikarense | calcaneum | 1    | Agate Spring Quarry | Harrison | Arikareean |
| AMNH   | 86090         | Menoceras | arikarense | podial | 2    | Agate Spring Quarry | Harrison | Arikareean |
| UW     | 52334         | Diceratherium | niobrarense | scapula | 1    | John Day Formation | John Day Formation | Whitneyan |
| UW     | 58203         | Diceratherium | niobrarense | scapula | 1    | south canyon | John Day Formation | Whitneyan |
| UCMP   | 2289          | Diceratherium | niobrarense | pelvis frag | 1    | Logan Butte | John Day Formation | Whitneyan |
| Prefix | Specimen Num. | Genus   | Species  | element | NISP | Locality Name   | Formation           | Age       |
|--------|---------------|---------|----------|---------|------|-----------------|----------------------|-----------|
| UW     | 26414         | Diceratherium† | niobrarense† | patella | 1    | Blue Basin      | John Day Formation   | Whitneyan |
| UW     | 26536         | Diceratherium† | niobrarense† | distal femur | 1 | John Day Formation | John Day Formation    | Whitneyan |
| UW     | 28151         | Diceratherium† | niobrarense† | femoral head | 1 | John Day Formation | John Day Formation    | Whitneyan |
| UW     | 52334         | Diceratherium† | niobrarense† | distal femur | 1 | John Day Formation | John Day Formation    | Whitneyan |
| UW     | 53301         | Diceratherium† | niobrarense† | tibia | 1 | picture gorge 14 | John Day Formation    | Whitneyan |
| UW     | 53302         | Diceratherium† | niobrarense† | proximal tibia | 1 | picture gorge 51 | John Day Formation    | Whitneyan |
| UW     | 53323         | Diceratherium† | niobrarense† | tibia (juvenile) | 1 | picture gorge 54 | John Day Formation    | Whitneyan |
| UW     | 53324         | Diceratherium† | niobrarense† | femur (juvenile) | 1 | picture gorge 54 | John Day Formation    | Whitneyan |
| UW     | 53325         | Diceratherium† | niobrarense† | distal femur | 1 | picture gorge 20 | John Day Formation    | Whitneyan |
| UW     | 53430         | Diceratherium† | niobrarense† | distal femur | 1 | picture gorge 54 | John Day Formation    | Whitneyan |
| UW     | 55086         | Diceratherium† | niobrarense† | tibia | 1 | North Wash Level 5 | John Day Formation    | Whitneyan |
| UW     | 58755         | Diceratherium† | niobrarense† | tibia | 1 | Blue Canyon      | John Day Formation    | Whitneyan |
| UW     | 58755         | Diceratherium† | niobrarense† | limb bone | 2 | Blue Canyon      | John Day Formation    | Whitneyan |
| UW     | 533315        | Diceratherium† | niobrarense† | humerus | 1 | picture gorge 12 | John Day Formation    | Whitneyan |
| UCMP   | 145           | Diceratherium† | niobrarense† | distal femur and podial | 1 | John Day Whitneyan General | John Day Whitneyan General | Whitneyan |
| UCMP   | 566           | Diceratherium† | niobrarense† | proximal radioulna | 1 | John Day Whitneyan General | John Day Whitneyan General | Whitneyan |
| UCMP   | 75260         | Diceratherium† | niobrarense† | proximal humerus | 1 | South Canyon 2   | John Day Formation    | Whitneyan |
| UCMP   | 75261         | Diceratherium† | niobrarense† | distal humerus | 1 | South Canyon 2   | John Day Formation    | Whitneyan |
| UCMP   | 75261         | Diceratherium† | niobrarense† | proximal humerus | 1 | South Canyon 2   | John Day Formation    | Whitneyan |
| UCMP   | 75282         | Diceratherium† | niobrarense† | femur | 1 | South Canyon 2   | John Day Formation    | Whitneyan |
| UCMP   | M1691         | Diceratherium† | niobrarense† | distal femur | 1 | Logan Butte      | John Day Formation    | Whitneyan |
| UCMP   | M1691         | Diceratherium† | niobrarense† | partial fibula | 1 | Logan Butte      | John Day Formation    | Whitneyan |
| UCMP   | M1691         | Diceratherium† | niobrarense† | tibia | 1 | Logan Butte      | John Day Formation    | Whitneyan |
| UCMP   | M2107         | Diceratherium† | niobrarense† | distal femur | 1 | Seigfried's 4    | John Day Formation    | Whitneyan |
| UW     | 26563         | Diceratherium† | niobrarense† | distal metapodial | 1 | John Day Formation | John Day Formation    | Whitneyan |
| UW     | 26879         | Diceratherium† | niobrarense† | distal metapodial | 1 | John Day Formation | John Day Formation    | Whitneyan |

(Continued)
| Prefix | Specimen Num. | Genus | Species | element | NISP | Locality Name | Formation | Age       |
|--------|---------------|-------|---------|---------|------|---------------|-----------|-----------|
| UW     | 43529         | Diceratherium† niobrarense† | metatarsal | 1       | John Day Formation | John Day Formation | Whitneyan |
| UW     | 52334         | Diceratherium† niobrarense† | metapodial | 1       | picture gorge | John Day Formation | Whitneyan |
| UW     | 52334         | Diceratherium† niobrarense† | distal metapodial | 1       | John Day Formation | John Day Formation | Whitneyan |
| UW     | 53322         | Diceratherium† niobrarense† | metapodial | 1       | picture gorge 16 | John Day Formation | Whitneyan |
| UW     | 55086         | Diceratherium† niobrarense† | metatarsal | 1       | North Wash Level 5 | John Day Formation | Whitneyan |
| UCMP   | 145           | Diceratherium† niobrarense† | right metatarsal 3 | 1       | John Day Whitneyan General | John Day Formation | Whitneyan |
| UCMP   | M1691         | Diceratherium† niobrarense† | left metapodial | 1       | Logan Butte | John Day Formation | Whitneyan |
| UCMP   | M1691         | Diceratherium† niobrarense† | metapodial | 5       | Logan Butte | John Day Formation | Whitneyan |
| UW     | 52334         | Diceratherium† niobrarense† | phalanx | 2       | John Day Formation | John Day Formation | Whitneyan |
| UW     | 53322         | Diceratherium† niobrarense† | phalanx | 1       | picture gorge 16 | John Day Formation | Whitneyan |
| UCMP   | 788           | Diceratherium† niobrarense† | phalanx | 1       | John Day Whitneyan General | John Day Formation | Whitneyan |
| UCMP   | 75035         | Diceratherium† niobrarense† | medial phalanx | 1       | South Canyon 2 | John Day Formation | Whitneyan |
| UCMP   | M1691         | Diceratherium† niobrarense† | phalanx | 3       | Logan Butte | John Day Formation | Whitneyan |
| UW     | 52334         | Diceratherium† niobrarense† | podial | 2       | John Day Formation | John Day Formation | Whitneyan |
| UW     | 53322         | Diceratherium† niobrarense† | podial | 2       | picture gorge 16 | John Day Formation | Whitneyan |
| UW     | 54947         | Diceratherium† niobrarense† | astragalus and partial calcanium | 1       | picture gorge 8'6" up | John Day Formation | Whitneyan |
| UW     | 54947         | Diceratherium† niobrarense† | podial | 2       | picture gorge 8'6" up | John Day Formation | Whitneyan |
| UW     | 55086         | Diceratherium† niobrarense† | podial | 2       | North Wash Level 5 | John Day Formation | Whitneyan |
| UW     | 75665         | Diceratherium† niobrarense† | distal podial | 1       | picture gorge 29 | John Day Formation | Whitneyan |
| UCMP   | 788           | Diceratherium† niobrarense† | tarsal | 1       | John Day Whitneyan General | John Day Formation | Whitneyan |
| UCMP   | 75033         | Diceratherium† niobrarense† | navicular | 1       | South Canyon 2 | John Day Formation | Whitneyan |
| UCMP   | 75035         | Diceratherium† niobrarense† | lunar | 1       | South Canyon 2 | John Day Formation | Whitneyan |
| UCMP   | 75120         | Diceratherium† niobrarense† | astragalus | 1       | South Canyon 2 | John Day Formation | Whitneyan |
| UCMP   | 76104         | Diceratherium† niobrarense† | podial | 2       | South Canyon 2 | John Day Formation | Whitneyan |
| UCMP   | 75260         | Diceratherium† niobrarense† | podial | 1       | South Canyon 2 | John Day Formation | Whitneyan |
| UCMP   | 75348         | Diceratherium† niobrarense† | middle podial | 1       | South Canyon 2 | John Day Formation | Whitneyan |

(Continued)
Table 2. (Continued)

| Prefix | Specimen Num. | Genus | Species | element | NISP | Locality Name | Formation | Age        |
|--------|---------------|-------|---------|---------|------|---------------|-----------|------------|
| UCMP   | 76104         | Diceratherium† niobrarense† | right podial | 1 | South Canyon 2 | John Day Formation | Whitneyain |
| UCMP   | M1691         | Diceratherium† niobrarense† | articulated astragalus and calcaneum | 1 | Logan Butte | John Day Formation | Whitneyain |
| UW     | 58755         | Diceratherium† niobrarense† | centrum | 1 | Blue Canyon | John Day Formation | Whitneyain |
| UCMP   | 22552         | Aphelops† mutilis† | left femur | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30166         | Aphelops† mutilis† | tibia | 1 | Higgins Quarry A | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | dist end of ulna | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | distal humerus | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30267         | Aphelops† mutilis† | left femur | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30268         | Aphelops† mutilis† | partial distal tibia | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | patella | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | tibia | 2 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | ulna | 2 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30267         | Aphelops† mutilis† | partial distal tibia | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30267         | Aphelops† mutilis† | patella | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30268         | Aphelops† mutilis† | patella | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | patella | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | tibia | 1 | Higgins Quarry A | Ogalla Group | Hemphilian |
| UCMP   | 30117         | Aphelops† mutilis† | ulna | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31118         | Aphelops† mutilis† | tibia | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31119         | Aphelops† mutilis† | humerus | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31120         | Aphelops† mutilis† | humerus | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31121         | Aphelops† mutilis† | humerus | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31122         | Aphelops† mutilis† | humerus | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31127         | Aphelops† mutilis† | patella | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31128         | Aphelops† mutilis† | patella | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31129         | Aphelops† mutilis† | patella | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | partial metacarpal | 4 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | metacarpal | 5 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31123         | Aphelops† mutilis† | metacarpal | 3 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 32066         | Aphelops† mutilis† | metatarsal | 11 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 32067         | Aphelops† mutilis† | metatarsal | 3 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 32068         | Aphelops† mutilis† | metatarsal | 3 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Aphelops† mutilis† | phalanx 3 | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30267         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30268         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30269         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30270         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30271         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30272         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30273         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30274         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30275         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31127         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31128         | Aphelops† mutilis† | phalanx | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |

(Continued)
| Prefix | Specimen Num. | Genus | Species | element | NISP | Locality Name | Formation | Age |
|--------|---------------|-------|---------|---------|------|---------------|-----------|-----|
| UCMP   | 31129         | Aphelops† | mutila† | phalanx | 1    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31130         | Aphelops† | mutila† | phalanx | 1    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31131         | Aphelops† | mutila† | phalanx | 1    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31132         | Aphelops† | mutila† | phalanx | 1    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31133         | Aphelops† | mutila† | phalanx | 1    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Teleoceras† | mutila† | carpals | 6    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Teleoceras† | mutila† | right calcaneum | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Teleoceras† | mutila† | carpal | 1    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30266         | Teleoceras† | mutila† | tarsal | 1    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 30267         | Teleoceras† | mutila† | calcaneum | 1 | Coffee Ranch Quarry 3 | Ogalla Group | Hemphilian |
| UCMP   | 30267         | Teleoceras† | mutila† | tarsal | 1    | Coffee Ranch Quarry 4 | Ogalla Group | Hemphilian |
| UCMP   | 30268         | Teleoceras† | mutila† | tarsal | 1    | Coffee Ranch Quarry 5 | Ogalla Group | Hemphilian |
| UCMP   | 30269         | Teleoceras† | mutila† | tarsal | 1    | Coffee Ranch Quarry 6 | Ogalla Group | Hemphilian |
| UCMP   | 30270         | Teleoceras† | mutila† | tarsal | 1    | Coffee Ranch Quarry 7 | Ogalla Group | Hemphilian |
| UCMP   | 31124         | Aphelops† | mutila† | astragalus | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31125         | Aphelops† | mutila† | astragalus | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31125         | Aphelops† | mutila† | calcaneum | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31125         | Teleoceras† | mutila† | calcaneum | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31126         | Teleoceras† | mutila† | calcaneum | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31127         | Teleoceras† | mutila† | calcaneum | 1 | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31127         | Teleoceras† | mutila† | carpal | 9    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 31128         | Teleoceras† | mutila† | tarsal | 1    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UCMP   | 32066         | Teleoceras† | mutila† | podial | 1    | Coffee Ranch Quarry 2 | Ogalla Group | Hemphilian |
| UO     | 2772          | Teleoceras† | hickš† | distal humerus | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UO     | 4163          | Teleoceras† | hickš† | proximal radius | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UO     | 9634          | Teleoceras† | hickš† | ulna | 1    | McKay Reservoir 1 | Shutler | Hemphilian |
| UO     | 17071         | Teleoceras† | hickš† | ulna | 1    | McKay Reservoir 1 | Shutler | Hemphilian |
| UO     | 17075         | Teleoceras† | hickš† | ulna | 1    | McKay Reservoir 1 | Shutler | Hemphilian |
| UO     | 49287         | Teleoceras† | hickš† | distal humerus | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UCMP   | 113504        | Teleoceras† | hickš† | humerus | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UCMP   | 113507        | Teleoceras† | hickš† | tibiofibula | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UCMP   | 113507        | Teleoceras† | hickš† | partial ulna | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UCMP   | 113518        | Teleoceras† | hickš† | tibia | 1    | McKay Reservoir 1 | Shutler | Hemphilian |
| UCMP   | 113519        | Teleoceras† | hickš† | partial ulna | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UCMP   | 113519        | Teleoceras† | hickš† | distal humerus | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UCMP   | 113519        | Teleoceras† | hickš† | proximal humerus | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UCMP   | 113526        | Teleoceras† | hickš† | distal humerus | 1 | McKay Reservoir 1 | Shutler | Hemphilian |
| UCMP   | 303           | Teleoceras† | hickš† | metapodial | 1 | McKay Reservoir 2 | Rattlesnake | Hemphilian |
| UCMP   | 306           | Teleoceras† | hickš† | metapodial | 1 | McKay Reservoir 3 | Rattlesnake | Hemphilian |
| UCMP   | 474           | Teleoceras† | hickš† | metapodial | 1 | McKay Reservoir 4 | Mascall | Barstovian |
| UCMP   | 475           | Teleoceras† | hickš† | metapodial | 1 | McKay Reservoir 5 | Mascall | Barstovian |
| UCMP   | 477           | Teleoceras† | hickš† | metapodial | 1 | McKay Reservoir 6 | Rattlesnake | Hemphilian |
| UO     | 5056          | Teleoceras† | hickš† | metapodial | 1 | McKay Reservoir 7 | Shutler | Hemphilian |
| UO     | 8049          | Teleoceras† | hickš† | metapodial | 1 | McKay Reservoir 8 | Shutler | Hemphilian |
| UO     | 8053          | Teleoceras† | hickš† | metapodial | 1 | McKay Reservoir 9 | Shutler | Hemphilian |
| UO     | 8142          | Teleoceras† | hickš† | metapodial | 1 | McKay Reservoir 10 | Shutler | Hemphilian |

(Continued)
Table 2. (Continued)

| Prefix | Specimen Num. | Genus | Species | element | NISP | Locality Name     | Formation   | Age      |
|--------|----------------|-------|---------|---------|------|-------------------|-------------|----------|
| UCMP   | 23181          | Teleoceras† | hicki† | metacarpal 3 | 1    | McKay Reservoir 11 | Rattlesnake 11 | Hemphilian |
| UCMP   | 23182          | Teleoceras† | hicki† | metatarsal 3 | 1    | McKay Reservoir 3 | Rattlesnake 11 | Hemphilian |
| UCMP   | 113514         | Teleoceras† | hicki† | metapodial | 1    | McKay Reservoir 4 | Shutler         | Hemphilian |
| UCMP   | 113517         | Teleoceras† | hicki† | metapodial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113520         | Teleoceras† | hicki† | metapodial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113521         | Teleoceras† | hicki† | metapodial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113522         | Teleoceras† | hicki† | metapodial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113523         | Teleoceras† | hicki† | metapodial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113524         | Teleoceras† | hicki† | metapodial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 10829          | Teleoceras† | hicki† | phalanx | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113505         | Teleoceras† | hicki† | phalanx | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113506         | Teleoceras† | hicki† | phalanx | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113509         | Teleoceras† | hicki† | phalanx | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 2094           | Teleoceras† | hicki† | calcaneum | 1   | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 4136           | Teleoceras† | hicki† | podial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 4167           | Teleoceras† | hicki† | podial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 8054           | Teleoceras† | hicki† | astragalus | 1   | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 17063          | Teleoceras† | hicki† | podial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 21886          | Teleoceras† | hicki† | astragalus | 1   | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 23178          | Teleoceras† | hicki† | lunar | 1    | McKay Reservoir 2 | Rattlesnake 16 | Hemphilian |
| UCMP   | 23179          | Teleoceras† | hicki† | calcaneum | 1   | McKay Reservoir 3 | Rattlesnake     | Hemphilian |
| UCMP   | 113510         | Teleoceras† | hicki† | pisiform | 1    | McKay Reservoir 4 | Shutler         | Hemphilian |
| UCMP   | 113511         | Teleoceras† | hicki† | carpal | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113512         | Teleoceras† | hicki† | podial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113513         | Teleoceras† | hicki† | podial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113514         | Teleoceras† | hicki† | carpal | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113515         | Teleoceras† | hicki† | pisiform | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113516         | Teleoceras† | hicki† | podial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113519         | Teleoceras† | hicki† | podial | 4    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113523         | Teleoceras† | hicki† | carpal | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 10397/ 5703    | Teleoceras† | hicki† | podial | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UCMP   | 113519         | Teleoceras† | hicki† | podial | 3    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | G1675          | Teleoceras† | hicki† | calcaneum | 1 | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | G1676          | Teleoceras† | hicki† | astragalus | 1   | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 4184           | Teleoceras† | hicki† | axis | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 25504          | Teleoceras† | hicki† | axis | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| UO     | 8055           | Teleoceras† | hicki† | NA | 1    | McKay Reservoir 1 | Shutler         | Hemphilian |
| AMNH   | 27757          | Diceros    | bicornis | metapodial | 9    | Kenya     | NA            | Recent    |
| AMNH   | 27757          | Diceros    | bicornis | patella | 2    | Kenya     | NA            | Recent    |
| AMNH   | 27757          | Diceros    | bicornis | calcaneum | 1    | Kenya     | NA            | Recent    |
| AMNH   | 27757          | Diceros    | bicornis | podial | 16   | Kenya     | NA            | Recent    |
| AMNH   | 27757          | Diceros    | bicornis | pisiform | 1    | Kenya     | NA            | Recent    |
| AMNH   | 27757          | Diceros    | bicornis | phalanx | 24   | Kenya     | NA            | Recent    |
| AMNH   | 27757          | Diceros    | bicornis | humerus | 1    | Kenya     | NA            | Recent    |
| AMNH   | 27757          | Diceros    | bicornis | radius | 1    | Kenya     | NA            | Recent    |
| AMNH   | 27757          | Diceros    | bicornis | ulna | 2    | Kenya     | NA            | Recent    |

(Continued)
horns, and was a cursorial browser [11, 23]. The rhinocerotid with the earliest first appearance datum (FAD) included in this study is the basal rhinocerotid *Trigonias osborni*. *T. osborni* also lacked horns and was substantially larger than *H. eximius* at about 677 kg [24,25]. *

*Menoceras arikarense* emigrated from Europe in the late Oligocene or early Miocene (24.8–20.43 Ma) and had a mass around 375 kg [24,25]. *M. arikarense* is notable for two firsts: horns and grazing [5]. *

*Diceratherium niobrarense* is larger than *M. arikarense* (about 1010 kg [5]). Although *D. niobrarense* also displays laterally paired rostral horns, it is thought be descended from *Subhyracodon* and is not considered a sister group of *M. arikarense* [5,18]. This rhinocerotid was present in North America in the early and middle Miocene (24.8–20.43 Ma) and was probably a browser [5]. Both *M. arikarense* and *D. niobrarense* show morphologies characteristic of increased graviportality: increased bone robusticity, more vertically-oriented pelvis [26], and widening rib cage [5]. Limb length also decreased relative to mass [5]. *

*Aphelops mutilis* and *Teleoceras hicksi* are similar to modern rhinos in graviportal morphology and robust limbs [5]. *A. mutilis* was a hornless aceratherine browser known from the middle Miocene to the beginning of the Pliocene (10.3–4.9 Ma) and is estimated to have weighed around 1840 kg. *T. hicksi* (10.3–4.9 Ma) is morphologically similar to aquatic hippos [5], but has highly hypsodont teeth [5] with enamel oxygen isotope ratios similar to terrestrial herbivores [29]. *T. hicksi* is estimated to have weighed around 1660 kg, is thought to have a small nasal horn and is one of the last rhinocerotids in the North American fossil record [30].

From the five modern taxa we examined in planning this study we chose *Diceros bicornis* (the black rhino) as the modern exemplar. *Diceros* (5.3332 Ma to present) weighs 800–1,350 kg [24] and is a browser with a prehensile lip specialized to grab foliage [26].

Table 2. (Continued)

| Prefix | Specimen Num. | Genus | Species | element | NISP | Locality Name | Formation | Age |
|--------|---------------|-------|---------|---------|------|---------------|-----------|-----|
| AMNH 27757 | Diceros bicornis | scapula | 1 | Kenya | NA | Recent |
| AMNH 27757 | Diceros bicornis | femur | 1 | Kenya | NA | Recent |
| AMNH 27757 | Diceros bicornis | fibula | 1 | Kenya | NA | Recent |
| AMNH 81805 | Diceros bicornis | ulna | 2 | South Africa | NA | Recent |
| AMNH 81805 | Diceros bicornis | radius | 1 | South Africa | NA | Recent |
| AMNH 81805 | Diceros bicornis | podial | 1 | South Africa | NA | Recent |
| AMNH 81805 | Diceros bicornis | calcaneum | 1 | South Africa | NA | Recent |
| AMNH 81805 | Diceros bicornis | metapodial | 1 | South Africa | NA | Recent |
| AMNH 34739 | Diceros bicornis | scapula | 1 | Kenya | NA | Recent |
| AMNH 34740 | Diceros bicornis | tibia (juvenile) | 1 | Kenya | NA | Recent |
| AMNH 34740 | Diceros bicornis | metapodial (juvenile) | 1 | Kenya | NA | Recent |
| AMNH 34740 | Diceros bicornis | calcaneum (juvenile) | 1 | Kenya | NA | Recent |
| AMNH 14136 | Diceros bicornis | metapodial | 1 | NA | NA | Recent |
| AMNH 113779 | Diceros bicornis | femur (fetal) | 1 | NA | NA | Recent |
| AMNH 113779 | Diceros bicornis | tibia (fetal) | 1 | NA | NA | Recent |
| AMNH 113779 | Diceros bicornis | scapula (fetal) | 1 | NA | NA | Recent |

Abbreviations: AMNH = American Museum of Natural History, UCMP = The University of California Museum of Paleontology, OU = The University of Oregon, UW = The University of Washington. A more detailed form of this table can be found in the supporting information.

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Data Collection Procedure

Diagnosing specific diseases from osteopathologies (often the only pathologies available for study in fossil taxa) is difficult, but not impossible. Certain recognized diseases and disorders can leave distinctive features; e.g., six fingers in a human skeleton are an indicator of polydactyly. The majority of diseases display a common range of pathologies and it is these unique combinations of pathologies that are most informative. For example, irregular holes in a bone can be caused by abnormal nutrient canals, bone infection, soft-tissue swelling, or preservation damage. Arthritis may cause bones to form these irregular holes as well as bone exostoses or thinning, lipping, and fibrous, candlewax, and lumpy bone textures. Arthritis is often labeled spondylarthropathy in non-human paleopathologic studies [17,31] to acknowledge that arthritis itself is not a specific disease, but can be caused by a range of environmental, genetic, and behavioral factors depending on the system under study [16,18,19].

Each specimen was digitally photographed with a Nikon D90 camera. The camera was hand held approximately perpendicular to the photographic plane. Elongate fossils (e.g. femora or
metapodials) were photographed in lateral view and fossils with irregular shapes (i.e. podials) were oriented in medial view. Proximal and distal articular surfaces were photographed as well for limb and foot elements. Vertebral elements were photographed in dorsal, ventral, proximal, and distal views. Extra photos were taken if a unique pathology was observed or for striking examples of specific pathologies.

The specimen number and corresponding photo numbers were recorded digitally and associated with a pathology index scoring and any qualitative observations (see supporting information). The presence or absence of pathology was recorded on site, while pathology severity scorings were determined from the digital photographs.

We quantitatively described the visible surface of each bone using a category, or binning, system. We sorted our initial qualitative descriptions of possible symptoms of disease into seven different categories. The seven categories were divided into ranks from 1 (regular bone) to 4 (severe) (Fig 2). These ranks are artificial, but should allow for consistent scoring. All scoring was completed by the first author. The seven categories are exostoses, lipping, bone texture, cavitation, foramen shape, foramen size, and articular surface modification. All categories except for ‘articular surface’ refer to the nonarticular surfaces of the bones. The categories were chosen following the methodology of Aufderheide [16], Rothschild [17, 31], and Bartosiewicz et al. [21]. Analogs of this procedure have been used for decades in anthropologic [21, 22, 32] and modern cattle [21] studies. Our goal was to quantitatively describe all irregularities observed in the osteology of the Rhinocerotidae, even if they could not immediately be categorized as a pathology.

**Category One: Exostoses.** Exostoses are formations of new bone on the surface of a bone, caused by inflammation of the periosteum. Exostoses appear as bumps or protuberances on an area of the bone that is expected to be smooth or relatively flat. This category includes ossification of the periosteum, ligaments, or muscle. Bones in rank one do not exhibit any exostoses. Bones in rank two show minor irregular bulging of bone. Bones in rank three show clear protrusions of irregular bone. Bones in rank four show a continuous irregular distortion of the non-articular surface of the bone.

**Category Two: Lipping.** Lipping occurs when osteophytes (commonly referred to as bone spurs) form as new bone on the margin of articular surfaces. They usually form as a series of merging osteophytes around the joint margin, but can occur singly as well. Bones in rank one do not exhibit any lipping. Bones in rank two show slight bulging of the bone adjacent to the articular surface. Bones in rank three show bulging of the bone surrounding the articular surface to the point where a prominent shelf is beginning to form. Bones in rank four show a prominent shelf adjacent to the articular surface. The shelf may be regular or irregular.

**Category Three: Textures.** Bone constantly remodels and rebuilds itself in response to localized stress. This can result in characteristic external textures. Care must be taken to not conflate exostoses (which has more to do with shape) with texture. Bones in rank one have a smooth texture. Bones in rank two have an elevated linear texture, termed fibrous. Bones in rank three have an elevated linear texture that is slightly bulging or uneven texture, likened to candle wax. Bones in rank four have an elevated, uneven, nonlinear texture.

**Category Four: Cavitation.** Cavitation is the first category concerned with loss of bone. A cavitation is a hole in the bone, usually caused by infection and/or decreased blood flow. Unlike the categories of foramen shape and size, these are relatively large areas of the bone that cannot be confused with vascularization. Bones in rank one do not exhibit any cavitation. Bones in rank two show a pockmarked appearance where the bone has lost integrity. Bones in rank three show small cavities. Bones in rank four show large cavities that may be linked together.

**Category Five: Articular Surface.** The articular surface forms the bony portion of a joint. Bones in rank one do not show any irregularities in the joint surface. Bones in rank two show a
pockmarked appearance where the cartilage has been worn away. Bones in rank three show bone loss on the articular surface. Bones in rank four show eburnation of the articular surface and/or osteophyte formation.
Category Six: Foramen Shape. We found bone cysts can easily be confounded with vascularization (called 'lucencies' in Regnault et al. 2–13 [13]), so we decided to describe the degree of foramen deformation instead of labeling all foramina as cysts. Cysting (pockets or holes where localized infections occurred [16,18]) was divided into two categories (foramen shape and size). Rank one consists of circular foramina on the surface of the bone. Rank two consists of elongate or ovoid foramina. Rank three consists of elongate foramina that are irregularly ovoid, but still linear. Rank four consists of irregular, nonlinear (or bent) foramina.

Category Seven: Foramen Size. Rank one consists of foramina of approximately the same size. Rank two consists of foramina which show little variation in size relative to one another. Rank three consists of foramina which show moderate variation in size relative to one another. Rank four consists of foramina which show a high degrees of variation in size relative to one another.

Each bone was also classified as appendicular and axial. To explore whether there were any overt patterns of regionalization in pathological expression, all appendicular elements were then divided into the functional categories: hindlimb or forelimb, and also developmental categories: girdle, stylopod, autopod, zeugopod. The overall percent expression of each category was tabulated and then compared relative to the total number of appendicular element.

Data Analysis

Each fossil was given a score of 1–4 for each pathology, and these scores were then averaged for each taxon and pathological category, yielding 49 results. These averaged scores were then added together for each taxon (i.e. the seven pathology categories were added together for each taxon) to create an index of pathology (IPa). The minimum score possible would therefore be seven (all pathological categories in a taxon having a score of one) and the maximum would be twenty-eight (all pathological categories in a taxon having a score of four). These average scores for each taxon do not behave as ordinal data, because they are subject to the central limit of means. That is, species averages of non-continuous data behave like continuous data, especially with large sample sizes. The smallest number of specimens we analyzed for one species was 65, more than adequate to produce this effect. Consequently, we decided it was appropriate to analyze these values using continuous-data approaches: linear regression and independent contrasts.

We tested whether mass was associated with increased osteopathologic expression in two ways. First, we ran a series of linear regressions in JMP [33] with estimated mass against each individual categorical score as well as the total index. Mass estimates for extinct taxa were calculated using the total molar length (M1-3) [34] from Radinsky 1967 for *Hyrachyus eximius* [23] and Prothero 2005 [5] for all other extinct taxa, which we found to be the most reliable of available body mass estimators. Other available proxies (femur length and humerus width) produced unreasonable mass estimates [35] for one or more of the included taxa, likely as a result of the changing degree of graviportality through the history of the rhino lineage.

The second test used Felsenstein’s [36] independent contrast (IC) method to examine the influence of shared ancestry on the relationship between mass and pathology. We constructed a fully resolved tree of just the taxa in our study by paring down the results of Cerdeño 1995 [8]. The tree was time-calibrated in RStudio [37] using the packages ‘ape’ [38] and ‘paleotree’ [28] with paleotree’s function TimePaleoPhy. The r code is available in the S2 File. We used the ‘Equal’ method within TimePaleoPhy, which prevents zero-length branches, and the setting ‘add.term = TRUE’, which gave us branch lengths that took LAD into consideration. FAD and LAD for the Equal method were determined by the temporal extent of the formation at the locality where the fossils were excavated. To implement the IC method, we used the package ‘ape’ [38], to calculate the absolute values of the difference for each pair of nodes for both mass and all seven types of pathologies, as well as for the overall IPa, under a Brownian Motion
model. The resulting contrasts for pathologic values were regressed against the contrast for the mass values. The $r^2$-squared and p-values for the non-phylogenetic linear regression versus the IC regression analysis were then compared.

**Results**

Overall, geologically older taxa show the smallest relative abundance of pathologic elements, while the greatest pathologic expression was seen in the more derived taxa, which were also the most massive taxa sampled in North America. The one exception is the extant species, *D. bicornis*, which appears later, yet is less massive and less pathologic overall than *A. mutilis* and *T. hicksi*.

When taxa are considered separately, *H. eximius* displayed low osteopathologic expression (~28%), most of which was expressed as cysting and exostoses in the podials. *T. osborni* and *D. niobrarens* also displayed a greater degree of pathologic expression in the distal elements. The *M. arikarens* fossil assemblage displayed prominent exostoses. In smaller elements (i.e. podials) the non-articular surfaces would be almost entirely composed of exostoses. *A. mutilis* and *T. hicksi* commonly contained large visible cysts and rank three, candlewax, bone texture. Only two fossils displayed eburnation, in *A. mutilis* on the articular surfaces of a proximal tibia (UCMP F-30266) and in *T. hicksi* on a distal humerus (UO F-2772). *A. mutilis* also had the highest percent expression of any one pathology (in this case, foramen shape), while *D. bicornis* had comparatively more foramen variation adjacent to the articular surfaces and fewer exostoses than the other robust taxa. One specimen (VPL M-8259) had flat ‘rice grain’ crystals on the proximal articular surface of right radius and ulna, as well as the distal articular surface of the humerus, a possible indication of gout [16, 18]. Tendon ossification was only seen in *A. mutilis* and *T. hicksi*. Of note, most of the articular surfaces of the synovial joints in both extinct and extant taxa appeared smooth and free of damage.

Overall index of pathology (IPa) scores were between 8 and 18, Table 3. The two oldest lineages, *H. eximius* and *T. osborni*, had an overall pathologic score of 8.8 and 11.06 respectively. The next oldest lineage, *D. niobrarens*, had an overall score of 12.81, while *M. arikarens* had an overall score of 13.31. *T. hicksi* had an overall score of 14.26, while *A. mutilis* had an overall score of 17.57. The modern rhino, *D. bicornis*, had an overall IPa of 12.23.

When we regressed mass for each taxon against each of the seven osteopathology categories Table 4, four of the pathologies (exostoses, abnormal textures, foramen shape, and foramen size variation) had p-values less than or equal to 0.05. A linear correlation of mass against the overall pathologic scores was found to be significant (p = 0.04) and accounted for about 52% of the variation ($r^2$ adj.). The IC analysis comparing mass and the seven osteopathology categories was also significant (p < 0.05) for the both foramen shape and the overall pathologic index, with mass accounting for 42% of the overall variation.

We were also interested in testing whether certain bones or regions of the appendicular skeleton (which comprises the majority of the data) displayed a greater amount of pathology than other bones or regions of the appendicular skeleton. We divided all appendicular elements into the functional categories: hindlimb or forelimb (Fig 3), and also developmental categories: girdle, stylopod, zeugopod, autopod (Fig 4). For example, if the stresses generating the osteopathology were greater in the distal parts of the limb, one might expect greater pathology in the autopod (manus and pes) than the stylopod (humerus and femur). We found no significant difference in pathological expression between different regions of the appendicular skeleton.

**Discussion**

In our study we found that mass can explain roughly 50% of the osteopathological expression. *A. mutilis*, surprisingly, had the highest pathology scores by a wide margin, while *T. hicksi,*
which was close to *A. mutilis* in estimated mass, had scores similar to the smaller *D. niobrar-ense* and *M. arikarense*. Both the overall expression of pathology and the subcategory of foramen shape were significant when regressed against mass regardless of whether phylogeny was taken into account or not. However, the $r^2$ value in the vicinity of 0.5 suggests that other factors besides mass, such as bone robusticity, cursoriality or environment, could play a significant role in pathological expression. There might be a tradeoff between a lineage increasing in size

| Table 3. Frequency of Pathology Scores and IPa grouped by Osteopathologies per Taxa. |
|-----------------------------------------------|
| **Exostoses** | **Lipping** | **Abnormal Bone Texture** | **Cavitation** | **Foramen Shape** | **Foramen Size** | **Articular Surface** | **Overall** |
| **H. eximius**† | 261 | 345 | 256 | 307 | 277 | 158 | 579 | 2183 |
| 2 | 127 | 46 | 125 | 81 | 102 | 292 | 16 | 789 |
| 3 | 3 | 0 | 9 | 4 | 13 | 15 | 1 | 45 |
| 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| IPa | 1.35 | 1.11 | 1.36 | 1.19 | 1.32 | 1.40 | 1.07 | 8.80 |
| **T. osborni**† | 19 | 78 | 17 | 86 | 56 | 52 | 95 | 403 |
| 2 | 88 | 34 | 81 | 17 | 50 | 42 | 16 | 328 |
| 3 | 7 | 2 | 15 | 11 | 8 | 20 | 3 | 66 |
| 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| IPa | 1.90 | 1.33 | 2 | 1.34 | 1.58 | 1.72 | 1.19 | 11.06 |
| **M. arikarense**† | 1 | 59 | 9 | 45 | 21 | 10 | 65 | 221 |
| 2 | 58 | 32 | 59 | 21 | 43 | 26 | 21 | 260 |
| 3 | 21 | 1 | 23 | 26 | 26 | 53 | 6 | 156 |
| 4 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 7 |
| IPa | 2.18 | 1.37 | 2.16 | 1.77 | 2.01 | 2.51 | 1.31 | 13.31 |
| **D. niobrararense**† | 1 | 33 | 3 | 36 | 25 | 26 | 52 | 200 |
| 2 | 41 | 36 | 45 | 24 | 33 | 29 | 20 | 245 |
| 3 | 19 | 6 | 23 | 14 | 17 | 20 | 3 | 122 |
| 4 | 1 | 0 | 4 | 1 | 0 | 0 | 0 | 33 |
| IPa | 2.10 | 1.61 | 2.38 | 1.69 | 1.85 | 1.88 | 1.31 | 12.81 |
| **A. mutilis**† | 1 | 61 | 10 | 35 | 3 | 0 | 73 | 182 |
| 2 | 47 | 49 | 44 | 19 | 25 | 12 | 39 | 235 |
| 3 | 73 | 20 | 53 | 44 | 81 | 74 | 10 | 355 |
| 4 | 11 | 1 | 23 | 33 | 22 | 45 | 1 | 136 |
| IPa | 2.69 | 1.75 | 2.96 | 2.54 | 2.86 | 3.26 | 1.53 | 17.57 |
| **T. hicksi**† | 1 | 54 | 9 | 27 | 9 | 9 | 70 | 190 |
| 2 | 34 | 26 | 34 | 36 | 33 | 20 | 10 | 193 |
| 3 | 31 | 2 | 37 | 18 | 38 | 46 | 2 | 174 |
| 4 | 5 | 0 | 2 | 0 | 2 | 7 | 0 | 17 |
| IPa | 2.49 | 1.37 | 2.43 | 1.82 | 2.4 | 2.59 | 1.169 | 14.26 |
| **D. bicornis** | 1 | 47 | 9 | 62 | 14 | 7 | 68 | 298 |
| 2 | 56 | 26 | 46 | 13 | 37 | 33 | 7 | 218 |
| 3 | 3 | 2 | 14 | 0 | 24 | 35 | 0 | 78 |
| 4 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 6 |
| IPa | 1.83 | 1.4 | 2.23 | 1.17 | 2.13 | 2.37 | 1.09 | 12.23 |

IPa = Index of Pathology, the average of all pathology scores (1 through 4) for all the individuals of a given taxa. Overall IPa is the sum of the seven individual averages. Frequency is unbolded, IPa is bolded.

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or weight and abnormal textures, lipping, and other pathologies that intuitively should be
selected against on an evolutionary scale. Lower levels of expression (categories 1 and 2) were
more common, but no taxon was entirely pathology-free. The maximum operational level of
different pathologies may be similar or drastically different in different vertebrate lineages,
which in turn could lead to diverse selection pressures.

Longevity could also be a factor in pathological expression. There is a positive correlation in
the Mammalia between body mass and lifespan, although there is a great amount of variation
[39]. The larger taxa may be living longer, which could increase the likelihood of osteoarthritis,
synovitis, traumatic injury, etc. Captive mammals that live longer than their wild counterparts
often display these pathologies [4, 13, 14, 15]. Pathology could be a reflection of ontogeny.
However, a longer lifespan does not necessarily increase only the geriatric portion of a mam-
mal’s life. In an animal with a longer lifespan bone would presumably stay healthy for the same
proportion of a mammal’s life as the shorter-lived counterpart, but this remains to be tested
[40].

Our main difficulty in this study was to establish a measurement method for pathology. In
anthropology several qualitative and quantitative metrics have been used to study paleopathol-
ogy [16, 18, 19]; paleontology also has no universal methodology for identifying and analyzing
paleopathologies, but several parallel methods [12, 13, 14, 17, 21, 27]. Our method uses a scor-
ing system that is focused on parsing out the severity of symptoms, not direct diagnoses of dis-
ease. It is possible to apply these separate pathology categories to studies across the vertebrate
kingdom. Comparison of pathological expression between these vastly different taxa could lead
to new insights into bone repair, species and lineage-level responses to pathology, and the uni-
formity of bone-related diseases over time.

Synovitis, not arthritis, may be the proximal cause of the pathologies observed. Notably, we
found that most of the pathology in the taxa we studied was located immediately adjacent to
the articular surface of joints and not in the articular surface itself. That is, the articular surface
itself appeared healthy (that is, not scarred or pitted) in all but five individual specimens even
in individuals with advanced exostoses and abnormal bone textures. This could indicate that
the joints (and therefore the organism) are functional well after pathologies begin to appear
and swelling of the synovium caused the observed cortical erosion [16].

The overall picture painted by our results shows a measureable increase in the percentage of
elements that display osteopathologies related to arthritis from the older to newer branches in
the North American rhinocerotid lineage, consistent with earlier observations [4, 13, 14, 15, 16,
17]. Our initial hypothesis was that more massive rhino species would display a greater

| Table 4. Linear Regression and Independent Contrast Regression against Mass. |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Overall         | Exostoses       | Lipping         | Abnormal Bone   | Cavitation       | Foramen Shape   | Foramen Size     | Articular       |
| Index           | Linear Contrasts|                 | Texture         |                 |                 |                 | Surface         |
| R² Adj.         |                  |                 |                 | F                | P                |                  |                 |
| F               | P                | F               | P                | F               | P                |                  |                 |
| Linear Contrasts| 0.5199           | 0.4772          | 0.2389           | 0.659            | 0.3325           | 0.6421           | 0.4797          |
| Adj             | 0.04087          | 0.05158         | 0.1502           | 0.0164           | 0.1023           | 0.01864          | 0.05091         |
| F               | 7.498            | 6.477           | 2.884            | 12.6             | 3.988            | 11.76            | 6.532           |
| P               | 0.05158          | 0.1502          | 0.0164           | 0.1023           | 0.01864          | 0.05091          | 0.5522          |
| Independent    | 0.4235           | 0.4011          | -0.01015         | 0.5236           | 0.2023           | 0.5263           | 0.3932          |
| Contrasts       | 0.03759          | 0.07522         | 0.3769           | 0.04003          | 0.1731           | 0.03942          | 0.07802         |
| R² Adj.         | 0.4235           | 0.4011          | -0.01015         | 0.5236           | 0.2023           | 0.5263           | 0.3932          |
| F               | 5.408            | 5.018           | 0.9397           | 70595            | 2.522            | 7.666            | 4.888           |
| P               | 0.03759          | 0.07522         | 0.3769           | 0.04003          | 0.1731           | 0.03942          | 0.07802         |

Linear Regression and Independent Contrast Regression Statistics against Mass. R²-adjusted, F Statistic and P values for linear and independent
counter (IC) regressions for each category of pathology are included.

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frequency of osteopathologies as increased loading pressure on the limbs caused microfractures that resulted in inflammation and abnormal bone textures. With our current sample, we found a significant correlation of pathology with mass, suggesting that increasing size in the lineage was partially responsible for osteopathologies. This study is not powerful enough to conclude if these pathologies are related primarily to arthritis or is a multifactorial response or a range of diseases. Because size increase is a common adaptation in terrestrial herbivores for both eating low-quality diets [26, 41, 42] and resisting predation pressure in open environments [26, 43], it...
seems that adaptations for food and predator avoidance may incur a cost in bone stress and osteopathology. The accumulation of pathologies in a lineage may no longer be solely a herald of disaster, but of adaptation as well.

Supporting Information

S1 File. Raw pathology Scores for all Rhinocerotidae specimens used in this study. Picture numbers correspond to digital photographs uploaded to Morphobank (project ID: 1238) [27]. Information available with permission from The American Museum of Natural History, The University of Washington Burke Museum, The University of Oregon Museum of Natural and Cultural History, and The University of Texas Jackson School of Geosciences Vertebrate Paleontology Laboratory. (XLSX)

S2 File. R Code and Required Files for Analysis. R Code can be run in RStudio [37] using the packages 'ape' [38] and 'paleotree' [28] with paleotree’s function TimePaleoPhy. Trees from Cerdeño (1995) [8]. (ZIP)

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Author Contributions

Conceived and designed the experiments: KTS SSBH EBD. Performed the experiments: KTS. Analyzed the data: KTS. Contributed reagents/materials/analysis tools: KTS SSBH EBD. Wrote the paper: KTS SSBH EBD.

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Fig 4. Comparison of limb regions. A color spectrum is used to indicate the percent of elements displaying any osteopathy in the stylopod, zeugopod, and autopod regions, respectively. The closer to the red portion of the color spectrum, the higher percentage. The closer to the violet portion of the color spectrum, the lower the percentage. Rhino figures do not display relative size.

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