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**Paleodietary reconstruction of *Equus simplicidens* from the Hagerman Horse
Quarry (Idaho, USA) highlights high abrasive habits in North American fossil
equids during the Pliocene**

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26 **Abstract**

27 The evolutionary history of equids represents a paradigmatic case of evolution through time
28 and space when, during the Cenozoic, fossil equids experimented with a variety of forms as well as
29 multiple dietary adaptations. Nowadays, only a single genus of Equidae (Subfamily Equinae, tribe
30 Equini) has survived, *Equus*, represented by wild zebras and asses and domesticated horses. In this
31 contribution, we undertake a comprehensive mesowear analysis on the *Equus simplicidens*
32 population from the Hagerman Horse Quarry, Idaho, Pliocene. Our sample includes sixty-two
33 individuals based on crania and maxillae. We used the classic mesowear method in scoring the first
34 or second molar paracone and calculating the average percentages of high versus low relief and
35 sharp versus round versus blunt cusps, but also scoring mesowear along a continuum that ranged
36 from sharp cusps with high relief to blunt cusps with low relief by comparing *E. simplicidens* and
37 extant ungulates. We applied the same methodology to a sample of living zebras, asses and horses
38 to increase our comparative sample. Our results show that the Hagerman *E. simplicidens* sample
39 had a high-abrasive diet as recorded in the living equid sample, and exhibited no significant
40 distinction between the different age classes sampled. For the first time, these results show that the
41 paleodietary behavior of *E. simplicidens* was similar to those of the living *Equus* species.

42

43 **1. Introduction**

44 The evolutionary history of equids represents a paradigmatic case of evolution through time
45 and space (MacFadden 1992, 2005; Mhlbachler et al. 2011; Bernor et al. 2021; Cirilli et al. 2022).
46 During the entire Cenozoic, equids experimented with a diversity of dietary adaptations, at the
47 genus and species levels (Mhlbachler et al. 2011; Semprebon et al., 2016; Bernor et al. 2021).
48 Currently, only a single genus of Equidae (Subfamily Equinae) has survived, *Equus*. The
49 evolutionary history of the genus *Equus* has been debated for over a century. Fossil species of
50 *Equus* have been referred to several other genera (or alternatively, subgenera), including *Plesippus*,
51 *Allohippus* and *Sussemionus* (Matthew 1924; Kretzoi, 1938; Eisenmann and Baylac 2000;

52 Eisenmann 2010), whereas the living species have been included in several additional subgenera,
53 such as *Dolichohippus*, *Quagga*, *Hippotigris*, *Hemionus* and *Asinus* (see Eisenmann 2022 for a
54 summary). Nevertheless, neither the most recent morphologically-based cladistic analysis (Cirilli et
55 al. 2021a) nor the genetic-based ones (Orlando et al. 2009, 2013; Vilstrup et al. 2013; Jónsson et al.
56 2014; Heintzmann et al. 2017) have supported these different taxonomic assignments, leading to the
57 conclusion that the species referred to in these different genera/subgenera should be included within
58 *Equus* without subgeneric assignments (Cirilli et al., 2021a).

59 Within this complicated taxonomic and evolutionary framework, a key role is played by the
60 Hagerman Horse Quarry (Pliocene, Idaho, USA). The Hagerman Horse Quarry (HHQ) consists of
61 several excavations in the upper section of the Glens Ferry Formation, close to the municipality of
62 Hagerman Idaho, USA (ca. 3.4 – 3.2 Ma, Hart and Brueseke 1999; Bell et al. 2004; Figure 1). As
63 reported by Akersten and Thomson (1992), several excavations have been conducted in the
64 fossiliferous layers of the Smithsonian Institution Hill, led by the Smithsonian Museum of Natural
65 History, Los Angeles County Museum, Idaho Museum of Natural History, Pacific Union College
66 excavations and several amateur collections. The HHQ was named after the enormous amount of
67 fossil horses collected there. As reported by McDonald (1996), a minimum number of 145
68 individuals were recognized between the collections of the Smithsonian Museum of Natural
69 History, Los Angeles County Museum and the Idaho Museum of Natural History, including
70 juvenile, young adult and fully adult individuals. The fossil horse species collected from the HHQ
71 has been referred variously to *Plesippus simplicidens* (Matthew 1924), *Plesippus shoshonensis*
72 (Gidley 1930; Gazin 1936; Eisenmann and Baylac 2000; Eisenmann 2022), *Equus shoshonensis*
73 (Ruez 2009a; Sun and Deng 2019) and *Equus simplicidens* (Skinner and Hibbard 1972; MacFadden
74 1992; Bernor et al. 2019; Cirilli et al. 2021a, 2021b, 2022).

75 In the present work, we provide a paleodietary reconstruction by means of mesowear
76 analyses of the HHQ sample housed at the Smithsonian Museum of Natural History of Washington
77 D.C. and at the American Museum of Natural History New York. Because different mesowear

78 methodologies exist, we compared the two most common methods to test their results against one
79 another: the traditional Fortelius and Solounias (2000) method and the modified mesowear ruler
80 (Michlbachler et al. 2011).

81 A comprehensive systematic study of the HHQ is ongoing by the authors of the present
82 contribution, and it will be the topic of future publications. In the present work, we follow the
83 identifications provided by previous authors (Skinner and Hibbard 1972; MacFadden 1992; Bernor
84 et al. 2019; Cirilli et al. 2021a, 2021b, 2022), referring this sample to *Equus simplicidens*.

85

86 2. Geological Setting

87 The HHQ is located on the west bank of the Snake River at Hagerman Fossil Beds National
88 Monument (hereafter HFBNM), Idaho, USA (Fig.1), where the Glenss Ferry Formation (GFF) is
89 exposed (McDonald 1996). The GFF contains lacustrine and fluvial sediments interbedded with
90 basaltic lava flows and is over 600 m thick at the type section near the town of Glenss Ferry. The
91 sediments comprise silts and muds, subordinate fine- to medium-grained sands, and local micritic
92 carbonate layers, volcanic ashes and diatomites (McDonald et al. 1996). At HFBNM, the GFF is flat
93 lying and it is composed of three members representing a lower member flood plain environment, a
94 middle member of marshy flood plain deposition and an upper member flood plain environment.
95 The lower member (about 67 m thick) lies on the Banbury Basalt, which constrains the lower limit
96 of the GFF (4.4 ± 0.6 and 4.9 ± 0.6 Ma; Ruez 2009b), and it is overlayed by the Peters Gulch
97 rhyolitic ash. The middle member (ca. 30 m thick) is interbedded between the lower Peters Gulch
98 ash and the higher Fossil Gulch dacitic ash. The upper member (ca. 90 m thick) extends from the
99 Fossil Gulch ash upward to the contact with the Tuana Gravel (McDonald et al. 1996). Hart and
100 Brueseke (1999) and Prassack and Walkup (2022) have provided the most recent $^{40}\text{Ar}/^{39}\text{Ar}$ ages for
101 the GFF at Hagerman, with an estimated age of ca. 3.84 ± 0.05 Ma for the Bed G (ca. 30 m above
102 the Peter Gulch Ash; Hart and Brueseke 1999; Prassack and Walkup 2022), ca. 3.68 ± 0.02 Ma for
103 the Shoestring Basalt (Bed I, between the Fossil Gulch Ash and the Deer Gulch basalt; Hart and

104 Brueseke 1999), ca. 3.44 ± 0.04 Ma for the Bed J (equivalent of the Deer Gulch basalt; Hart and
105 Brueseke 1999; Prassack and Walkup 2022) and ca. 3.2 Ma for the tephra HA97-1B (Hart and
106 Brueseke 1999), correlative with the Horse Quarry Ash Ka832 of Evernden et al. (1964) which also
107 yielded an estimated age of 3.2 Ma. The HHQ is constrained between the Bed J (ca. 3.44 ± 0.04
108 Ma) and the tephra HA97-1B (= Horse Quarry Ash, ca. 3.2 Ma) and placed in the upper member of
109 the GFF in a normal interval of the geomagnetic time scale (Evernden et al., 1964; Neville et al.
110 1979; McDonald et al. 1996; McDonald, 1996; Hart and Brueseke 1999; Bell et al. 2004; Ruez
111 2009b; Fig. 1B).

112

113 **3. Material and Methods**

114 **3.1. Comparative samples**

115 The samples studied in this work originate from the Smithsonian excavations at the HHQ
116 (Fig. 2), and are stored at the Smithsonian Museum of Natural History and Museum Support Center
117 (MSC), Washington D.C., USA (USNM), and at the American Museum of Natural History, New
118 York, USA (AMNH). The AMNH collection was previously part of the USNM collection. The
119 collection was made during the 1929, 1930, 1931, and 1934 field seasons. The 1929 and 1930 field
120 seasons were under the direction of Gidley, the 1931 season was led by Boss, and Gazin supervised
121 the final season in 1934 (Akersten and Thompson 1992; McDonald 1996). The material studied
122 originates from the “Main Quarry” (Fig. 2; Akersten and Thompson 1992) from a lens of reddish
123 and bog-iron stained sand sediments (Gazin 1936), but also contains specimens from the “Southern
124 Quarries” from the Gazin field campaign (Fig. 2). The Southern Quarries, including the “Green
125 Sandstone Quarry” and the “White Sandstone Quarry”, were excavated at the same stratigraphic
126 horizon as the “Main Quarry” (Gazin 1936), and are characterized by a concretionary layer with a
127 considerable portion of the material firmly cemented in large blocks of gray to white limy sand
128 (Gazin 1936: pp. 284). Therefore, it can be reasonably concluded that the assemblage that we report
129 on here originates from a single stratigraphic level (Fig. 2).

130 The fossil sample studied herein includes 62 crania, with at least the upper second molar
131 (M2) erupted (see Table 1). The sample has been divided into three age classes: juveniles,
132 characterized by the presence of upper deciduous premolars (dP2-dP4) with M1 and M2 emerging
133 or in crypt; young adults, characterized by the absence of upper deciduous premolars and by the
134 presence of P2-M2 and M3 not completely erupted: adults, with P2-M3 erupted and in wear. The
135 complete sample is reported in Table 1.

136 In addition to the *E. simplicidens* fossil sample, we applied the mesowear method to a
137 sample of 69 extant *Equus*, including specimens of: *Equus africanus*, *Equus hemionus*, *Equus*
138 *hemionus onager*, *Equus kiang*, *Equus grevyi*, *Equus quagga boehmi*, *Equus quagga antiquorum*,
139 *Equus quagga burchelli*, *Equus quagga selousi*, *Equus zebra*, *Equus zebra hartmannae* and *Equus*
140 *przewalskii*. Only adult and wild individuals were included, while zoo specimens were excluded
141 from the analysis. The complete sample is reported in Supplementary Table 1 and figured in
142 Supplementary materials.

143

144 3.2. Mesowear analysis

145 Mesowear analysis is a method for categorizing the gross dental wear of ungulate molars by
146 evaluating both the occlusal relief and relative sharpness of molar cusp apices to estimate gross
147 molar wear that accumulates on molars during an individual animal's lifespan (see Ackermans et al.
148 2020). The method is a measure of total dietary abrasion incurred during the lifetime of an
149 individual animal and, thus, abrasive elements intrinsic to plants or the coating of food items by
150 exogenous grit (Fortelius and Solounias, 2000). Most mesowear studies score molars
151 macroscopically from the buccal side of maxillary molar teeth (Fortelius and Solounias, 2000).
152 Mesowear is based on tooth facet development which is caused by the relative amounts of attritive
153 (tooth-on-tooth) versus abrasive (food-on-tooth) wear incurred by dental enamel during mastication.
154 Mesowear is scored by categorizing the shape of the buccal apex (paracone) of the second upper
155 molar cusps in adult individuals that display normal occlusion of the M1 and M2. Two variables are

156 assessed: (i) buccal apical shape of the paracone (scored as either sharp, rounded, or blunt) and (ii)
157 the occlusal relief (defined as the distance between paracone and metacone cusp apices and the
158 inter-cusp valley across the mesostyle-protocone horizontal plane). Sharp cusp apices (and therefore
159 high occlusal relief) are found when attrition dominates over abrasion (i.e., when relative soft food
160 items are consumed as in leaf browsing). Relatively rounded or even blunt cusps are observed when
161 the attritive signal is masked by relatively abrasive food items.

162 Mesowear scores were obtained using our two selected methods. First, following the
163 methodology of Fortelius and Solounias (2000) we scored the M2 paracone and calculating the
164 average percentages of high versus low relief and sharp versus round versus blunt cusps. Second, by
165 modifying the traditional technique because cusp shape and occlusal relief have been found not to
166 be independent variables. Moreover, if the paracone was damaged, M2 metacone was chosen for the
167 analysis (see USNM16991, USNM11988 and USNM13838), whereas if both of the M2 cusps were
168 broken, M1 was selected for scoring (USNM13842, USNM16982, USNM16990, USNM16991 and
169 USNM12573). Only in one case (USNM13838), the P4 was selected for the analysis, due to the
170 poor preservation of the M1 and M2. The stable mesowear signal across tooth position has been
171 tested previously for horses, showing no significant differences in mesowear scores among tooth
172 positions (Rivals et al. (2015). We preferentially use M2, but when M2 cusps are not adequately
173 preserved use P4 or M1. In addition, scoring mesowear variables without standardization of the
174 boundaries that define various shape categories has been shown to incur more interobserver error
175 (Mihlbachler et al., 2011). Consequently, we also scored mesowear along a continuum that ranged
176 from sharp cusps with high relief to blunt cusps with low relief by comparing *E. simplicidens* and
177 extant ungulates to a “mesowear ruler” (Mihlbachler et al., 2011). The original mesowear ruler was
178 developed using seven modern *Equus* tooth cusps that encompassed a range from sharp cusps with
179 high relief (state 0) to blunt cusps with no relief (stage 6). When cusps were found to have a
180 negative relief (i.e., concave upward cusp apex), stage 7 was assigned. A mesowear score was
181 calculated from each extant and fossil tooth sample by averaging individual scores per taxon. Lower

mesowear scores near 0 (i.e., mostly high relief and sharp cusp apices) are due to more dietary attrition versus abrasion (ex: low abrasion browsers), whereas higher abrasion scores near 6 or 7 (i.e., low relief with blunt cusps) would be seen in extreme grazers. Scores falling in between these two extremes are seen in coarser browsers, mixed feeders and non-extreme grazers. We use this methodology herein, but also recognize intermediate scores in 0.5 increments assigned in cases when the observed cusp shape cannot be assigned to one of the seven original steps but appears to fall in between two steps (i.e., 0.5, 1.5, 2.5, 3.5, 4.5, 5.5, 6.5). Scores were obtained via consensus scoring between the three authors.

We calculated hierarchical cluster analyses to compare the mesowear results for Hagerman *E. simplicidens* with extant ungulates that have known diets (i.e., data from a set of “typical” living species from Fortelius and Solounias (2000) and Mihlbachler et al. (2011) and additional extant *Equus* species using both mesowear methodologies (see above). Moreover, we provide a comparison of the mesowear scores of *E. simplicidens* from the HHQ with a selection of North America taxa of the genera *Pliohippus*, *Dinohippus* and *Equus* (data from Mihlbachler et al. 2011).

Univariate statistical analyses, ANOVA, and Tukey's post-hoc test were undertaken to identify potential significant differences between different age classes of *E. simplicidens*, in order to understand whether the inclusion of subadult and juvenile teeth with the adult tooth sample could be used to increase sample size without leading to a statistically significant disparity of results. PAST4 software (Hammer et al., 2001) was used and for all statistical tests (ANOVA and Tukey's pairwise comparisons), the significance level was set at $p = 0.05$.

3.3. Anatomical abbreviations

UTR: upper cheek tooth row; I1: premaxillary first incisor; I2: premaxillary second incisor; I3: premaxillary third incisor; P2: maxillary second premolar; P3: maxillary third premolar; P4: maxillary fourth premolar; M1: maxillary first molar; M2: maxillary second molar; M3: maxillary third molar; rt: right; lt: left.

208

209 3.3. Institutional repositories

210 **USNM:** United States National Museum of Natural History, Smithsonian Institution, Washington
211 D.C., USA. **AMNH F:AM:** American Museum of Natural History, Frick Collection of fossil
212 Mammals, New York, USA. **MSNG:** Museo di Scienze Naturali di Genova Giacomo Doria,
213 Genova, Italy.

214

215 4. Results

216 The upper cheek tooth rows of the HHQ *E. simplicidens* sample are illustrated in Figures 3-
217 8. Figure 3 shows all the juvenile specimens, Figure 4 all the young adult individuals, and Figures
218 5-8 all the fully adult ones. Age classes follow the description provided in the Material and Methods
219 and reported in Table 1. Among the 62 specimens analyzed, one shows a mesowear score of 3.5
220 (USNM12155: young adult), two of 4.0 (USNM16990: juvenile; USNM222302: adult), eight of 4.5
221 (USNM12497 - USNM13841 - USNM16991: juveniles; USNM16997: young adult; USNM12501 -
222 USNM12543 - USNM12573 - USNM16983: adults), five of 5.0 (USNM16982: juvenile;
223 USNM16985: young adult; USNM12499 - USNM12539 - USNM785642: adults) twenty-four of
224 5.5 (USNM12502- USNM12517 - USNM13842: juveniles; USNM12518 - USNM12542 -
225 USNM13832 - USNM16989 - USNM16994: young adults; AMNHFAM32551 - AMNHFAM32556
226 - USNM11986 - USNM11989 - USNM12500 - USNM12522 - USNM12534 - USNM12547 -
227 USNM12576 - USNM13791 - USNM13792 - USNM16984 - USNM16987 - USNM17000 -
228 USNM785640 - USNM785641: adults), seventeen of 6.0 (USNM12515 - USNM12521 -
229 USNM17003: young adults; USNM11988 - USNM12506 - USNM12528 - USNM12529 -
230 USNM12535 - USNM12536 - USNM12544 - USNM12546 - USNM12548 - USNM13835 -
231 USNM13838 - USNM13848 - USNM16992 - USNM16995: adults), two of 6.5 (USNM12525 -
232 USNM13793: adults) and three of 7.0 (USNM16998: juvenile; AMNHFAM32553 - USNM12538:
233 adults), for an overall average score of 5.5 (see Table 1 and Figs. 3-8).

234 Figure 9 show the results of the comparison between HHQ *E. simplicidens* and living
235 ungulate species following the Fortelius and Solounias (2000) methodology. Figure 9A displays the
236 results of a hierarchical cluster analysis comparing traditional mesowear variables of 27 “typical”
237 ungulate species of known diet (after Fortelius and Solounias, 2000) with the same variables in *E.*
238 *simplicidens* (the latter shown in red). Four main clusters are seen – extreme grazers (e.g. *E. grevyi*;
239 orange), non-extreme grazers (e.g. *Kobus ellipsiprymnus*; yellow), browsers (e.g. *Alces alces*; blue),
240 and mixed feeders (e.g. *Gazella granti*; green). The Hagerman *E. simplicidens* clusters with the
241 extreme grazing species, close to the modern *E. grevyi* and *E. quagga burchelli*. Figures 9B-J depict
242 a comparison of high vs. low relief and cusp shapes using the traditional mesowear variables
243 between the different age classes here selected for absolute values (Fig. 9B-E) and percentages
244 (Figs. 9F-J). What is notable in Figures 9B-J are the low percentages of high occlusal relief and low
245 percentages of sharp cusps indicating an abrasion-dominated diet. Juveniles and young adults
246 exhibit higher values of round cusp shapes compared to sharp and blunt shapes (Figs. 9B-C, F-G),
247 whereas adults have more blunt cusp shapes than the round and sharp ones (Figs. 9D and H). In
248 total, round cusp shapes are more common than the sharp and blunt ones (Figs. 9E and J).

249 Table 2 shows *E. simplicidens* mesowear results divided into age classes. Herein, no
250 significant statistical differences are observed in mesowear scores between various age classes of *E.*
251 *simplicidens* and a sample of *E. simplicidens* where all age classes were combined (ANOVA; $p =$
252 0.1994; Table 2). Tukey’s pairwise comparisons also showed no significant statistical differences
253 between different age classes of *E. simplicidens* ($p = 0.6827$) (Table S2). In addition, a Kruskal-
254 Wallis test for equal medians showed no significant statistical differences between sample medians
255 ($p = 0.1465$) (Table S2).

256 Figures 10 and 11 show the results of the comparison between *E. simplicidens* from the
257 HHQ and living ungulate species following the Muhlbachler et al. (2011) ruler method. These
258 results agree with the traditional Fortelius and Solounias (2000) method, with no statistically
259 significant differences. In Fig. 10A, the variability of the mesowear score shown by the adult

260 individuals of *E. simplicidens* includes the mesowear values of the juvenile and young adults,
261 suggesting no distinction between the different age classes of this sample in using the mesowear
262 score of Muhlbachler et al. (2011). Moreover, *E. simplicidens* shows the same mesowear values of
263 modern zebras (*E. grevyi* and *E. quagga* spp.) and, in general, also with the other living species, *E.*
264 *zebra*, *E. hemionus* spp., *E. kiang*, *E. africanus* and *E. ferus przewalskii* (Fig. 10B). Figure 11A
265 shows the results of a hierarchical cluster analysis using the same “typical” ungulate species of
266 known diet but comparing mesowear ruler scores of Muhlbachler et al. (2011). Results are similar to
267 Figure 9A with a separation of extreme grazers (orange), non-extreme grazers (yellow), mixed
268 feeders (green) and browsers (blue). *Equus simplicidens* clusters with extreme grazers. Figure 11B
269 depicts the mesowear ruler scores of extant ungulate leaf browsers, mixed feeders and grazers (after
270 Rivals et al. 2009: Fig. 3) with added taxa of the extant genus *Equus* measured in this study
271 compared to *E. simplicidens*. Again, *E. simplicidens* clusters closest with extant extreme grazers
272 (particularly *E. grevyi* and *E. quagga burchelli*). All the analyses provided herein place the HHQ *E.*
273 *simplicidens* population within the grazer and extreme-grazer living taxa, and in particular with the
274 living *Equus* species.

275 Figure 12 shows the comparison of HHQ *E. simplicidens* with a selection of *Pliohippus*,
276 *Dinohippus* and *Equus* taxa from the Late Miocene – Pleistocene of North America (data from
277 Muhlbachler et al. 2011). Figure 12A depicts the total mesowear scores of the taxa considered in the
278 analysis, whereas Figure 12B shows only the mean value of the mesowear scores. As can be seen in
279 the graphs, *E. simplicidens* from the HHQ has mesowear values comparable with other *Equus*
280 species, whereas the species of the genera *Pliohippus* and *Dinohippus* shows more mixed-feeding
281 to browser adaptations (Fig. 12A-B). However, it should be noted that the *Dinohippus* species show
282 a wide range of adaptation, from browser to grazer, although the majority indicate a mixed-feeding
283 diet. Nevertheless, some of them such as *Dinohippus leydianus* from Edson Quarry and Optima /
284 Guymon and *Dinohippus interpolatus* from the Coffee Ranch site have mesowear values between 3
285 to 6, indicating that these populations might have fed on a more abrasive vegetation than others.

Figure 12C (modified from Figure 1 in Muhlbachler et al., 2011) shows the position of the HHQ *E. simplicidens* with the mesowear trend line of fossil equids from the Pliocene and Pleistocene of North America. As exhibited in the image, the HHQ sample has higher mesowear values than the mean trend shown by the Pliocene North American horses, represented by *Nannippus aztecus* (Bone Valley Formation, Florida; mixed-feeder to grazer), *Pseudhipparion simpsoni* (Bone Valley Formation, Florida; mixed-feeder to grazer), *Neohipparion eurystyle* (Bone Valley Formation, Florida; extreme grazer), *Cormohipparion emsliei* (Bone Valley Formation, Florida; ; mixed-feeder), *E. simplicidens* (Sand Drew Local Fauna, Nebraska; mixed-feeder to grazer) *Equus* sp. (Dry and Northern Whitlock Mtn Localities, Arizona; mixed-feeder to grazer / St. David Formation, Benson Area, Arizona; mixed-feeder to grazer) and *Nannippus peninsulatus* (Ogalalla Group, Texas; mixed-feeder to grazer) (see Semprebon et al. 2016 for a more comprehensive explanation).

297

298 5. Discussion

Equus first appeared in North America during the Early Blancan (ca. 4.0 Ma; Miller, 1980; Azzaroli and Voorhies 1993; Morgan and Spencer 2003; Bell et al. 2004; Rook et al. 2019), derived from the genus *Dinohippus* (MacFadden 1984, 2006; MacFadden and Carranza-Castañeda 2002; Carranza-Castañeda 2019; Cirilli et al. 2021a). Monodactyly initially emerged in North America with the genus *Pliohippus* in the Barstovian 2 of the North America Land Mammal Ages (ca. 15 Ma), wherein the early members of this genus (*Pl. mirabilis* and *Pl. pernix*) exhibit a tridactyl foot with the lateral digits apparently nonfunctional in their locomotion (Solounias et al. 2018; Janis and Bernor 2019). Nevertheless, definitive monodactyly, interpreted as the absence of the lateral digits except fused splints, appeared in the Late Miocene with the genus *Dinohippus* (*D. leydianus*) at ca. 7 Ma (Equini) that evolved alongside tridactyl equids during the Late Miocene (Janis and Bernor, 2019). *Equus* had a foot anatomy adapted for elastic energy storage that facilitated a persistent trotting/roaming behavior and evolved through the Late Miocene and Pliocene in dry, open country environments that prevailed in North America. These Late Miocene conditions contrasted with the

312 more forested and woodland conditions that prevailed in Eurasia and Africa in the Late Miocene
313 and supported an extensive radiation of tridactyl hipparionine horses (Janis and Bernor, 2019;
314 Bernor et al., 2021; Cirilli et al. 2022). Although several taxonomic Plio-Pleistocene Equini genera
315 have been proposed (Eisenmann and Baylac 2000; Barron-Ortiz et al. 2019; Eisenmann 2010,
316 2022), the current most parsimonious hypothesis supports the Pliocene North America species be
317 included in the genus *Equus*, with *E. simplicidens* being the earliest known representative (Cirilli et
318 al. 2021a, 2022). Bernor et al. (2019) and Cirilli et al. (2021a, 2021b) reviewed and re-affirmed
319 Azzaroli and Voorhies (1993) assertion that HHQ *E. simplicidens* was the most likely evolutionary
320 source for European *Equus stenonis* which, in turn, was the likely source for the radiation of the
321 East African Early Pleistocene *Equus koobiforensis* and, more broadly, for modern asses and zebras,
322 derived from Eurasian stenonine horses (Bernor et al. 2019; Cirilli et al. 2021a, 2021b). Azzaroli
323 and Voorhies (1993), Bernor et al. (2019) and Cirilli et al. (2021a, 2021b) support the hypothesis
324 that the North American *E. simplicidens* was a zebra-like equid, as previously indicated by Skinner
325 and Hibbard (1972) and McDonald (1996).

326 Our results on *E. simplicidens* paleodiet are consistent with this view. Firstly, an abrasion-
327 dominated grass diet is compatible with the low percentages of high occlusal relief and low
328 percentages of sharp cusps (Fig. 9B). Secondly, *E. simplicidens* clusters with extreme grazers and
329 closest to *E. grevyi* in a hierarchical cluster analysis with extant ungulates of known diet using
330 traditional mesowear variables (Fig. 9A) and is nestled between *E. grevyi* and *E. quagga* spp. using
331 the mesowear “ruler” (Fig. 11). Also interesting is that no significant differences were found in
332 mesowear scores between various age classes of *E. simplicidens* and a sample of *E. simplicidens*
333 where all age classes were combined to test whether the incorporation of subadults and juvenile
334 teeth with adult teeth could potentially be used to increase sample sizes (Fig. 10A and Table S2).
335 Furthermore, the HHQ *E. simplicidens* exhibits a grazing adaptation as the other North American
336 *Equus* species, different from the large paleodietary range (mixed-feeding to browsing) shown by
337 *Pliohippus* and *Dinohippus* (Fig. 12A-B).

Overall, the results obtained from this study are in agreement with others reported using different methodologies, such as isotopic and microwear applications (MacFadden et al. 1999; Semprebon et al. 2016). In Semprebon et al. (2016) Late Miocene and Pliocene genera (*Dinohippus* and *Equus*) were identified as mixed feeders to grazers, based on microwear analyses. Nevertheless, MacFadden et al. (1999) demonstrated that some individuals of the large *Dinohippus* (*D. mexicanus*) from the Bone Valley Formation were feeding on C₄ grasses, although showing a microwear browsing signal, and other populations of *Dinohippus* of Mexico were principally grazers (Wang et al. 1994). The authors suggested that the subsequent transition to widespread grazing in *Equus* occurred rapidly during the Early Pliocene in North America (MacFadden et al. 1999). As reported by Mithlbackler et al. (2011), the radiation of the C₄ grasslands in the Great Plains of North America occurred between the very Late Miocene and the Early Pliocene, a timespan when the fossil equids were exploiting new feeding strategies.

The recognition that HHQ *E. simplicidens* was an extreme like modern zebras and asses is in agreement with this paleoenvironmental and paleoecological interpretation of Late Miocene and Early Pliocene of North American paleoenvironments, supporting the hypothesis articulated by Mithlbackler et al. (2011) that high-abrasion diets persisted since ca. 4 Ma in fossil and living horses. Furthermore, this new paleodietary evidence suggests that *E. simplicidens* was a zebra-like form, similar to *E. grevyi*. This is also in agreement with the body size reconstructions reported by Saarinen et al. (2021) and Cirilli et al. (2021b, 2022, 2024), wherein both species have body size estimates between 300 and 400 kg. Consequently, the suggestion by Cirilli et al. (2021a) that North American Pliocene *E. simplicidens* represents the likely ancestral stock for the origin of Eurasian stenonine horses and ultimately African *E. grevyi*, and the zebra-ass clade is supported here.

360

361 6. Conclusions

362 Dietary assessment of *E. simplicidens* is made using both the traditional mesowear variables
363 and the mesowear “ruler”. These methods closely concur in our interpretation that the Hagerman *E.*

364 *simplicidens* was an extreme abrasion-dominated grazer most similar to extant zebras (particularly
365 *E. grevyi*). Using a consensus approach to scoring mesowear and recognizing intermediate “ruler”
366 wear stages facilitated a refined scoring system among observers. We found no significant statistical
367 differences when subadults and juvenile teeth were incorporated with adult teeth thus showing the
368 potential that juvenile and subadults might be used to increase sample size in *Equus* dietary studies:
369 to wit, once adult teeth emerge, the horse assumes its common diet. Our mesowear-based dietary
370 studies have demonstrated that Pliocene North American *E. simplicidens* had a diet akin to extant
371 asses and zebras and support previous assertions that *E. simplicidens* was a North American zebra
372 (Skinner and Hibbard 1972; McDonald, 1996).

373

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390

391 **References**

- 392 Ackermans, N.L., Martin, L.F., Codron, D., Hummel, J., Kircher, P.R., Richter, H., Kaiser, T.M.,
393 Clauss, M., Hatt, J., 2020. Mesowear represents a lifetime signal in sheep (*Ovis aries*) within
394 a long-term feeding experiment. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 553, 109793.
- 395 Akersten, W.A., Thompson, M.E., 1992. The Hagerman Horse Quarry: History, status, potential,
396 and recommendations for the future: Idaho Museum of Natural History Paleontology
397 Reports 2, 1–109.
- 398 Azzaroli, A., Voorhies, M.R., 1993. The genus *Equus* in North America. The Blancan species.
399 *Palaeontogr. Ital.* 80, 175-198.
- 400 Barrón–Ortiz, C.I., Avilla, L.S., Jass, C.N., Bravo–Cuevas, V.M., Machado, H. and Mothé, D.,
401 2019. What is *Equus*? Reconciling taxonomy and phylogenetic analyses. *Front. Ecol. Evol.*
402 7, 343.
- 403 Bell, C.J., Lundelius, E.L. Jr., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez, D.R. Jr.,
404 Semken, H.A. Jr., Webb, S.D., Zakrewski, R.J. 2004. The Blancan, Irvingtonian, and
405 Rancholabrean Mammal Ages. In: Woodburne, M.O. (Eds.), *Late Cretaceous and Cenozoic*
406 *Mammals of North America: Biostratigraphy and Geochronology*. Columbia University
407 Press, New York, pp. 232–314.
- 408 Bernor, R.L., Cirilli, O., Jukar, A.M., Potts, R., Buskianidze, M., Rook, L., 2019. Evolution of early
409 *Equus* in Italy, Georgia, the Indian subcontinent, East Africa, and the origins of African
410 zebras. *Front. Ecol. Evol.* 7, 166.
- 411 Bernor, R.L., Kaya, F., Kaakinen, A., Saarinen, J., Fortelius, M., 2021. Old World hipparion
412 evolution, biogeography, climatology and ecology. *Earth Sci. Rev.* 221, 103748.

- 413 Carranza–Castañeda, O. 2019. *Dinohippus mexicanus* (early–late, late, and latest Hemphillian) and
414 the transition to genus *Equus*, in Central Mexico faunas. *Front. Earth Sci.* 7, 89.
- 415 Cirilli, O., Pandolfi, L., Rook, L., Bernor, R.L., 2021a. Old World *Equus* evolution and the origin of
416 the zebra-ass clade. *Sci. Rep.* 11, 10156.
- 417 Cirilli, O., Saarinen, J., Pandolfi, L., Rook, L., Bernor, R.L., 2021b. An updated review on *Equus*
418 *stenonis* (Mammalia, Perissodactyla): new implications for the European Early Pleistocene
419 *Equus* taxonomy and paleoecology, and remarks on the Old World *Equus* evolution. *Quat.*
420 *Sci. Rev.* 269, 107155.
- 421 Cirilli, O., Machado, H., Arroyo-Cabrales, J., Barrón-Ortiz, C.I., Davis, E., Jass, C.N., Jukar, A.M.,
422 Landry, Z., Marin-Leyva, A.H., Pandolfi, L., Pushkina, D., Rook, L., Saarinen, J., Scott, E.,
423 Semperebon, G., Strani, F., Villavicencio, N.A., Kaya, F., Bernor, R.L., 2022. Evolution of
424 the family Equidae, subfamily Equinae, in North, Central and South America, Eurasia and
425 Africa during the Plio-Pleistocene. *Biology* 11, 1258.
- 426 Cirilli, O., Saarinen, J., Bernor, R.L., 2024. Lost in the collections. A critical re-appraisal on *Equus*
427 *major* provides a new perspective on the paleobiogeography of the Plio-Pleistocene
428 European equids and on the *Equus* Datum. *Quat. Sci. Rev.* 323, 108428.
- 429 Eisenmann, V., 2010. *Sussemionus*, a new subgenus of *Equus* (Perissodactyla, mammalia). *C. R.*
430 *Biol.* 333, 235–240.
- 431 Eisenmann, V., 2022. Old world fossil *Equus* (Perissodactyla, Mammalia), extant wild relatives and
432 incertae sedis forms. *Quaternary* 5, 38.
- 433 Eisenmann, V., Baylac, M., 2000. Extant and fossil *Equus* (Mammalia, Perissodactyla) skulls: a
434 morphometric definition of the genus *Equus*. *Zool. Scripta* 29, 89e100.
- 435 Evernden, J.F., Savage, D.E., Curtis, G.H., James, G.T., 1964. Potassium–argon dates and the
436 Cenozoic mammalian chronology of North America: *Am. J. Sci.* 262, 145–198.

437 Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the
 438 abrasioneattrition wear gradient: a new method for reconstructing paleodiets. *Am. Mus.*
 439 *Novit.* 3301, 1–35.

440 Gazin, C.L., 1936. A study of the fossil horses remains from the Upper Pliocene of Idaho.
 441 *Proceedings of the United States National Museum* 83, 281–320.

442 Gidley, J. W., 1930, A new Pliocene horse from Idaho: *J. Mammal.* 11, 300–303.

443 Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package
 444 for education and data analysis. *Palaeont. Electr.* 4, 9.

445 Hart, W.K., Brueseke, M.E., 1999. Analysis and dating of volcanic horizons from Hagerman Fossil
 446 Beds National Monument and a revised interpretation of eastern Glenns Ferry Formation
 447 chronostratigraphy: a report of work accomplished and scientific results. *Nat. Park Serv.*
 448 *Rep.* 1443A, 1–37

449 Heintzman, P.D., Zazula, G.D., MacPhee, R.D., Scott, E., Cahill, J.A., McHorse, B.K., Kapp, J.D.,
 450 Stiller, M., Wooller, M.J., Orlando, L., Southon, J., Froese, D.G., Shapiro, B. 2017. A new
 451 genus of horse from Pleistocene North America. *eLife* 6, e29944.

452 Janis, C.M., Bernor, R.L., 2019. The Evolution of Equid Monodactyly: A Review Including a New
 453 Hypothesis. *Front. Ecol. Evol* 7, 119.

454 Jónsson, H., Schubert, M., Seguin-Orlando, A., Ginolhac, A., Petersen, L., Fumagalli, M.,
 455 Albrechtsen, A., Petersen, B., Korneliussen, T.S.; Vilstrup, J.T.; Learg, T., Mykag, J.L.,
 456 Lundquistg, J., Millerh, D.C., Alfarhani, A.H., Alquraishii, S.A., Al-Rasheidi, K.A.S.,
 457 Stagegaardj, J., Strausssk, G., Bertelsenl, M.F., Sicheritz-Pontenf, T., Antczakh, D.F.,
 458 Baileyg, E., Nielsenc, R., Willersleva, E., Orlando, L., 2014. Speciation with gene flow in
 459 equids despite extensive chromosomal plasticity. *Proc. Natl. Acad. Sci. USA* 111, 18655–60.

460 Kretzoi, M., 1938. Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtfaua. Annales
 461 Musei Nationalis Hungarici. Pars Mineralogica, Geologica, Palaeontologica 31, 88–157.

462 MacFadden, B.J. 1984. *Astrohippus* and *Dinohippus* from the Yepómera local fauna (Hemphillian,
 463 Mexico) and implications for the phylogeny of one-toed horses, J. Vert. Paleontol. 4, 273-
 464 283.

465 MacFadden, B.J. 1992. Fossil Horses: Systematics, Paleobiology, and Evolution of the Family
 466 Equidae; Cambridge University Press: Cambridge, UK.

467 MacFadden, B.J., 2005. Fossil Horses – Evidence for Evolution. Science 307, 1728 – 1730.

468 MacFadden, B.J., Carranza–Castañeda, O., 2002. Cranium of *Dinohippus mexicanus* (Mammalia:
 469 Equidae) from the Early Pliocene (latest Hemphillian) of Central Mexico, and the origin of
 470 *Equus*. Bull. Fla. Mus. Nat. Hist. 43, 163–185.

471 MacFadden, B., Solounias, N., Cerling, T.E., 1999. Ancient Diets, Ecology, and Extinction of 5-
 472 Million-Year-Old Horses from Florida. Science 283, 824–827.

473 Matthew, W.D., 1924. A new link in the ancestry of the horse. Am. Mus. Nov. 131, 130–131.

474 McDonald, H. 1996. Population structure of the late Pliocene (Blancan) zebra *Equus simplicidens*
 475 (Perissodactyla: Equidae) from the Hagerman Horse Quarry, Idaho. In: Stewart, K.M.,
 476 Seymour, K.L. (Eds.), Paleoecology and Paleoenvironments of Late Cenozoic Mammals:
 477 Tributes to the Career of CS (Rufus) Churcher. University of Toronto Press, Toronto, pp.
 478 134–155.

479 McDonald, G.H., Link, P.K., Lee, D.E. 1996. An overview of the geology and paleontology of the
 480 Pliocene Glenns Ferry Formation, Hagerman Fossil Beds National Monument: Northwest
 481 Geology 26, 16–45.

482 Muhlbachler, C., Rivals, F., Solounias, N., Semperebon, G.M. 2011. Dietary change and evolution of
483 horses in North America. *Science* 331, 1178–1181.

484 Miller, W.E., 1980. The late Pliocene Las Tunas local fauna from southernmost Baja California,
485 Mexico. *J. Paleont.* 54, 762-805.

486 Morgan, G.S., Spencer, G.L., 2003. Mammalian Biochronology of Blancan and Irvingtonian
487 (Pliocene and Early Pleistocene) Faunas from New Mexico. *Bull. Am. Mus. Nat. Hist.* 279,
488 269-320.

489 Orlando, L.; Metcalf, J.L.; Alberdi, M.T.; Telles-Antunes, M.; Bonjean, D.; Otte, M.; Martin, F.;
490 Eisenmann, V.; Mashkour, M.; Morello, F.; Prado, J.L., Salas-Gismondi, R., Shockey, B.J.
491 Wrinn, P.J., Vasil'ev, S.K., Ovodov, N.D., Cherry, M.I., Hopwood, B., Male, D., Austin, J.J.,
492 Hanni, C., Cooper, A., 2009. Revising the recent evolutionary history of equids using
493 ancient DNA. *Proc. Natl. Acad. Sci. USA* 106, 21754–21759.

494 Orlando, L., Ginolhac, A., Zhang, G., Froese, D., Albrechtsen, A., Stiller, M., Schubert, M.,
495 Cappellini, E., Petersen, B., Moltke, I., Johnson, P.L.F., Fumagalli, M., Vilstrup, J.T.,
496 Raghavan, M., Korneliussen, T., Malaspinas, A.S., Vogt, J., Szklarczyk, D., Kelstrup, C.D,
497 Vinther, J., Dolocan, A., Stenderup, J., Velazquez, A.M.V., Cahill, J., Rasmussen, M., Wang,
498 X., Min, J., Zazula, G.D.M, Seguin–Orlando, A., Mortensen, C., Magnussen, K., Thompson,
499 K.F., Weinstock, J., Gregersen, K., Røed, K.H., Eisenmann, V., Rubin, C.J., Miller, D.C.,
500 Antczak, D.F., Bertelsen, M.F., Brunak, S., Al–Rasheid, K.A.S., Ryder, O., Andersson, L.,
501 Mundy, J., Krogh, A., Gilbert, M.T.P., Kjær, K., Sicheritz–Ponten, T., Juhl Jensen, L., Olsen,
502 J.V., Hofreiter, M., Nielsen, R., Shapiro, B., Wang, J., Willerslev, E. 2013. Recalibrating
503 *Equus* evolution using the genome sequence of an early Middle Pleistocene horse. *Nature*
504 499, 74–80.

505 Rivals, F., Schulz, E., Kaiser, T.M., 2009. Late and middle Pleistocene ungulates dietary diversity in
506 Western Europe indicate variations of Neanderthal paleoenvironments through time and
507 space. *Quat. Sci. Rev.* 28, 3388-3400.

508 Rivals, F., Julien, M.-A., Kuitens, M., Van Kolfschoten, T., Serangeli, J., Drucker, D.G., Bocherens,
509 H., Conard, N.J., 2015. Investigation of equid paleodiet from Schöningen 13 II-4 through
510 dental wear and isotopic analyses: Archaeological implications. *J. Hum. Evol.* 89, 129-137.

511 Rook, L., Bernor, R.L., Avilla, L.D., Cirilli, O., Flynn, L., Jukar, A.M., Sanders, W., Scott, E.,
512 Wang, X., 2019. Mammal biochronology (land mammal auroeound the world from the late
513 miocene to middle Pleistocene and major events in horse evolutionary history. *Front. Ecol.*
514 *Evol.* 7, 268.

515 Ruez, D.R., 2009a. Revision of the Blancan (Pliocene) mammals from Hagerman Fossil Beds
516 National Monument, Idaho. *Journal of the Idaho Academy of Science* 45, 1-143.

517 Ruez, D.R. 2009b. Framework for stratigraphic analysis of Pliocene fossiliferous deposits at
518 Hagerman Fossil Beds National Monument, Idaho. *Rocky Mountain Geology* 44, 33–70.

519 Semprebon, G.M., Rivals, F., Solounias, N., Hulbert, R.C., 2016. Paleodietary reconstruction of
520 fossil horses from the Eocene through Pleistocene of North America. *Palaeogeogr.*
521 *Palaeoclim. Palaeoecol.* 442, 110-127.

522 Skinner, M.P., Hibbard, C.W., 1972. Early Pleistocene pre-glacial and glacial rocks and faunas of
523 north-central Nebraska. *Bull. Am. Mus. Nat. Hist.* 148, 1–148.

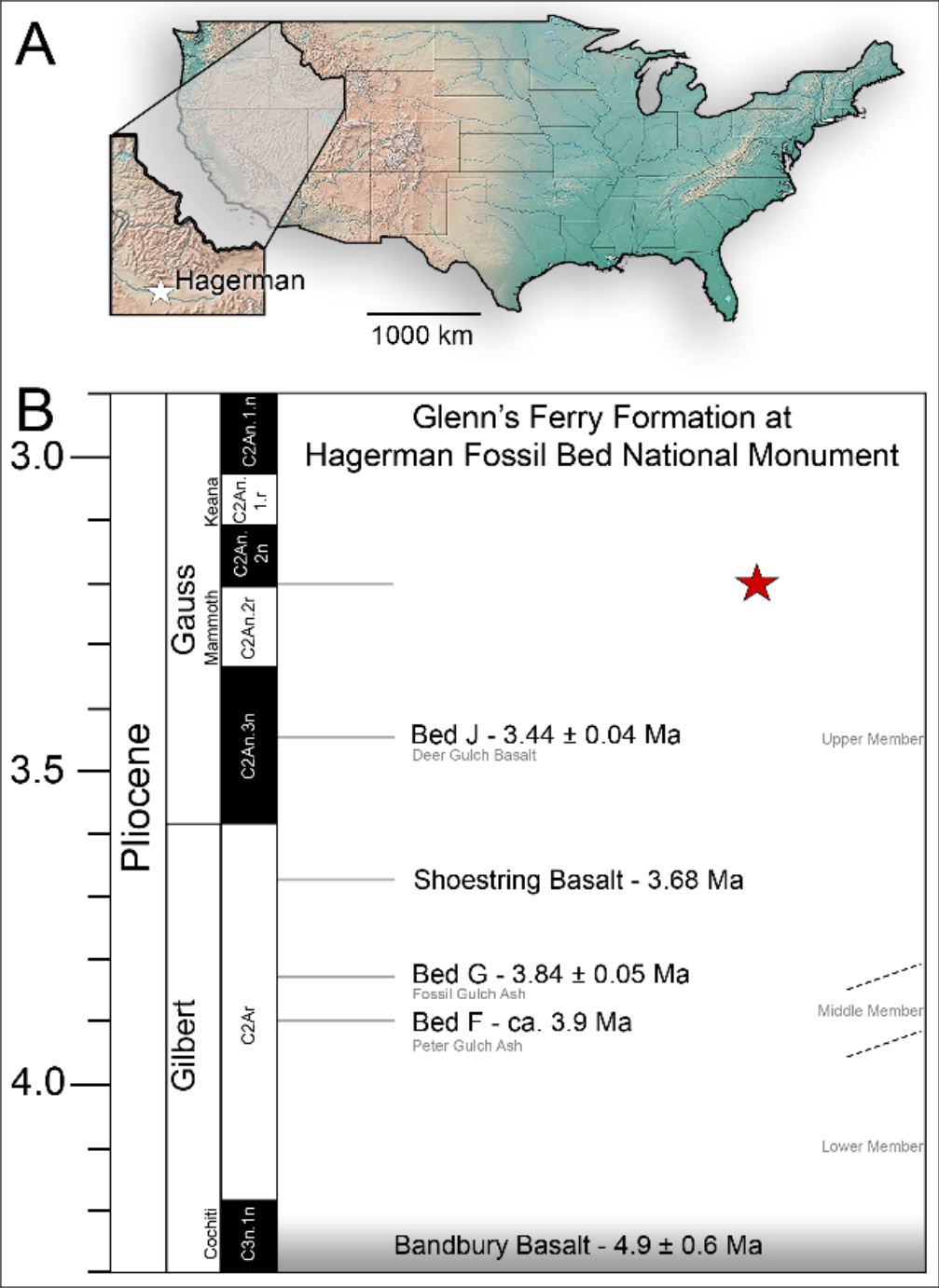
524 Solounias, N., Danowitz, M., Stachtiaris, E., Khurana, A., Araim, M., Sayegh, M., Natale, J., 2018.
525 The evolution and anatomy of the horse manus with an emphasis on digit reduction. *R. Soc.*
526 *Open Sci.* 5:171782.

527 Sun, B., Deng, T., 2019. The *Equus* Datum and early radiation of *Equus* in China. *Front. Ecol. Evol.*
528 7, 429.

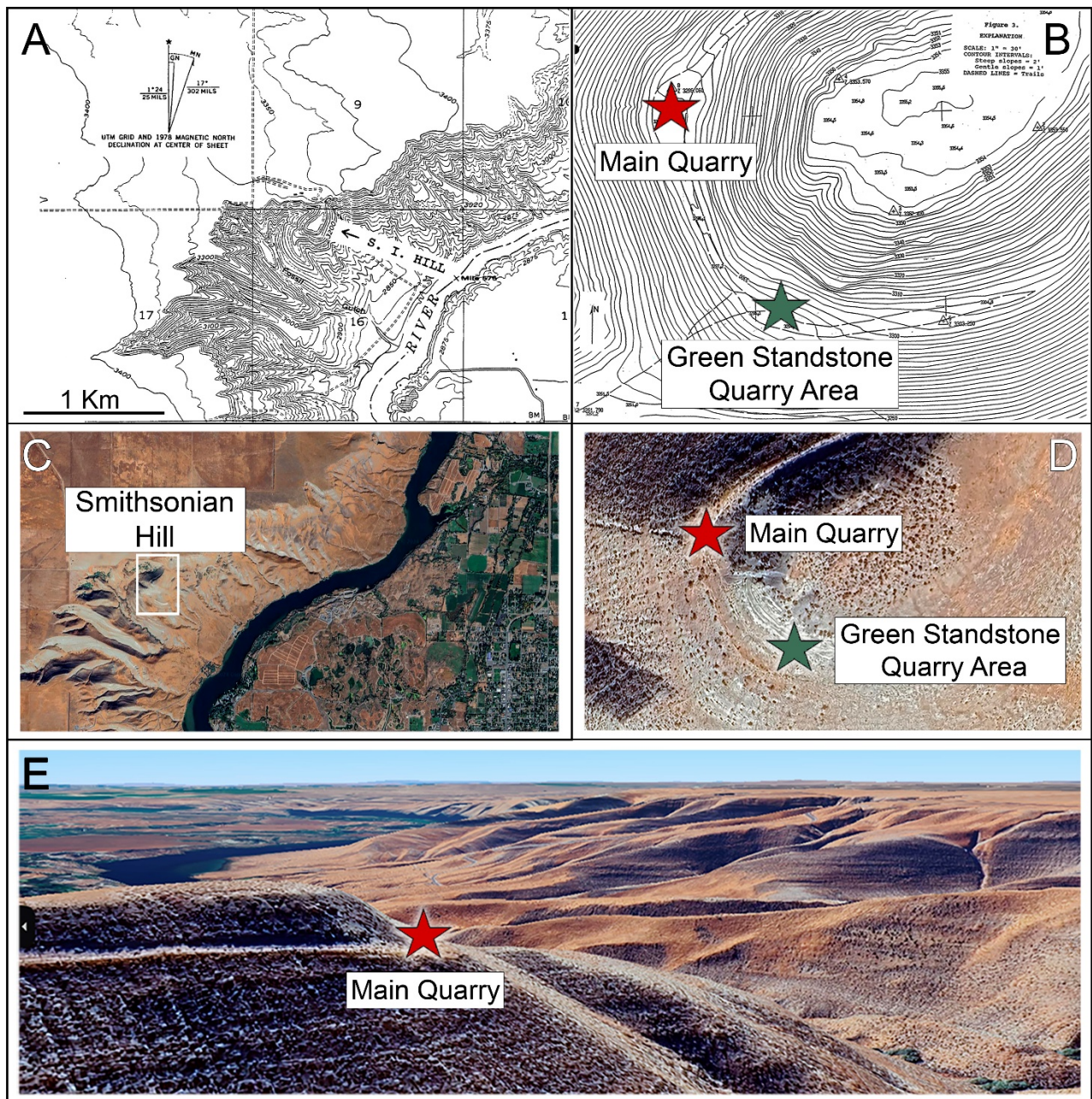
529 Vilstrup, J.L., Seguin–Orlando, A., Stiller, M., Ginolhac, A., Raghavan, M., Nielsen, S.C.A,
530 Weinstock, J., Froese, D., Vasiliev, S.V., Ovodov, N.K., Clary, J., Helgen, K.M., Fleischer,
531 R.C., Cooper, A., Shapiro, B. Orlando, L., 2013. Mitochondrial phylogenomics of modern
532 and ancient equids. PLoS ONE 8: e55950.

533 Wang, Y., Cerling, T. E., MacFadden, B.J. 1994. Fossil horses and carbon isotopes: new evidences
534 for Cenozoic dietary, habitat, and ecosystem changes in North America. *Palaeogeogr.*
535 *Palaeoclimatol. Palaeoecol.* 107, 269 – 279.

536

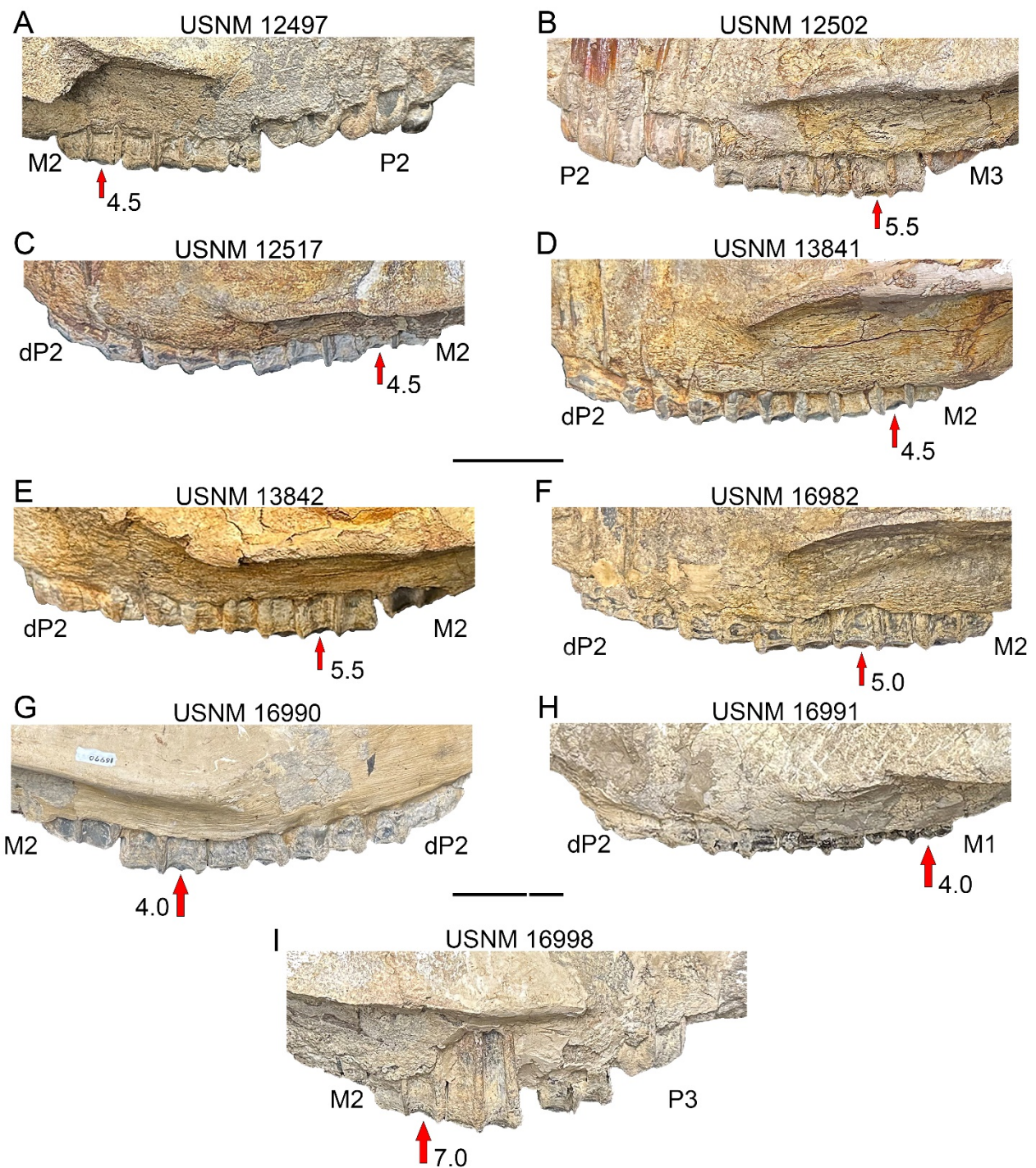


538
539 Figure 1. Geographic map, geochronology and location of the Hagerman Horse Quarry at the
540 Hagerman Fossil Beds National Monument, Idaho, USA. A) Geographic map of Hagerman Fossil
541 Beds National Monument, Idaho, USA. B) Geochronology of the Glenn's Ferry Formation at the
542 Hagerman Fossil Beds National Monument. Ages reported from Evernden et al., (1964); Neville et
543 al., (1979); McDonald et al., (1996); McDonald, (1996); Hart and Brueseke (1999); Bell et al.,
544 (2004) and Ruez (2009b). Scale bar 1000 km.



545
 546 Figure 2. Location of the Main Quarry and of the Green Sandstone Quarry Area on the Smithsonian
 547 Institution Hill (A-B edited from Akersten and Thompson 1992). C-E) Physical location of the
 548 Main Quarry and of the Green Sandstone Quarry Area on the Smithsonian Institution Hill (images
 549 from Google Earth). Scale bar 1 km.

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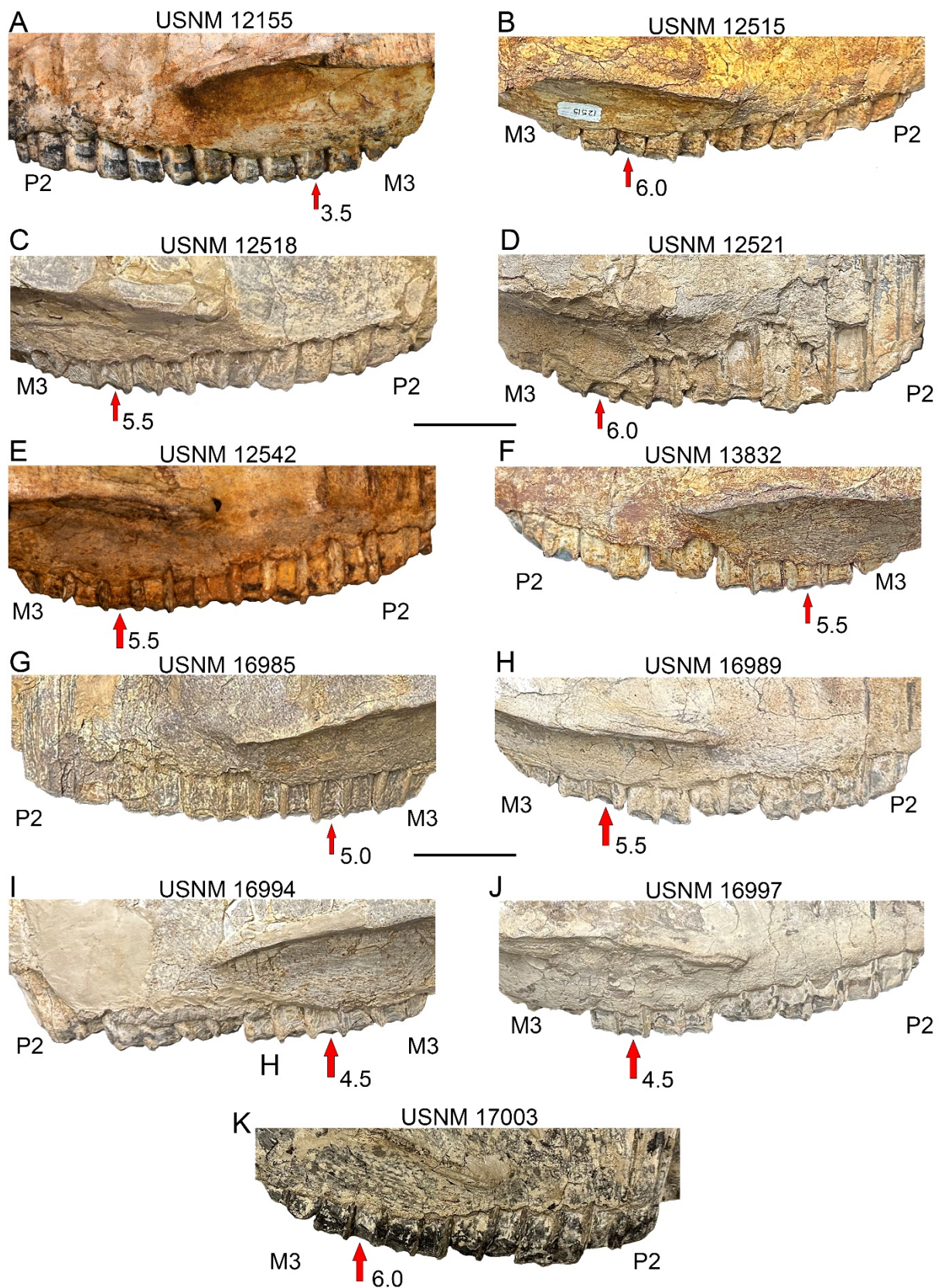
551

552 Figure 3. Lateral view of the upper cheek tooth rows of juvenile individuals of *Equus simplicidens*
 553 from Hagerman Horse Quarry (USNM12497 – USNM16998). The juvenile definition refers to
 554 material and methods. Scale bar 5 cm.

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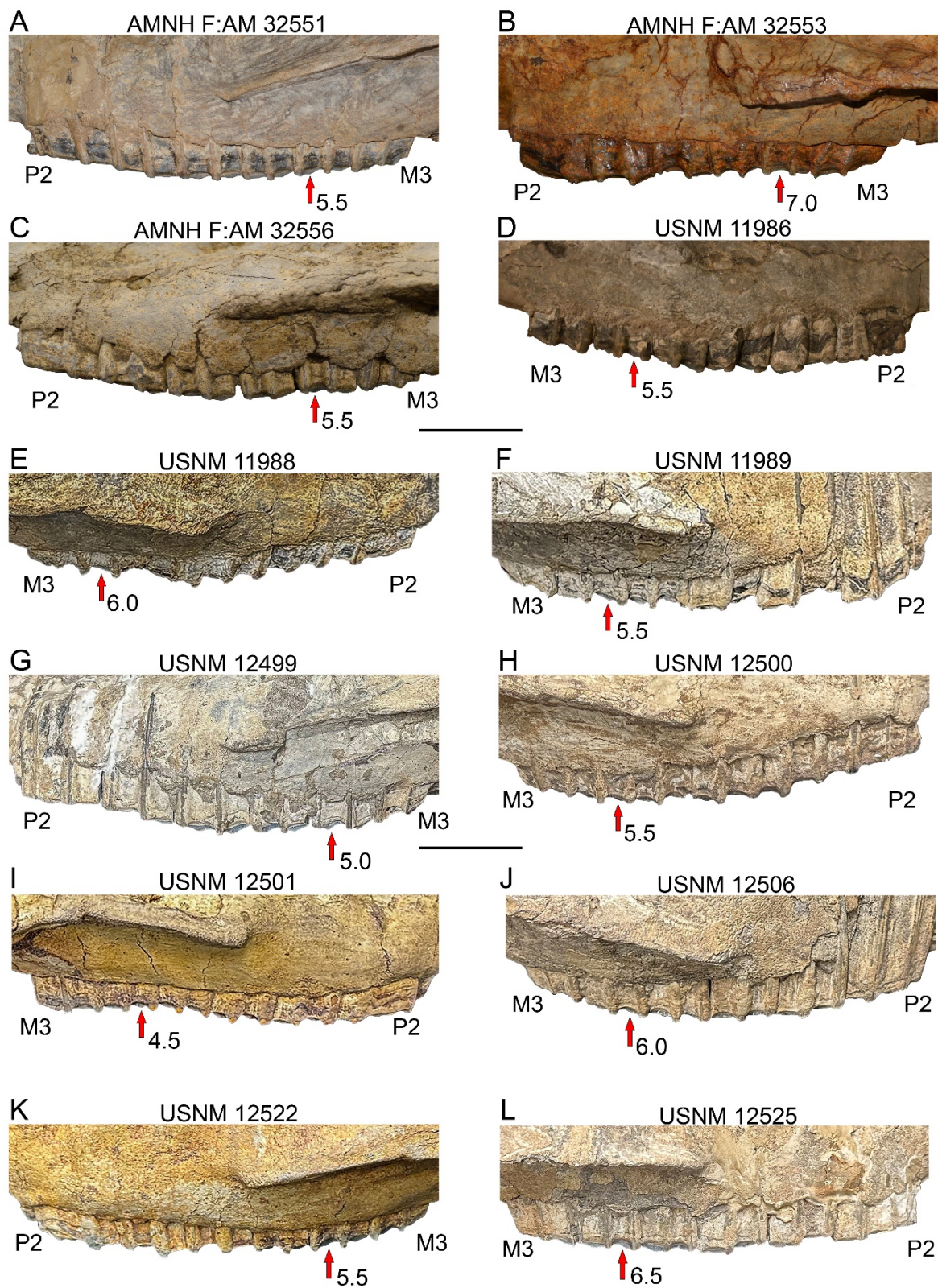
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559 Figure 4. Lateral view of the upper cheek tooth rows of young adult individuals of *Equus*
 560 *simplicidens* from Hagerman Horse Quarry (USNM12155 – USNM17003). The young adult
 561 definition refers to material and methods. Scale bar 5 cm.



562

563 Figure 5. Lateral view of the upper cheek tooth rows of fully adult individuals of *Equus*
 564 *simplicidens* from Hagerman Horse Quarry (AMNHF:AM32551 – USNM12525). The adult
 565 definition refers to material and methods. Scale bar 5 cm.

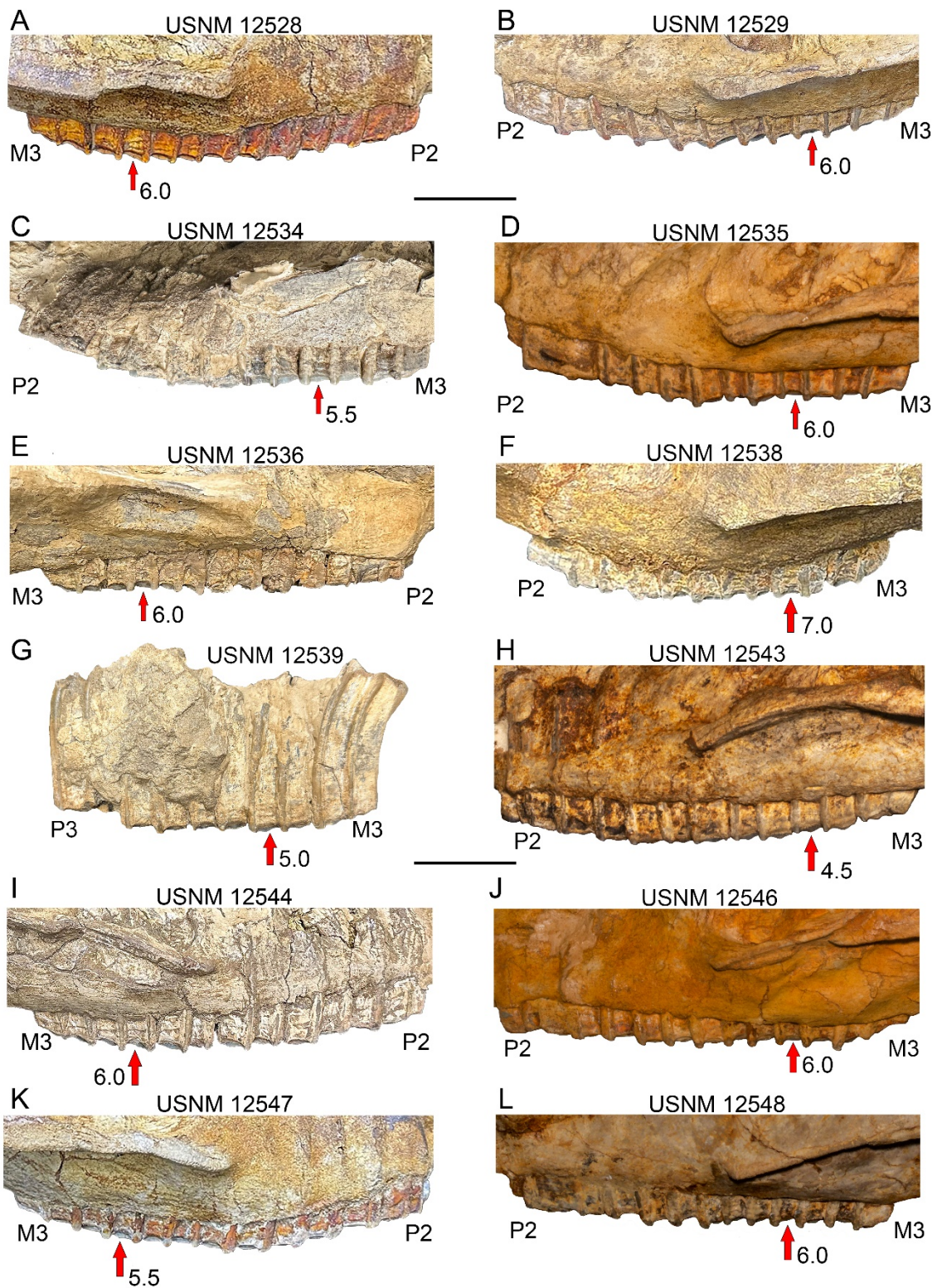


Figure 6. Lateral view of the upper cheek tooth rows of fully adult individuals of *Equus simplicidens* from Hagerman Horse Quarry (USNM12528 – USNM12548). The adult definition refers to material and methods. Scale bar 5 cm.

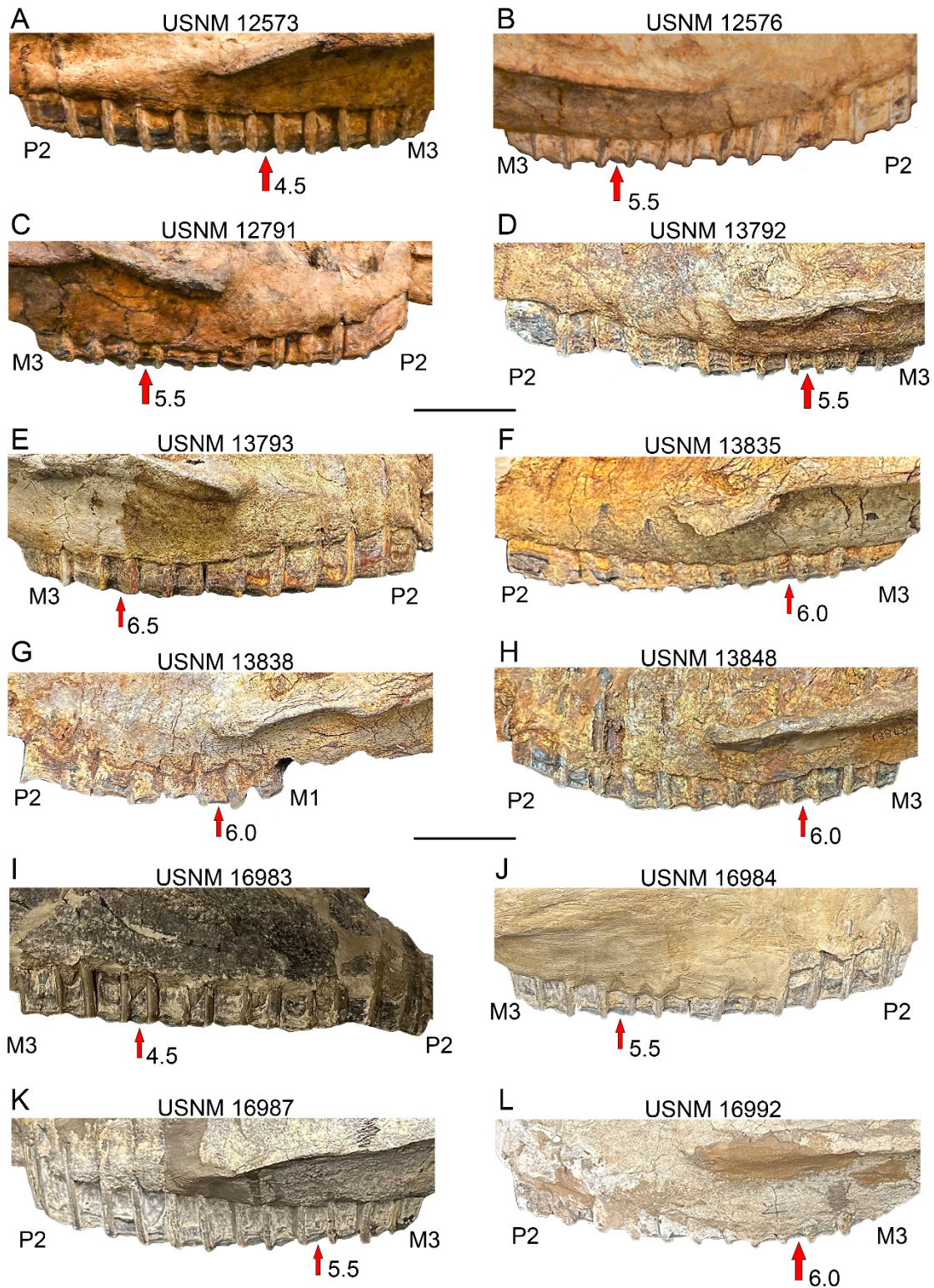
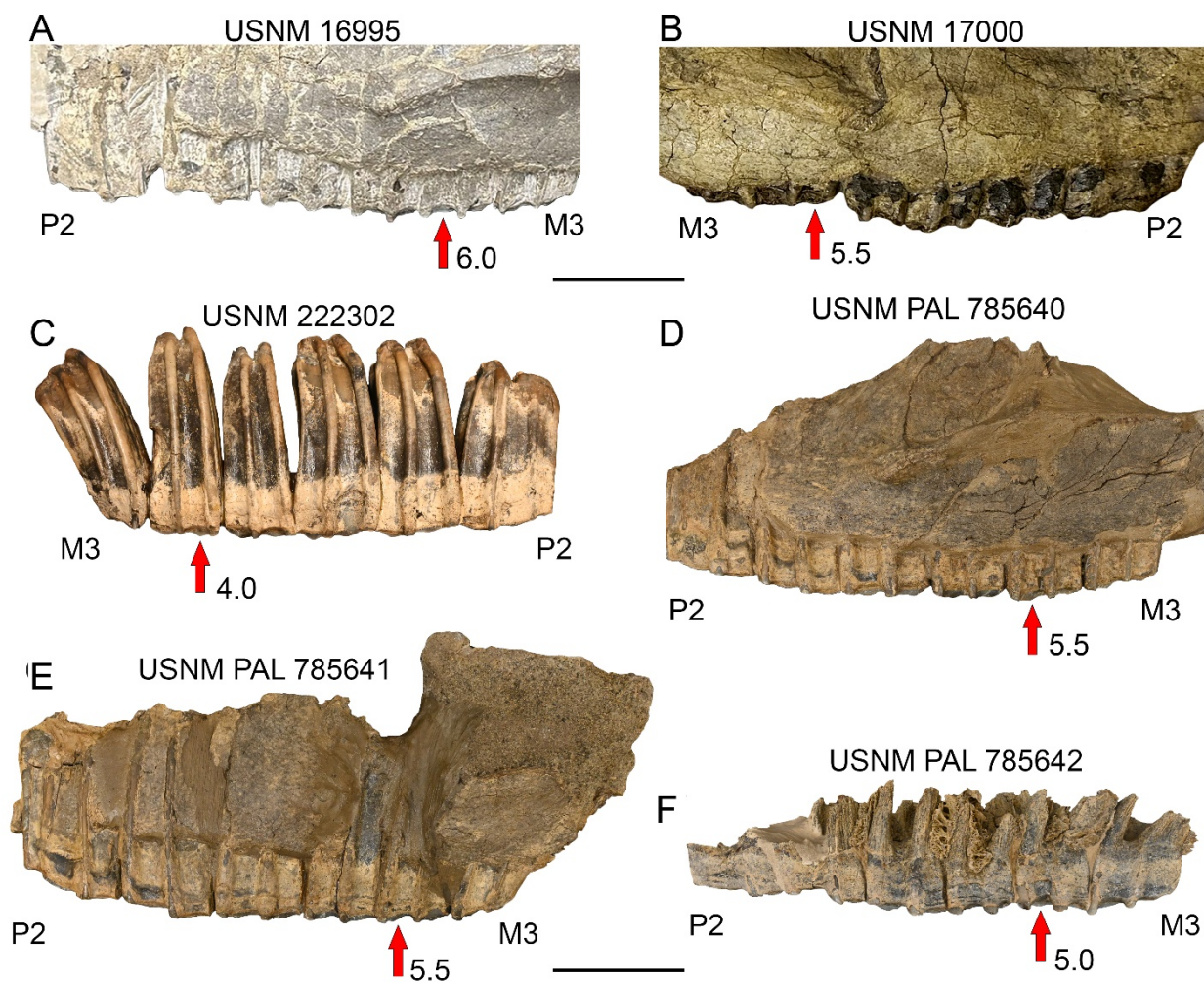


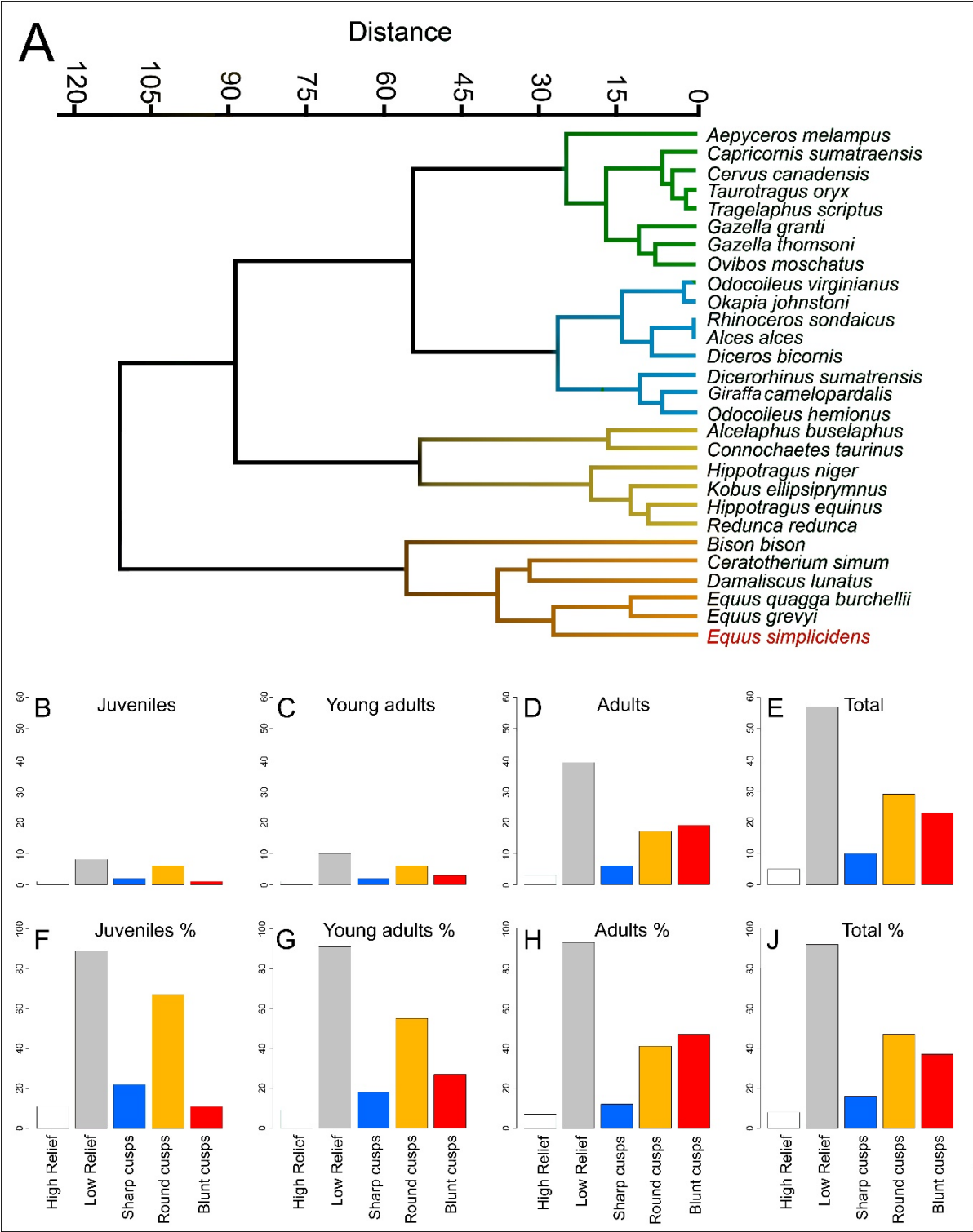
Figure 7. Lateral view of the upper cheek tooth rows of fully adult individuals of *Equus simplicidens* from Hagerman Horse Quarry (USNM12573 – USNM16992). The adult definition refers to material and methods. Scale bar 5 cm.



576

577 Figure 8. Lateral view of the upper cheek tooth rows of fully adult individuals of *Equus*
 578 *simplicidens* from Hagerman Horse Quarry (USNM16995 – USNMPAL785642). The adult
 579 definition refers to material and methods. Scale bar 5 cm.

580



581

582 Figure 9. A) Cluster analysis of *E. simplicidens* compared to typical extant ungulates with known

583 diets using traditional mesowear variables of high relief, sharp cusps, round cusps, and blunt cusps.

584 Green: mixed feeders; Blue: browsers; yellow: non extreme grazers; orange: extreme grazers. B-J)

585 Bar graph depicting row values (B-E) and percentages (F-J) of high versus low occlusal relief and

586 sharp vs. round vs. blunt cusps.

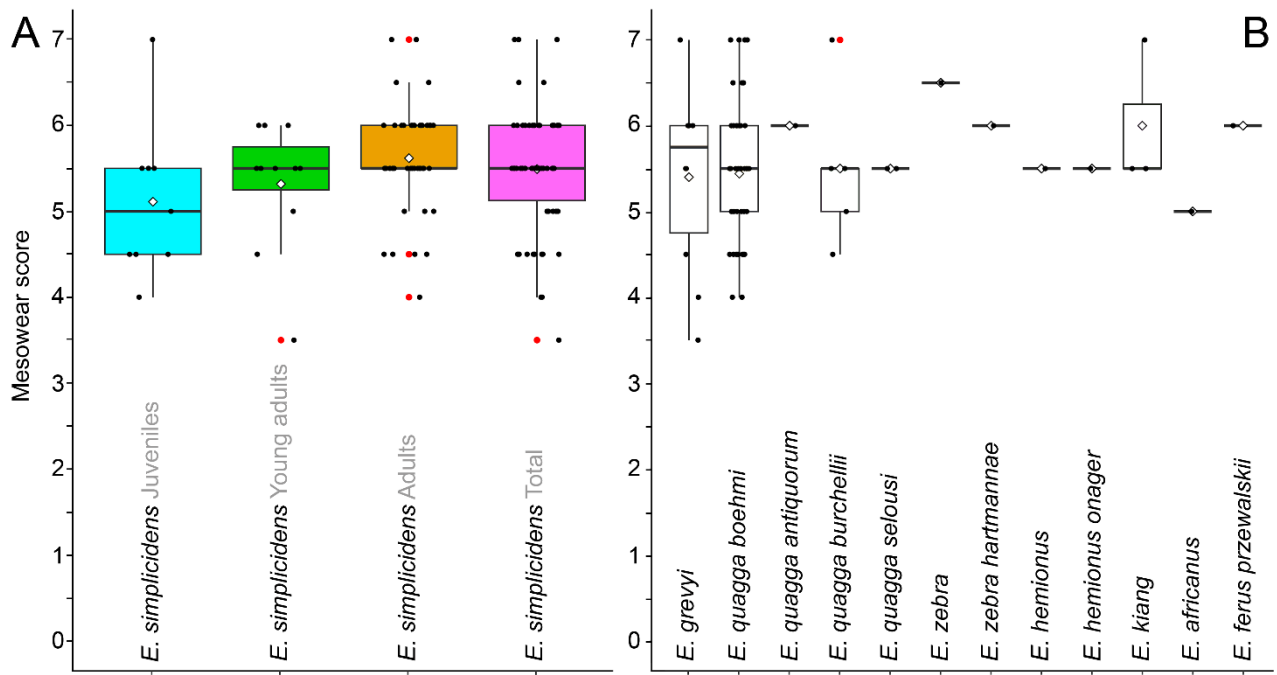


Figure 10. Boxplots comparing the mesowear score values in the different age classes of *Equus simplicidens* from the Hagerman Horse Quarry (A) with living species of the genus *Equus* (B).

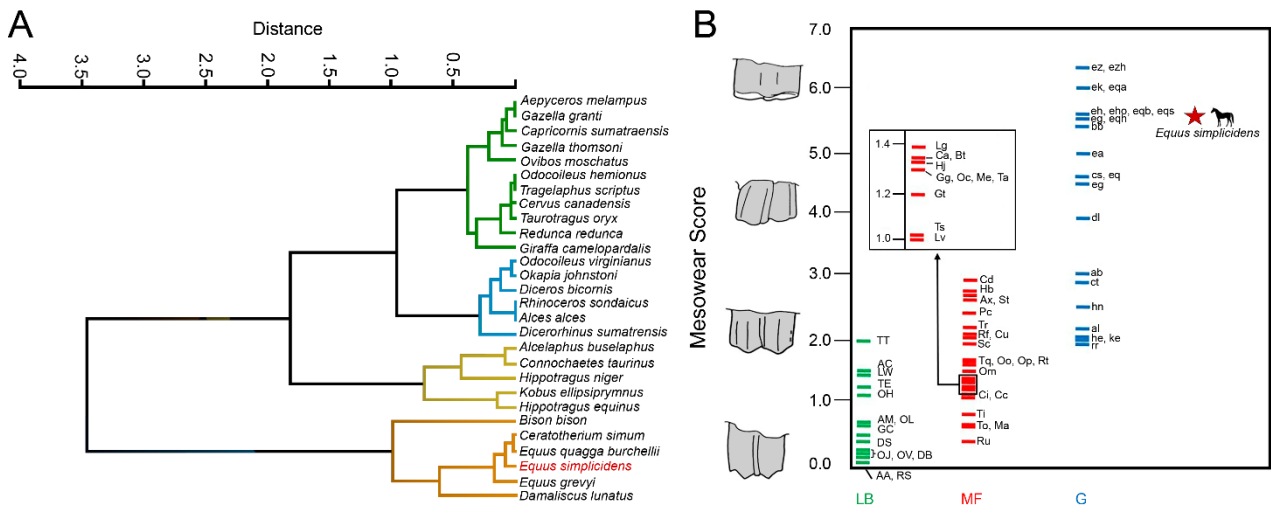
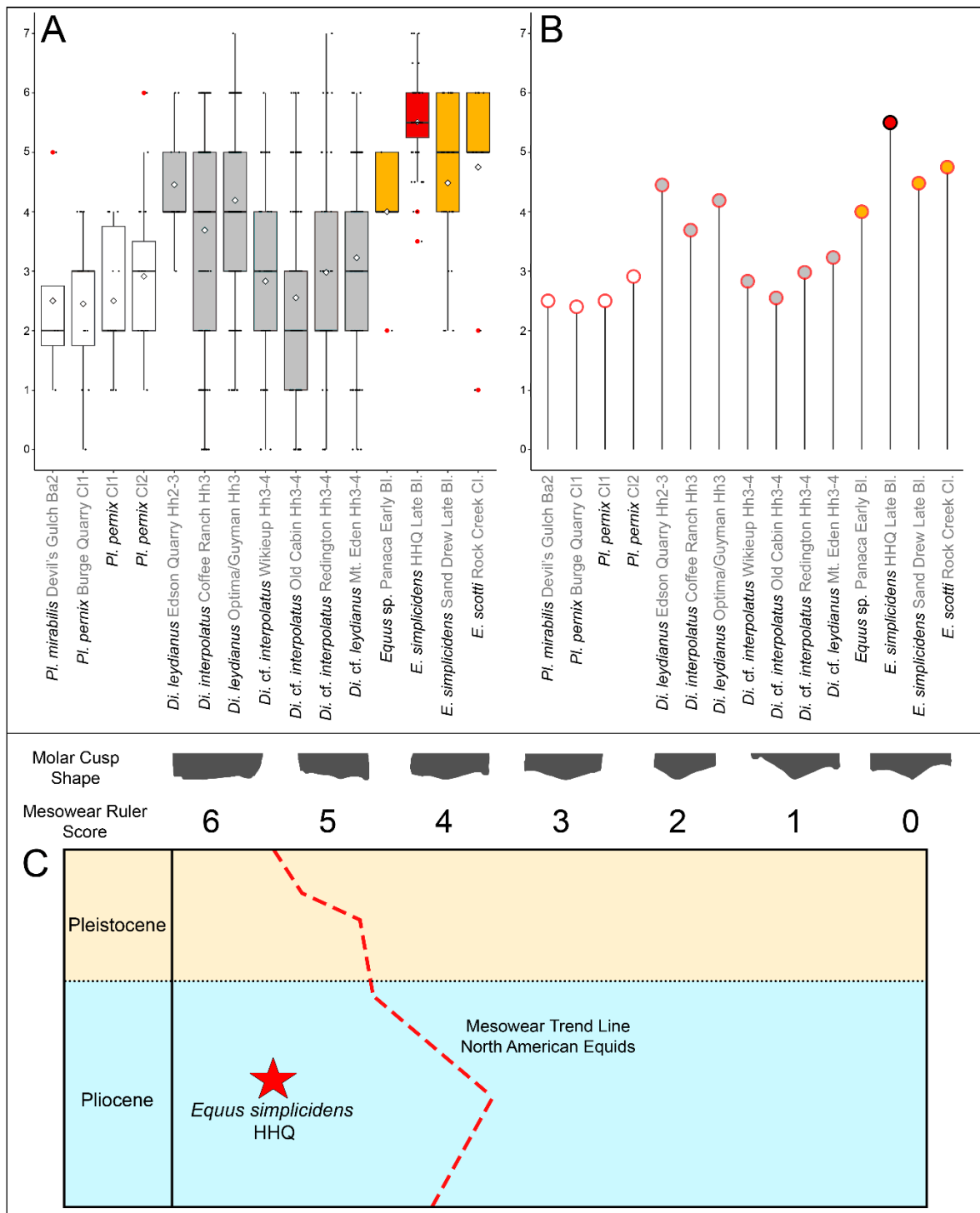


Figure 11. A) Cluster analysis results of *Equus simplicidens* compared to typical extant ungulates with known diets using mesowear scores. Green: mixed feeders; Blue: browsers; yellow: non extreme grazers; orange: extreme grazers. B) Mesowear scores based on the extant reference species from Fortelius and Solounias (2000) and the fossil samples of *E. simplicidens* from Hagerman: lowercase letters depict grazers, uppercase letters depict browsers, and a mixture of upper and lower case letters depict mixed feeders. **Ba** = *Bison antiquus*, **Ca** = *Camelops* sp., **Cs** = *Cervalces scotti*, **Eq** = *Equus* sp., **Ov** = *Odocoileus virginianus*, **Pm** = *Palaeolama mirifica*, **Rt** = *Rangifer tarandus*. Extant taxa are classified as leaf browsers (LB), mixed feeders (MF) and grazers (G). Browsers: **AA** = *Alces alces*, **AM** = *Antilocapra americana*, **DB** = *Diceros bicornis*, **DS** = *Dicerorhinus sumatrensis*, **GC** = *Giraffa camelopardalis*, **LW** = *Litocranius walleri*, **OH** = *Odocoileus hemionus*, **OJ** = *Okapia johnstoni*, **OL** = *Capreolus capreolus*, **OV** = *Odocoileus virginianus*, **RS** = *Rhinoceros sondaicus*, **TE** = *Tragelaphus euryceros*, **TT** = *Tragelaphus strepsiceros*. Grazers: **ab** = *Alcelaphus buselaphus*, **al** = *Sigmoceros lichtensteinii*, **bb** = *Bison bison*, **cs** = *Ceratotherium simum*, **ct** = *Connochaetes taurinus*, **dl** = *Damaliscus lunatus*, **eg** = *Equus grevyi*, **eq** = *Equus quagga*, **he** = *Hippotragus equinus*, **hn** = *Hippotragus niger*, **ke** = *Kobus ellipsiprymnus*, **rr** = *Redunca redunca*. Mixed feeders: **Ax** = *eCervus duvauceli*, **Ci** = *Capra ibex*, **Cu** = *Cervus unicolor*, **Gg** = *Gazella granti*, **Gt** = *Gazella thomsoni*, **Hj** = *Hemitragus jemlahicus*, **Lv** = *Lama vicugna*, **Ma** = *Antidorcas marsupialis*, **Me** = *Aepyceros melampus*, **Oc** = *Ovis*

617 *canadensis*, **Om** = *Ovibos moschatus*, **Oo** = *Ourebia ourebi*, **Op** = *Ovis ammon poli*, **Pc** = *Procavia*
618 *capensis*, **Rf** = *Redunca fulvorufula*, **Rt** = *Rangifer tarandus*, **Ru** = *Rhinoceros unicornis*, **Sc** =
619 *Syncerus caffer*, **St** = *Saiga tatarica*, **Ta** = *Tragelaphus angasi*, **Ti** = *Tragelaphus imberbis*, **To** =
620 *Taurotragus oryx*, **Tq** = *Tetracerus quadricornis*, **Tr** = *Boselaphus tragocamelus*. Additional equid
621 extant taxa from this study. Grazers: **ea** = *Equus africanus*, **ecp** = *Equus caballus przewalskii*, **eh** =
622 *Equus hemionus*, **eho** = *Equus hemionus onager*, **eq** = *Equus kiang*, **eq** = *Equus grevyi*, **eqh** = *Equus*
623 *quagga boehmi*, **eqa** = *Equus quagga antiquorum*, **eqb** = *Equus quagga burchelli*, **eqs** = *Equus*
624 *quagga selouisi*, **ez** = *Equus zebra*, **ezh** = *Equus zebra hartmannae*.
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627 Figure 12. Mesowear comparison of *Equus simplicidens* from Hagerman Horse Quarry with North
 628 American taxa of the genera *Pliohippus*, *Dinohippus* and *Equus* (data from Muhlbacler et al. 2011).
 629 A) Total mesowear values comparison. B) Mean mesowear values comparison. C) Comparison of
 630 the Hagerman Horse Quarry with the Mesowear Trend Line of the North American fossil equids
 631 (Modified from Figure 1 in Muhlbacler et al., 2011).

632 **Tables**

633 Table 1. Complete sample of *Equus simplicidens* from the Hagerman Horse Quarry excavated by
 634 the Smithsonian Natural History Museum with mesowear scoring.

Catalogue Number	Class	Sex	Tooth Row	Side	Tooth Position	Cusp	Cusp Shape	Relief	Mesowear Score
USNM1249 7	Juvenile	indeterminate	dP1 / P2-P3 erupted / dP4 / M1-M2 / M3 in crypt	lt.	M2	paracone	round	high	4,5
USNM1250 2	Juvenile	indeterminate	dP1 / P2-P3 erupted / dP4 / M1-2 / M3 in crypt	lt.	M2	paracone	sharp	low	5,5
USNM1251 7	Juvenile	indeterminate	dP1-dP4 / M1-M2 / M3 in crypt	lt.	M2	paracone	sharp	low	5,5
USNM1384 1	Juvenile	female	dP1-dP4 / M1-2 / M3 in crypt	lt.	M2	paracone	round	low	4,5
USNM1384 2	Juvenile	female	dP1-dP4 / M1 / M2 emerging from crypt	lt.	M1	paracone	round	low	5,5
USNM1698 2	Juvenile	male	dI1-dI2 / dP1-dP4 / M1 / M2 erupted	lt.	M1	paracone	round	low	5,0
USNM1699 0	Juvenile	indeterminate	dP2-dP4 / M1 / M2 emerging from crypt	rt.	M1	paracone	round	low	4,0
USNM1699 1	Juvenile	female	dP1-dP4 / M1 / M2 in crypt	rt.	M1	metacone	round	low	4,5
USNM1699 8	Juvenile	male	P2-P3 emerging / dP4 / M1 / M2 erupted	rt.	M2	paracone	blunt	low	7,0
USNM1215 5	Young adult	female	dp1-M2 / M3 emerging	lt.	M2	paracone	round	high	3,5
USNM1251 5	Young adult	indeterminate	P2-M2 / M3 emerging from crypt	rt.	M2	paracone	blunt	low	6,0
USNM1251 8	Young adult	indeterminate	dP1 / P2-M2 / M3 erupted	rt.	M2	paracone	round	low	5,5

USNM1252 1	Young adult	ind et	dP1 / P2-M2 / M3 erupted	rt.	M2	parac one	blunt	low	6,0
USNM1254 2	Young adult	mal e	dP1 / P2-M2 / M3 erupted	lt.	M2	parac one	round	low	5,5
USNM1383 2	Young adult	ind et	dP1 / P2-P3 / P4 emerging / M1-M2 / M3 emerging from crypt	rt.	M2	parac one	round	low	5,5
USNM1698 5	Young adult	fem ale	P2-M2/ M3 erupted	rt.	M2	parac one	sharp	low	5,0
USNM1698 9	Young adult	ind et	dp1 / P2-P3 / P4 erupted / M1- M2 / M3 emergent	rt.	M2	parac one	sharp	low	5,5
USNM1699 4	Young adult	ind et	dP1 / P2-M2 / M3 emergent	lt.	M2	parac one	round	low	5,5
USNM1699 7	Young adult	mal e	dP1 / P2-P3/ P4 emerged / M1-M2 / M3 emergent	rt.	M2	parac one	round	low	4,5
USNM1700 3	Young adult	fem ale	P2-P3 / P4 erupted / M1-M2 / M3 erupted	rt.	M2	parac one	blunt	low	6,0
AMNHFA M32551	Adult	fem ale	dP1-M3	lt.	M2	parac one	round	low	5,5
AMNHFA M32553	Adult	mal e	P2-M3	lt.	M2	parac one	blunt	low	7,0
AMNHFA M32556	Adult	mal e	dP1/ P2-M3	lt.	M2	parac one	round	low	5,5
USNM1198 6	Adult	mal e	dP1/ P2-M3	rt	M2	parac one	sharp	low	5,5
USNM1198 8	Adult	fem ale	dP1-M3	rt.	M2	metac one	blunt	low	6,0
USNM1198 9	Adult	fem ale	dP1 / P2-M3	rt.	M2	parac one	sharp	low	5,5

USNM1249 9	Adult	fem ale	dP1 / P2-M3	lt.	M2	parac one	sharp	high	5,0
USNM1250 0	Adult	male	dp1/ P2-M3	rt.	M2	parac one	round	low	5,5
USNM1250 1	Adult	male	dP1 / P2-M3	lt.	M2	parac one	round	low	4,5
USNM1250 6	Adult	ind et	P2-M3	rt.	M2	parac one	blunt	low	6,0
USNM1252 2	Adult	male	P2-M3	lt.	M2	parac one	round	low	5,5
USNM1252 5	Adult	male	dP1 / P2-M3	rt.	M2	parac one	blunt	low	6,5
USNM1252 8	Adult	fem ale	dP1 / P2-M3	rt.	M2	parac one	blunt	low	6,0
USNM1252 9	Adult	ind et	P2-M3	lt.	M2	parac one	blunt	low	6,0
USNM1253 4	Adult	fem ale	dP1 / P2-M3	lt.	M2	parac one	blunt	low	5,5
USNM1253 5	Adult	fem ale	dP1 / P2-M3	lt.	M2	parac one	blunt	low	6,0
USNM1253 6	Adult	adu lt	P2-M3	rt.	M2	parac one	blunt	low	6,0
USNM1253 8	Adult	male	P2-M3	lt.	M2	parac one	blunt	low	7,0
USNM1253 9	Adult	ind et	P3-M3	lt.	M2	parac one	round	low	5,0
USNM1254 3	Adult	fem ale	dP1 / P2-M3	lt.	M2	parac one	sharp	low	4,5
USNM1254 4	Adult	fem ale	P2-M3	rt.	M2	parac one	blunt	low	6,0

USNM1254 6	Adult	fem ale	dP1 / P2-M3	lt.	M2	parac one	blunt	low	6,0
USNM1254 7	Adult	fem ale	dP1 / P2-M3	rt.	M2	parac one	round	low	5,5
USNM1254 8	Adult	fem ale	dP1 / P2-M3	lt.	M2	parac one	blunt	low	6,0
USNM1257 3	Adult	mal e	P2-M3	rt.	M1	parac one	round	low	4,5
USNM1257 6	Adult	fem ale	dP1 / P2-M3	rt.	M2	parac one	round	low	5,5
USNM1379 1	Adult	fem ale	dP1 / P2-M3	lt.	M2	parac one	round	low	5,5
USNM1379 2	Adult	fem ale	P2-M3	lt.	M2	parac one	round	low	5,5
USNM1379 3	Adult	fem ale	dP1 / P2-M3	rt.	M2	parac one	blunt	low	6,5
USNM1383 5	Adult	fem ale	P2-M3	lt.	M2	parac one	blunt	low	6,0
USNM1383 8	Adult	mal e	P2-M1	rt.	P4	metac one	blunt	low	6,0
USNM1384 8	Adult	fem ale	P2-M3	lt.	M2	parac one	blunt	low	6,0
USNM1698 3	Adult	fem ale	P2-M3	rt.	M2	parac one	round	high	4,5
USNM1698 4	Adult	fem ale	dP1 / P2-M3	rt.	M2	parac one	round	low	5,5
USNM1698 7	Adult	fem ale	P2-M3	lt.	M2	parac one	sharp	low	5,5
USNM1699 2	Adult	mal e	P2-M3	lt.	M2	parac one	blunt	low	6,0

USNM1699 5	Adult	fem ale	P2-M3	lt.	M2	parac one	blunt	low	6,0
USNM1700 0	Adult	mal e	P2-M3	rt.	M2	parac one	round	low	5,5
USNM2223 02	Adult	ind et	P2-M3	rt	M2	parac one	round	hig h	4,0
USNM7856 40	Adult	ind et	P2-M3	lt.	M2	parac one	sharp	low	5,5
USNM7856 41	Adult	ind et	P2-M3	lt.	M2	parac one	round	low	5,5
USNM7856 42	Adult	ind et	P2-M3	lt.	M2	parac one	round	low	5,0
Mesowear Mean									5,5

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637 Table 2. *Equus simplicidens* mesowear results divided into age classes.

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Taxon	N	Average Mesowear Score	%High Relief	% Low Relief	% Sharp Cusps	% Round cusps	% Blunt cusps
Adults	42	5.6	7	93	12	41	47
Subadults	11	5.3	9	91	18	55	27
Juveniles	9	5.1	11	89	22	67	11
Combined age classes	62	5.5	8	92	16	47	37

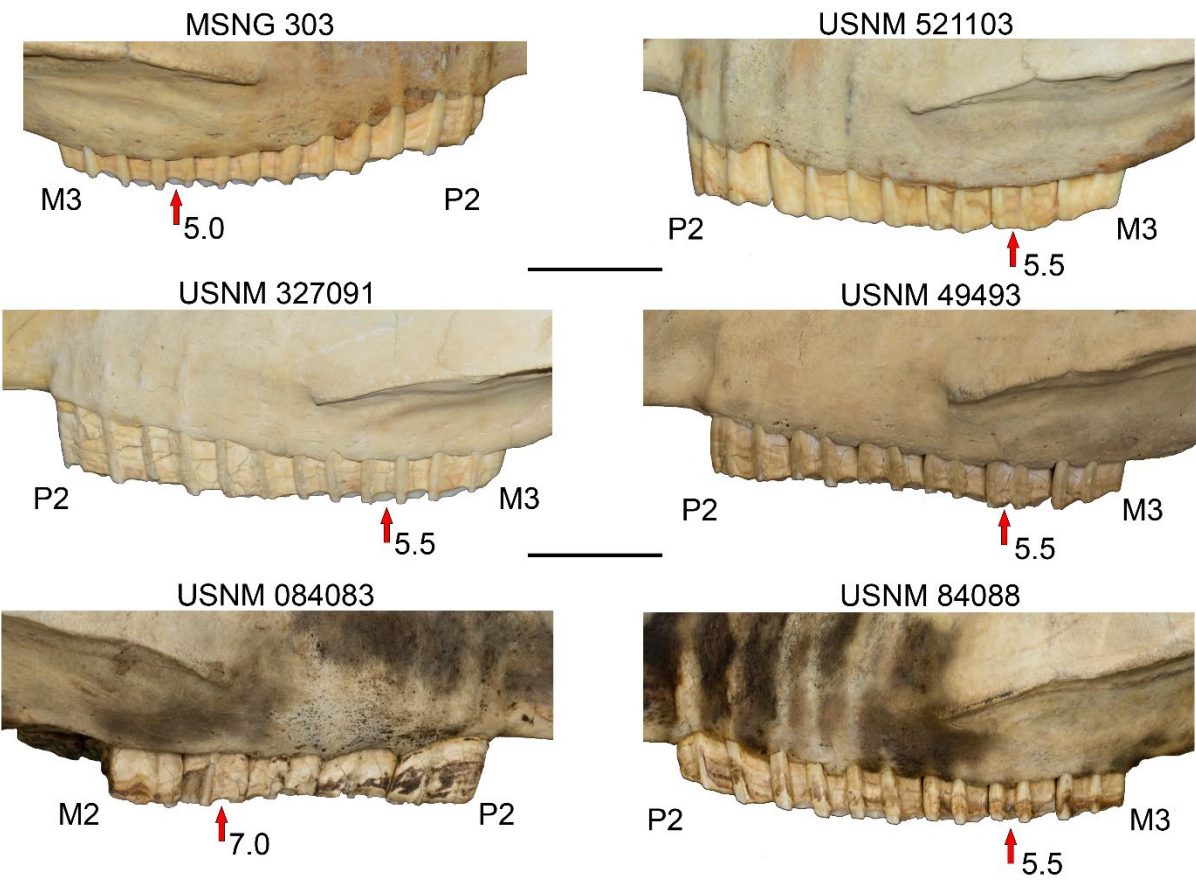
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641 **Supplementary Information**

642 Supplementary Information 1. Images of the lateral upper cheek tooth rows of the wild living *Equus*
643 species scored in the present work.

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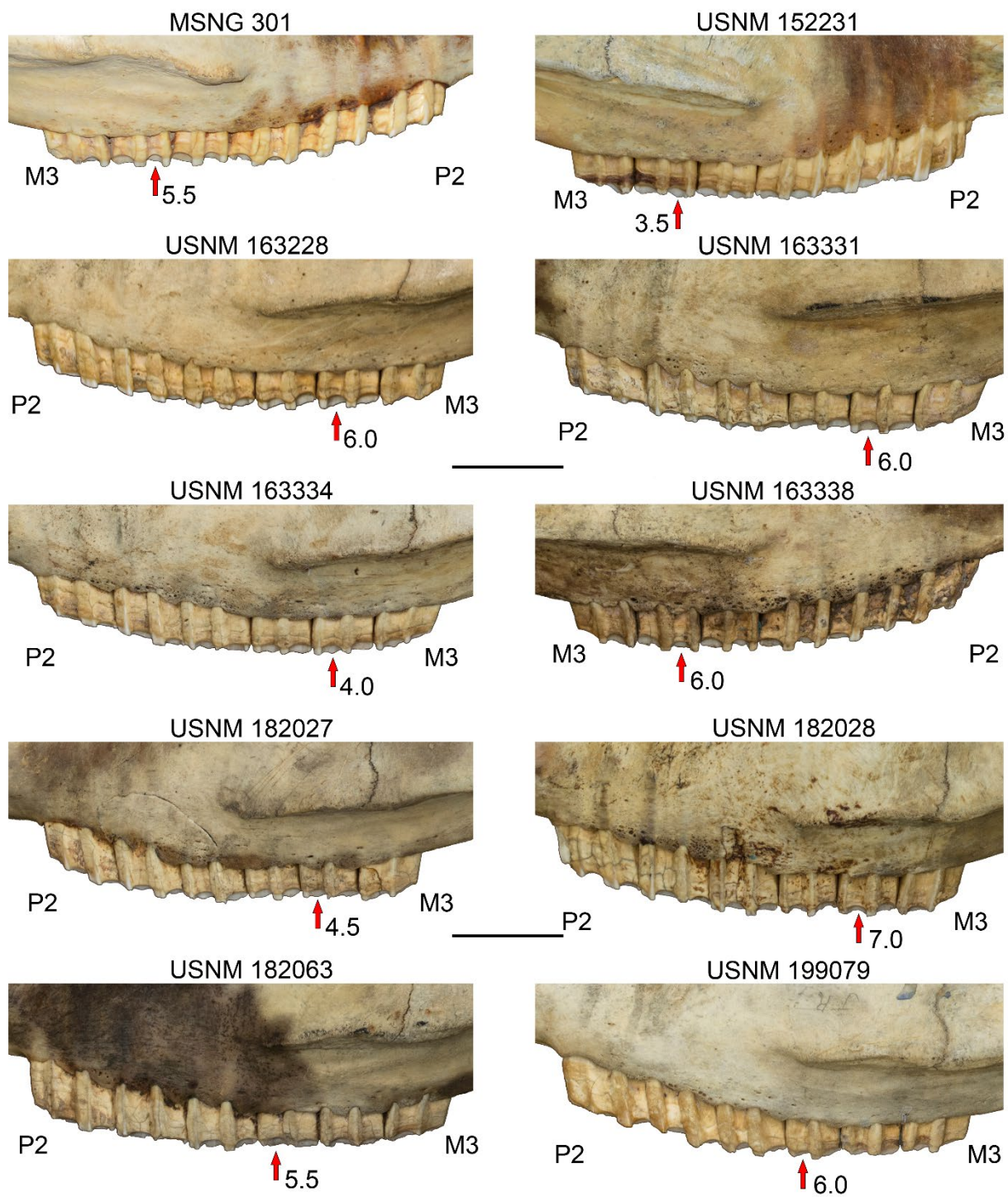


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646 Lateral view of the upper cheek tooth rows of living wild equids. MSNG303: *Equus africanus*;
647 USNM521103: *Equus hemionus*; USNM327901: *Equus hemionus onager*; USNMA49493 -
648 USNM084083 - USNM84088: *Equus kiang*. Scale bar 5 cm.

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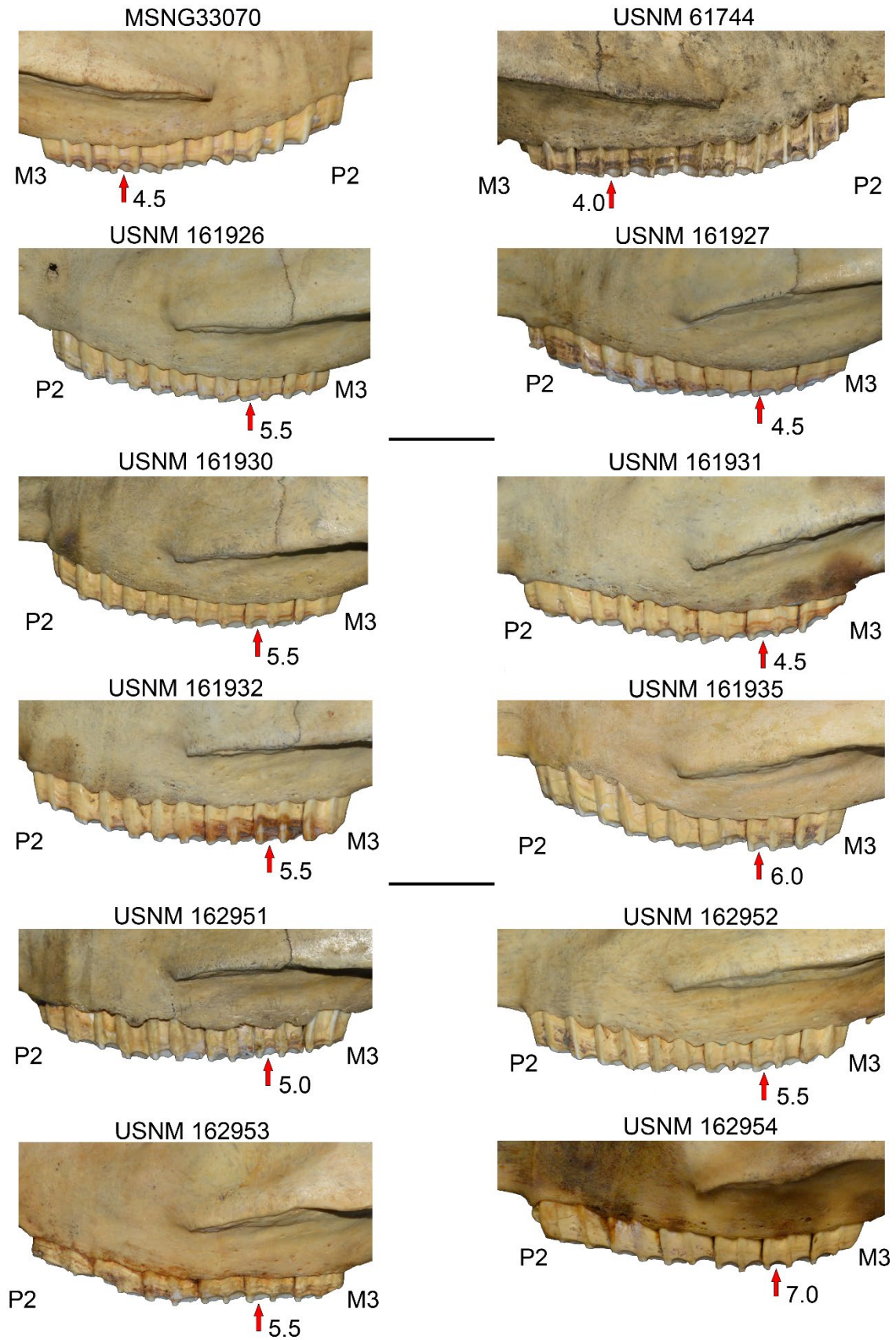
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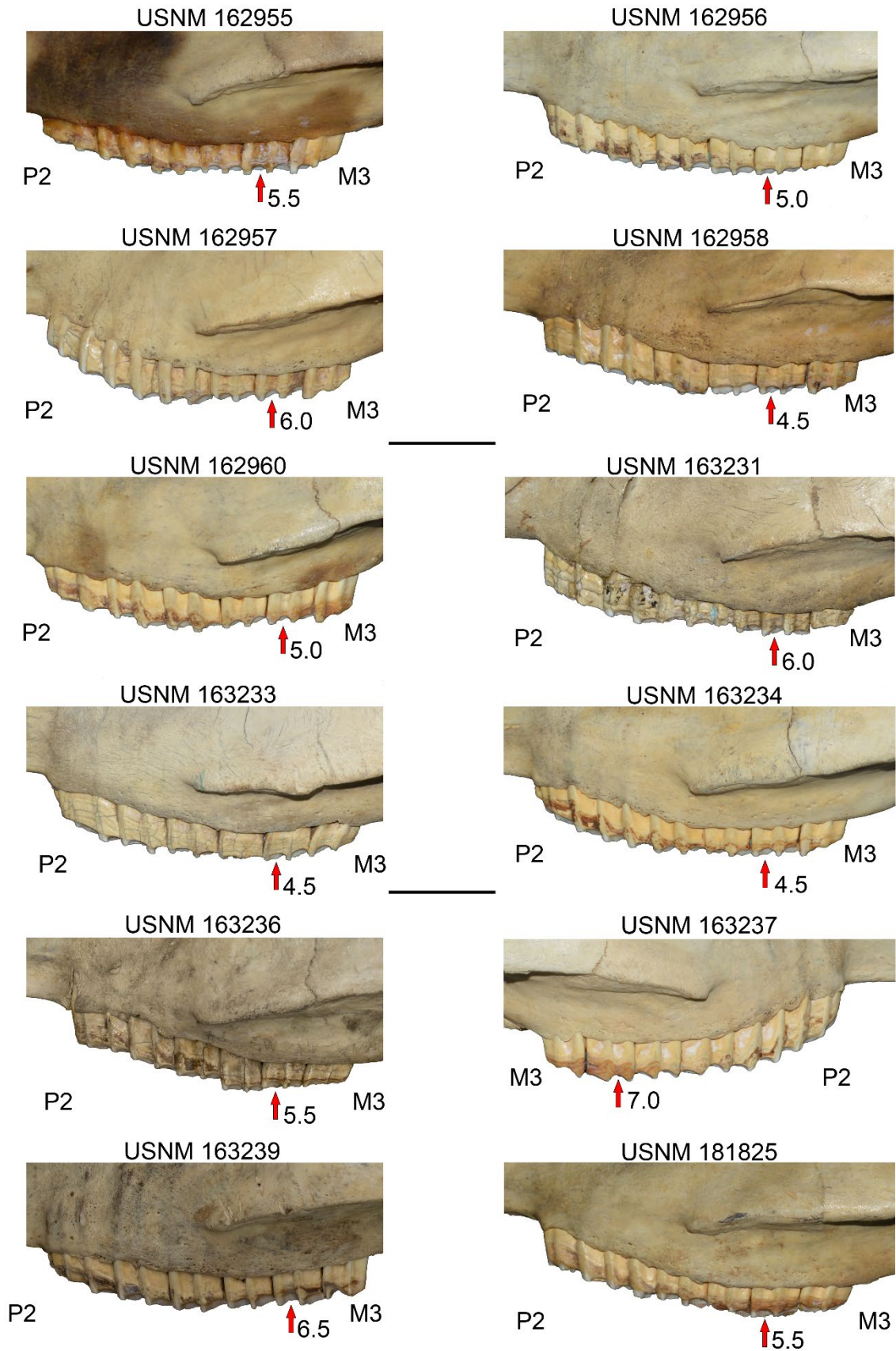
652 Lateral view of the upper cheek tooth rows of living *Equus grevyi*. Scale bar 5 cm.

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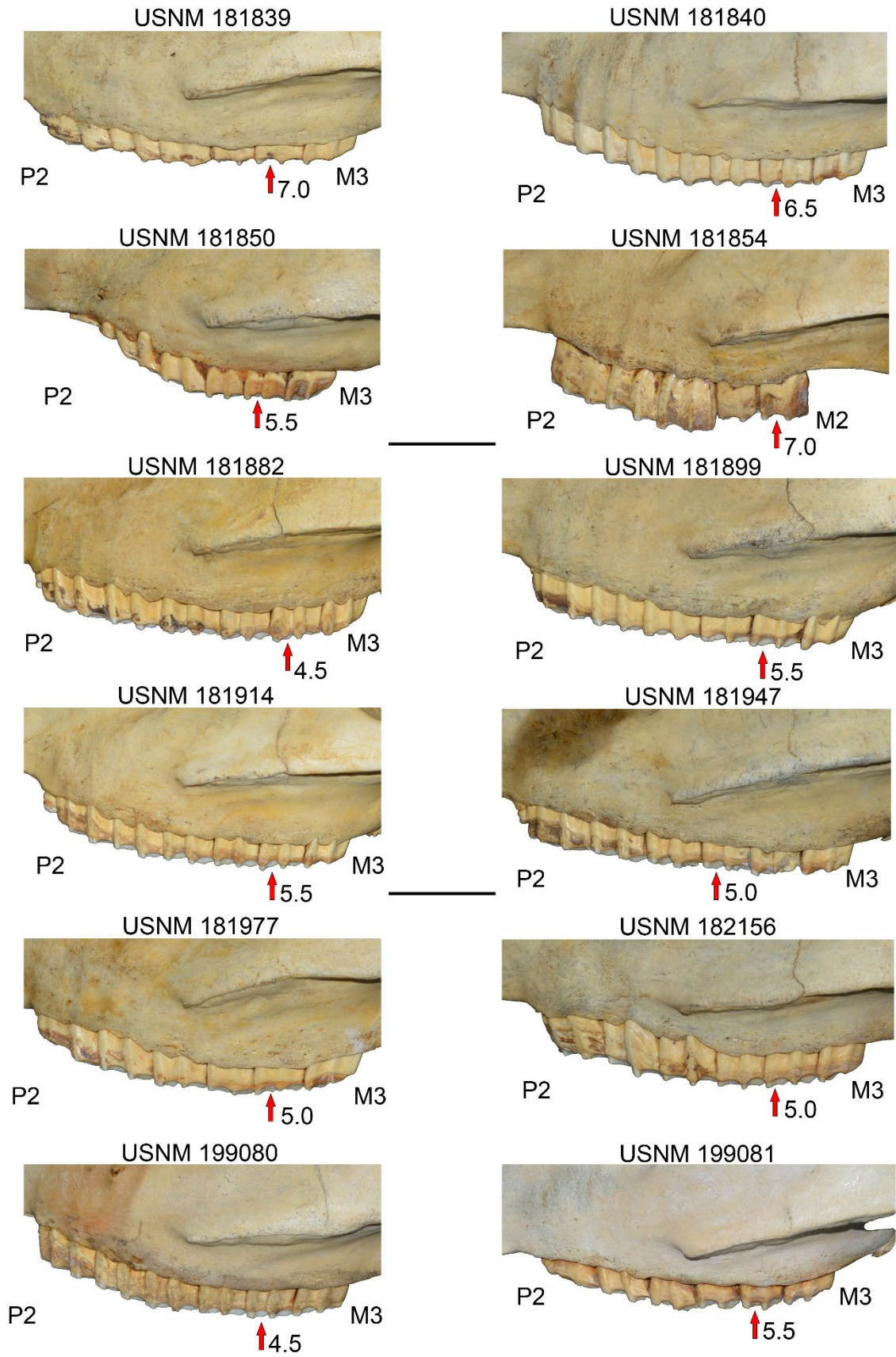
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655 Lateral view of the upper cheek tooth rows of living *Equus quagga boehmi*. Scale bar 5 cm.



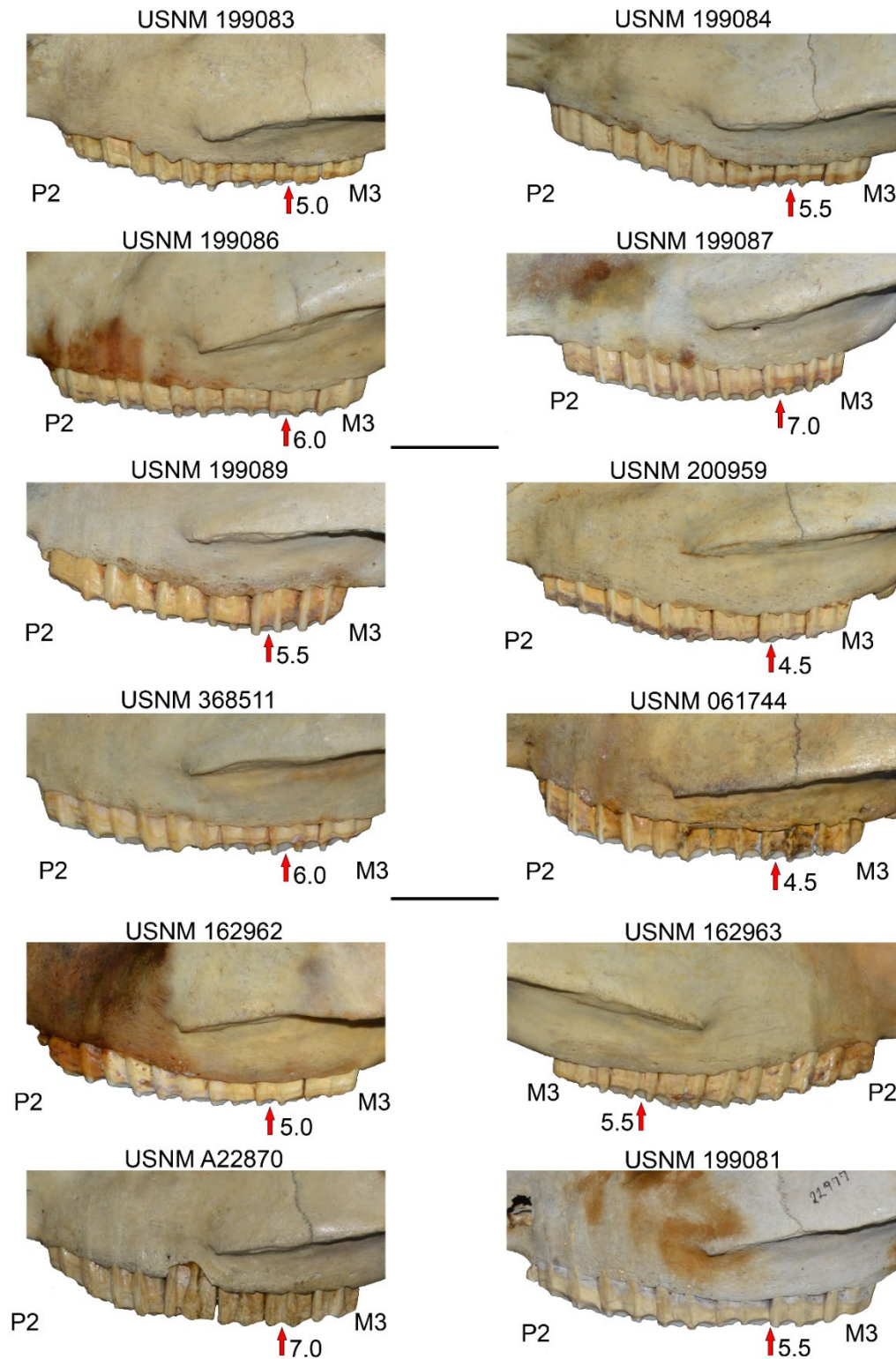
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657 Lateral view of the upper cheek tooth rows of living *Equus quagga boehmi*. Scale bar 5 cm.



658

659 Lateral view of the upper cheek tooth rows of living *Equus quagga boehmi*. Scale bar 5 cm.



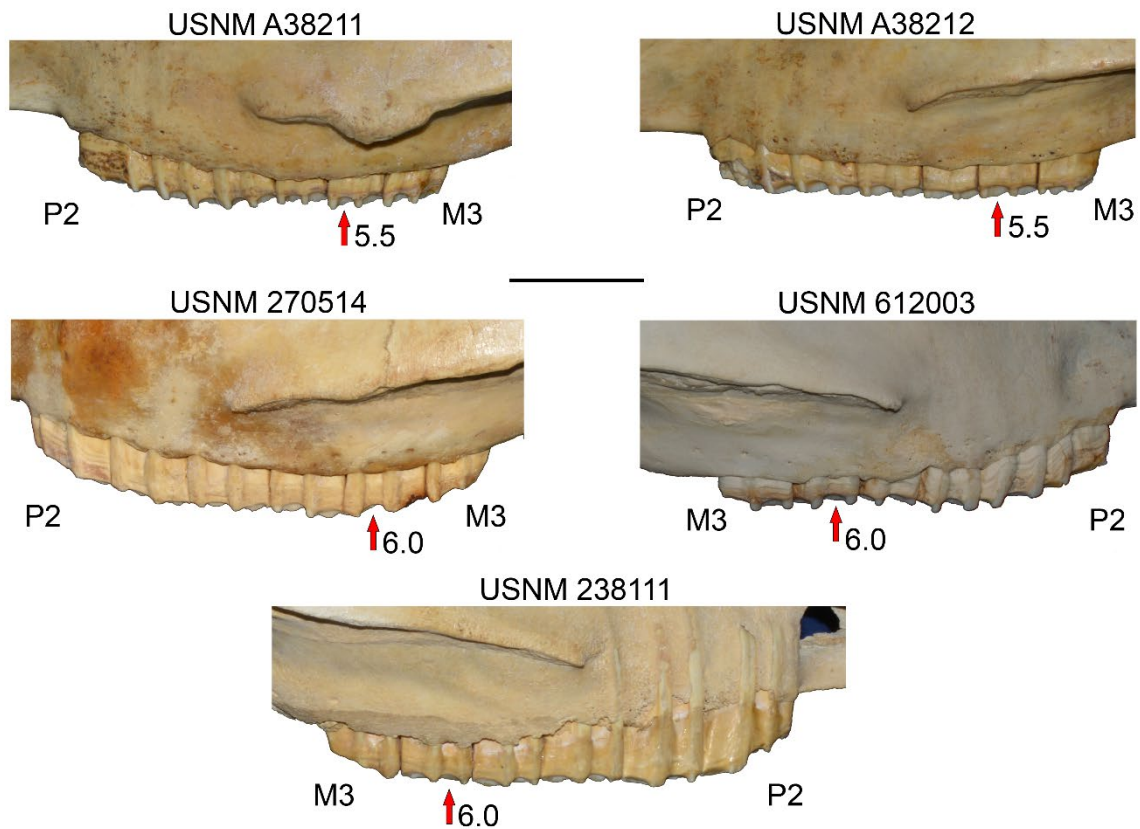
660

661 Lateral view of the upper cheek tooth rows of living *Equus quagga boehmi* (USNM199083

662 - USNM199084 - USNM199086 - USNM199087 - USNM199089 - USNM200959), *Equus quagga*

663 *antiquorum* (USNM368511) and *Equus quagga burchelli* (USNM061744 - USNM162962 -

664 USNM162963 - USNMA22870 - USNMA22977). Scale bar 5 cm.



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666 Lateral view of the upper cheek tooth rows of living *Equus quagga selousi* (USNMA38211 -
 667 USNMA38212), *Equus zebra* (USNM270514), *Equus zebra hartmannae* (USNM612003) and
 668 *Equus przewalskii* (USNM238111). Scale bar 5 cm.

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677 Supplementary Table 1. Complete sample of wild living *Equus* species with mesowear scoring.

Catalogue Number	Species	Age (Ma)	Age skulls	Sex	Locality	Right Tooth Row	Left Tooth Row	Tooth Position	Side	Cusp	Cusp Shape	Relief	Mesowear Score
MSNG303	<i>Equus africanus</i>	0.0	Adult	female	Assaorta, Eritrea	P2-M3	P2-M3	M2	rt.	paracone	blunt	low	5,0
USNM521103	<i>Equus hemionus</i>	0.0	Adult	female	Unknown (wild)	P2-M3	P2-M3	M2	lt.	paracone	round	low	5,5
USNM327901	<i>Equus hemionus onager</i>	0.0	Adult	female	Khorashan Dasht I Kavir, Iran	P2-M3	P2-M3	M2	lt.	paracone	round	low	5,5
USNMA49493	<i>Equus kiang</i>	0.0	Adult	male	Jammu and Kashmir	P2-M3	P2-M3	M2	lt.	paracone	round	low	5,5
USNM084083	<i>Equus kiang</i>	0.0	Adult	male	Jammu and Kashmir	P2-M3	P2-M3	M1	rt.	paracone	blunt	low	7,0
USNM84088	<i>Equus kiang</i>	0.0	Adult	female	Jammu and Kashmir	P2-M3	P2-M3	M2	lt.	paracone	blunt	low	5,5
MSNG301	<i>Equus grevyi</i>	0.0	Adult	female	Scioa, Ethiopia	P2-M3	P2-M3	M2	rt.	paracone	blunt	low	5,5
USNM152231	<i>Equus grevyi</i>	0.0	Adult	female	unknown (wild)	P2-M3	P2-M3	M2	rt.	paracone	sharp	high	3,5
USNM163228	<i>Equus grevyi</i>	0.0	Adult	female	Nguaso Nyiro, Nyiro River	P2-M3	P2-M3	M2	lt.	paracone	blunt	low	6,0
USNM163331	<i>Equus grevyi</i>	0.0	Adult	female	Nguaso Nyiro, Nyiro River	P2-M3	P2-M3	M2	lt.	paracone	blunt	low	6,0
USNM163334	<i>Equus grevyi</i>	0.0	Adult	female	Nguaso Nyiro, Nyiro River	P2-M3	P2-M3	M2	lt.	paracone	round	low	4,0
USNM163338	<i>Equus grevyi</i>	0.0	Adult	male	Nguaso Nyiro, Roosevelt	P2-M3	P2-M3	M2	rt.	paracone	blunt	low	6,0
USNM182027	<i>Equus grevyi</i>	0.0	Adult	male	Nguaso Nyiro, Nyiro River	P2-M3	P2-M3	M2	lt.	paracone	round	low	4,5
USNM182028	<i>Equus grevyi</i>	0.0	Adult	female	Nguaso Nyiro, Nyiro River	P2-M3	P2-M3	M2	lt.	paracone	blunt	low	7,0
USNM182063	<i>Equus grevyi</i>	0.0	Adult	male	Nguaso Nyiro, Nyiro River	P2-M3	P2-M3	M1	lt.	paracone	sharp	low	5,5
USNM199079	<i>Equus grevyi</i>	0.0	Adult	male	Nguaso Nyiro, Nyiro River	P2-M3	P2-M3	M1	lt.	paracone	blunt	low	6,0
MSNG33070	<i>Equus quagga boehmi</i>	0.0	Adult	male	Javello, Ethiopia	P2-M3	P2-M3	M2	rt.	paracone	round	low	4,5
USNM61744	<i>Equus quagga boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	rt.	paracone	round	low	4,0
USNM161926	<i>Equus quagga boehmi</i>	0.0	Adult	male	Kitanga Farm, Kenya	P2-M3	P2-M3	M2	lt.	paracone	blunt	low	6,0
USNM161927	<i>Equus quagga boehmi</i>	0.0	Adult	female	Kitanga Farm, Kenya	P2-M3	P2-M3	M2	lt.	paracone	round	low	4,5
USNM161930	<i>Equus quagga boehmi</i>	0.0	Adult	male	Kamiti Farm, Kenya	P2-M3	P2-M3	M2	lt.	paracone	round	low	5,5
USNM161931	<i>Equus quagga boehmi</i>	0.0	Adult	male	Kamiti Farm, Kenya	P2-M3	P2-M3	M2	lt.	paracone	round	low	4,0

USNM1619 32	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Kamiti Farm, Kenya	P2-M3	P2-M3	M2	lt.	parac one	sharp	low	5,5
USNM1619 35	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Kapiti plains, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	6,0
USNM1629 51	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	sharp	low	5,0
USNM1629 52	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,5
USNM1629 53	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,5
USNM1629 54	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	7,0
USNM1629 55	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	sharp	low	5,5
USNM1629 56	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,0
USNM1629 57	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	female	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	6,0
USNM1629 58	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	female	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	4,5
USNM1629 60	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M1	lt.	parac one	round	low	5,0
USNM1632 31	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nairobi, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	6,0
USNM1632 33	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Kasorongai River, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	4,5
USNM1632 34	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	4,5
USNM1632 36	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Ulucania Hills	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,5
USNM1632 37	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	female	Ulucania Hills	P2-M3	P2-M3	M2	rt.	parac one	blunt	low	7,0
USNM1632 39	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	female	Lake Baringo	P2-M3	P2-M3	M2	lt.	meta cone	blunt	low	6,5
USNM1818 25	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Mtoto Andei, Kenya	P2-M3	P2-M3	M2	lt.	parac one	sharp	low	5,5
USNM1818 39	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Suswa Plains, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	7,0
USNM1818 40	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	female	Suswa Plains, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	6,5
USNM1818 50	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,5
USNM1818 54	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	female	Nguaso Nyiro, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	7,0
USNM1818 82	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Palm Springs, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	4,5
USNM1818 99	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	male	Kabalot Hill, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,5
USNM1819 14	<i>Equus quagga</i> <i>boehmi</i>	0.0	Adult	female	Kabalot Hill, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,5

USNM1819 47	<i>Equus quagga boehmi</i>	0.0	Adult	male	Telak River, Kenya	P2-M3	P2-M3	M1	lt.	parac one	sharp	low	5,0
USNM1819 77	<i>Equus quagga boehmi</i>	0.0	Adult	male	Telak River, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,0
USNM1821 56	<i>Equus quagga boehmi</i>	0.0	Adult	male	Archers Post, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,0
USNM1990 80	<i>Equus quagga boehmi</i>	0.0	Adult	male	Athi Plains, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	4,5
USNM1990 81	<i>Equus quagga boehmi</i>	0.0	Adult	male	Athi Plains, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	6,0
USNM1990 83	<i>Equus quagga boehmi</i>	0.0	Adult	male	Athi Plains, Kenya	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,0
USNM1990 84	<i>Equus quagga boehmi</i>	0.0	Adult	female	Athi Plains, Kenya	P2-M3	P2-M3	M2	lt.	parac one	sharp	low	5,0
USNM1990 86	<i>Equus quagga boehmi</i>	0.0	Adult	female	Tana River, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	6,0
USNM1990 87	<i>Equus quagga boehmi</i>	0.0	Adult	male	Tana River, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	6,5
USNM1990 89	<i>Equus quagga boehmi</i>	0.0	Adult	male	Guas Ngishu Plateau, Kenya	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	6,0
USNM2009 59	<i>Equus quagga boehmi</i>	0.0	Adult	male	Serengeti Plains, Tanzania	P2-M3	P2-M3	M2	lt.	parac one	round	high	4,5
USNM3685 11	<i>Equus quagga antiquorum</i>	0.0	Adult	male	Javerga, Botswana	P2-M3	P2-M3	M2	lt.	meta cone	blunt	low	6,0
USNM0617 44	<i>Equus quagga burchellii</i>	0.0	Adult	male	Manica&Sofala, Beira, Moore	P2-M3	P2-M3	M2	lt.	parac one	round	low	4,5
USNM1629 62	<i>Equus quagga burchellii</i>	0.0	Adult	female	Unknown (wild)	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,0
USNM1629 63	<i>Equus quagga burchellii</i>	0.0	Adult	female	Unknown (wild)	P2-M3	P2-M3	M2	rt.	parac one	round	low	5,5
USNMA228 70	<i>Equus quagga burchellii</i>	0.0	Adult	male	Unknown, Lucas (wild)	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	7,0
USNMA229 77	<i>Equus quagga burchellii</i>	0.0	Adult	male	Unknown (wild)	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,5
USNMA382 11	<i>Equus quagga selouisi</i>	0.0	Adult	male	Zambesi River	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,5
USNMA382 12	<i>Equus quagga selouisi</i>	0.0	Adult	female	Zambesi River	P2-M3	P2-M3	M2	lt.	parac one	round	low	5,5
USNM2705 14	<i>Equus zebra</i>	0.0	Adult	female	Unknown (wild)	P2-M3	P2-M3	M2	lt.	parac one	blunt	low	6,5
USNM6120 03	<i>Equus zebra hartmannae</i>	0.0	Adult	female	Namibia	P2-M3	P2-M3	M2	rt.	parac one	blunt	low	6,0
USNM2381 11	<i>Equus caballus przewalskii</i>	0.0	Adult	male	Mongolia	P2-M3	P2-M3	M2	rt.	parac one	blunt	low	6,0

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681 Supplementary Table 2. ANOVA and Tukey’s Test on the different age classes for *Equus*
682 *simplicidens* from the Hagerman Horse Quarry.

ANOVA Test for equal means on <i>E. simplicidens</i> from HHQ.						
	Sum of Squares	df	Mean square	F	<i>p</i>	
Between groups:	2.31595	3	0.771984	1.565	0.2013	
Within groups:	59.176	120	0.493133			
Total:	61.4919	123				
Levene’s test for homogeneity of variance, from means <i>p</i>: 0.6827						
Levene’s test from medians <i>p</i>: 0.7066						
Welch F test in the case of unequal variances <i>F</i> = 1.197, <i>df</i> = 23.48, <i>p</i> = 0.3324						
Bayes factor: 0.0958 (strong evidence for equal means)						

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Tukey’s Test for Pairwise Mean Comparisons on <i>E. simplicidens</i> from HHQ.				
	Adult	Subadult	Juvenile	Combined Age Classes
Adult		0.587	0.2055	0.8018
Subadult	1.789		0.9132	0.8738
Juvenile	2.785	0.9278		0.4286
Combined Age Classes	1.281	1.07	2.15	

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Extant <i>Equus</i> Taxa Mesowear Scores							
Taxon	N	Mesowear Score	%High Relief	% Low Relief	% Sharp Cusps	% Round Cusps	%Blunt Cusps
<i>Equus africanus</i>	1	5.0	0	100	0	0	100
<i>Equus hemionus</i>	1	5.5	0	100	0	100	0
<i>Equus caballus przewalskii</i>	1	6.0	0	100	0	0	100
<i>Equus hemionus anoager</i>	1	5.5	0	100	0	100	
<i>Equus kiang</i>	3	6.0	0	100	0	33	67
<i>Equus grevyi</i>	10	5.4	0	100	20	20	60
<i>Equus quagga boehini</i>	42	5.4	2	98	14	54	31
<i>Equus quagga antiquorum</i>	1	6.0	0	100	0	0	100
<i>Equus quagga burchelli</i>	5	5.5	0	100	0	80	20
<i>Equus quagga selouisi</i>	2	5.5	0	100	0	100	0
<i>Equus zebra</i>	1	6.5	0	100	0	0	100
<i>Equus zebra hartmannae</i>	1	6.3	0	100	0	0	100