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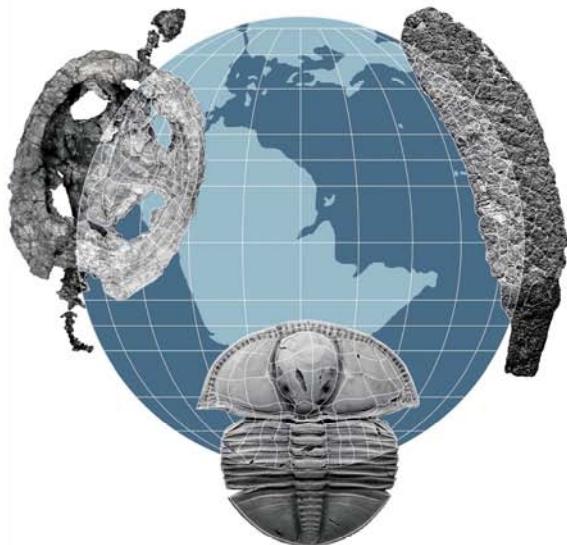


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**WAS *EQUUS CEDRALENSIS* A NON-STILT LEGGED HORSE? TAXONOMICAL  
IMPLICATIONS FOR THE MEXICAN PLEISTOCENE HORSES**

**FUE *EQUUS CEDRALENSIS* UN CABALLO DE PATAS NO ZANCONAS?  
IMPLICACIONES TAXONÓMICAS PARA LOS CABALLOS PLEISTOCÉNICOS  
MEXICANOS**

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HORSE

**Key words.** Pleistocene. Rancholabrean. *Equus*. Mexico. North America.

**Palabras clave.** Pleistoceno. Rancholabreano. *Equus*. Mexico. Norteamérica.

THE SMALL-SIZED horse *Equus cedralensis* was erected based on specimens from the late Pleistocene locality of El Cedral, San Luis Potosí, in north-central Mexico (Figure 1). The species was diagnosed as one of the smallest North American horse species, with teeth that are morphologically very similar to the other horses found at Cedral (i.e., *Equus conversidens* and *E. mexicanus*) but smaller in size (Alberdi et al., 2014). Its postcranials are also small in size, without stilt-legged metapodials, which are less slender than those of *E. francisci* (Alberdi et al., 2014).

Studies on Pleistocene *Equus* teeth morphology recognized a very similar size and enamel pattern between the *E. cedralensis* and *E. francisci* specimens (Barrón-Ortiz et al., 2017; Priego-Vargas et al., 2017), raising the possibility that the new Mexican species is a synonymy of *E. francisci*, but given its non-stilt legged status, it was tentatively considered a valid species (Priego-Vargas et al., 2017).

Based on paleogenomic and morphometric analyses, a new genus of horse for the Pleistocene of North America was erected: *Haringtonhippus francisci* (= *Equus francisci*); this was a New World stilt-legged equid that inhabited a vast area, from Alaska to Texas (Figure 1). In Mexico this equid was tentatively identified in San Josecito Cave, Nuevo León, based on a short mitochondrial DNA sequence (Heintzman et al., 2017), and recently it was identified in southern Mexico based on morphological characters (Jiménez-Hidalgo et al., 2019); it is possible that *Equus cedralensis* is a junior synonym of *Haringtonhippus francisci*.

With the aim of establishing if *E. cedralensis* is a non-stilt legged small horse species, we performed multivariate and univariate analyses of metatarsals from several stilt-legged and stout-legged Pleistocene equid species from North America, including this Mexican species.

## MATERIALS AND METHODS

We analyzed 332 metatarsals from caballine (*Equus* spp.) and non-caballine (*Haringtonhippus francisci*) Pleistocene horses, including 23 specimens of *Equus cedralensis* from Alberdi et al. (2014). The geographical extent of the samples was comprised of 13 North American sites, including two Mexican *Equus cedralensis* localities (Figure 1). The list of specimens, localities, and bibliographic references used in this work are in the Supplementary Online File.

We performed a principal component analysis (PCA) with the variables: greatest length (GL), proximal breadth (Bp), distal breadth (Bd), and smallest breadth of the diaphysis (SD), following Von Den Driesch (1976) and Eisenmann et al. (1988), in order to evaluate the morphological variation of stilt-legged horses (*Haringtonhippus francisci*), stout-legged horses (*Equus* spp.), and *E. cedralensis*, and also to find the most significant variables to discriminate among these horses.

Additionally, we performed a linear discriminant analysis (DA), using the same variables for the PCA, with the categories “stilt-legged” and “stout-legged”. We employed common covariance as the discriminant method, given that all variables were in covariance (i.e. they proceeded from the same bone element), to designate the *E. cedralensis* individuals as either stilt-legged or stout-legged horses. To test statistic differences among the multivariate centroids of the categories, we performed a Pillai's Trace test.

Following the results of the PCA, we developed a robustness index with the variables that displayed the highest eigenvector values in each principal component (PC1 and PC2). Then, we proceeded to compare the stilt-legged horses and stout-legged horses with the *E. cedralensis* sample, with one-way ANOVA and a Tukey-Kramer test.

To test if latitude has any influence in the robustness index, we analyzed the data of the stilt-legged horses and *E. cedralensis* from five selected sites, ranging from 64° to 18° latitude. Finally, we compared these sites with a one-way ANOVA and a Tukey-Kramer test.

All statistical tests were performed with JMP 8.0 (SAS Institute, Inc., <https://www.jmp.com>). In all cases, the level of significance was  $\alpha=0.05$ .

## RESULTS

The PCA showed that the overall metatarsal morphospace of *E. cedralensis* overlaps with both the stilt and stout-legged horses (Figure 2.1). The PCA eigenvectors are in Table 1.

The DA showed that 77.7% of the *E. cedralensis* sample were classified as stilt-legged horses (*Haringtonhippus francisci*), while 22.2% were classified as stout-legged horses. Two specimens (INAH DP-3078d and INAH DP-4730d) are close to the *Haringtonhippus francisci* holotype (Figure 2.2). Also, the DA showed statistically significant differences among the stilt and stout-legged groups (Prob>F= <0.0001).

The ANOVA of the robustness index (Figure 2.3), showed statistically significant differences among the categories of stilt-legged, stout-legged and *E. cedralensis* (Prob > F= <0.0001). The Tukey-Kramer test showed no statistically significant differences between *E. cedralensis* and the stilt-legged horses (Prob > F= 0.0923), but it showed statistically significant differences between *E. cedralensis* and the stout-legged horses, as well as between stilt and stout-legged horses (Prob > F= <0.0001 in both cases).

Finally, we tested if the geographical provenance of the stilt-legged horses (*Haringtonhippus francisci*) and *E. cedralensis* (classified as a stilt-legged horse in our analysis) had any influence in the robustness index (Figure 2.4). We found no statistically

significant differences among most of the samples (Table 2), the only exception being the comparison of the samples from Valsequillo (Puebla) and Natural Trap Cave (Wyoming), which show statistically significant differences (Prob > F= <0.0210).

## DISCUSSION

Our results indicate that *Equus cedralensis* was a stilt-legged horse, not different from *Haringtonippus francisci*; therefore, the autapomorphy that diagnosed the species is no longer valid, giving that its dental morphology is very similar to *H. francisci*, as was shown by Barrón-Ortiz et al. (2017) and Priego-Vargas et al. (2017). Consequently, we propose that the Mexican specimens described and figured by Alberdi et al. (2014) as *E. cedralensis* should be referred as *Haringtonippus francisci*, in accordance with the Statement of the Principle of Priority (ICZN, 1999: Article 23).

Recently, Marín-Leyva et al. (2019) reached a similar conclusion using a geometric morphometrics approach for Mexican Pleistocene equids, in which *E. cedralensis* is a stilt-legged, slender equid species.

Some metatarsal specimens identified as *E. cedralensis* by Alberdi et al. (2014) were within the morphospace of *E. conversidens* in our analysis (Figure 2.2), suggesting that they were misidentified. Barrón-Ortiz et al. (2017) also identified some teeth specimens as *E. conversidens* that were originally identified as *E. cedralensis*.

Our analysis showed that there is no latitudinal robustness cline among the stilt-legged samples from diverse North American localities (64° N- 18°N). The results of our study indicate that *Haringtonippus francisci* had a very broad geographic range during the Pleistocene in North America, from Alaska to southern Mexico, and that only one small-sized stilt-legged species of equid roamed Mexico, *H. francisci*.

## **CONCLUSIONS**

The species *Equus cedralensis* was diagnosed as having stouter metapodials than those of *E. francisci*, but our analyses of a large sample of stout-legged and stilt-legged equid specimens along with *E. cedralensis* from several localities of the Pleistocene of North America showed that it is a stilt-legged equid. Therefore, *Equus cedralensis* should be considered a junior synonym of *Haringtonhippus francisci*, because its dental morphology and size is very similar to that of *H. francisci* and lacks any other diagnostic character that allows it to be distinguished as a valid species.

## **ACKNOWLEDGEMENTS**

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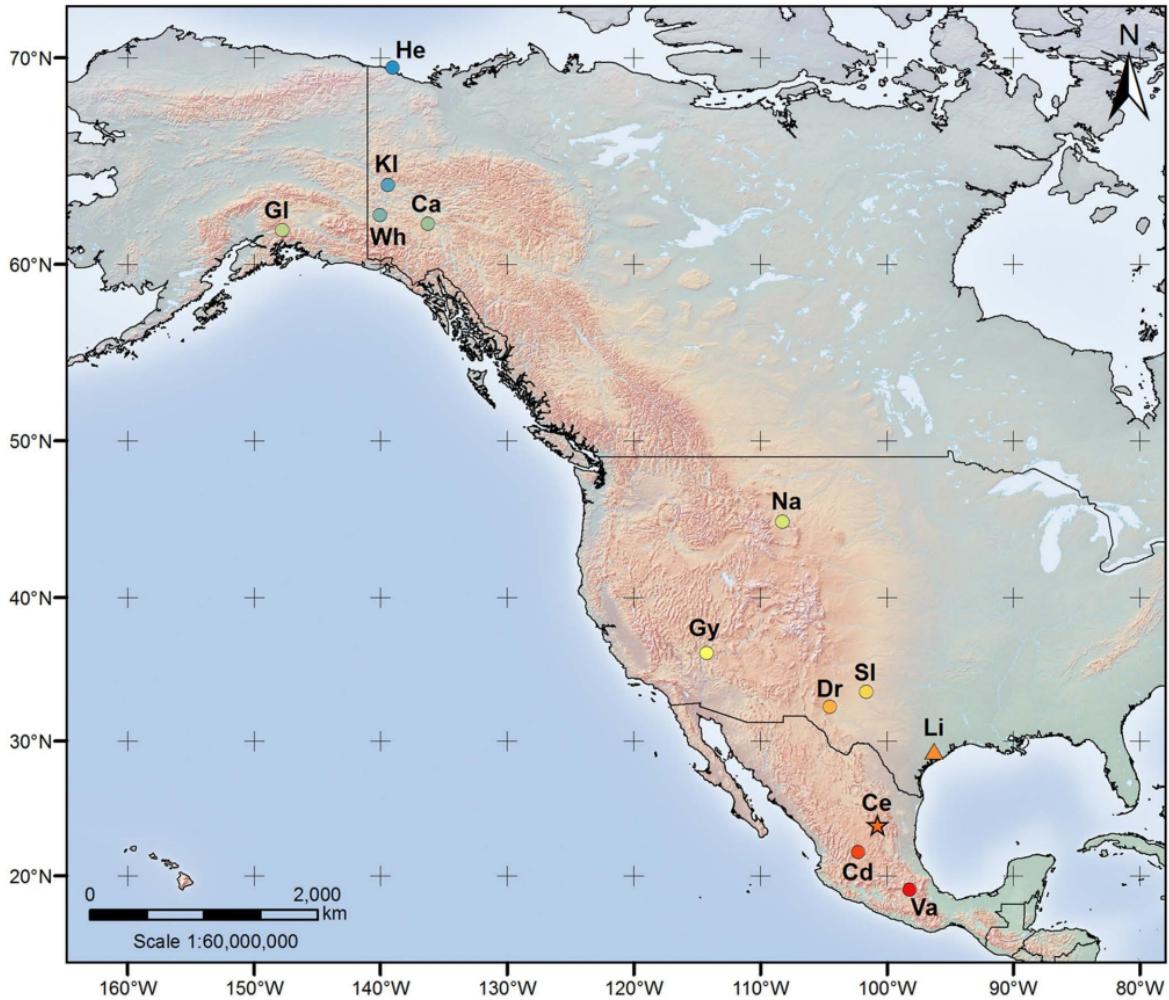
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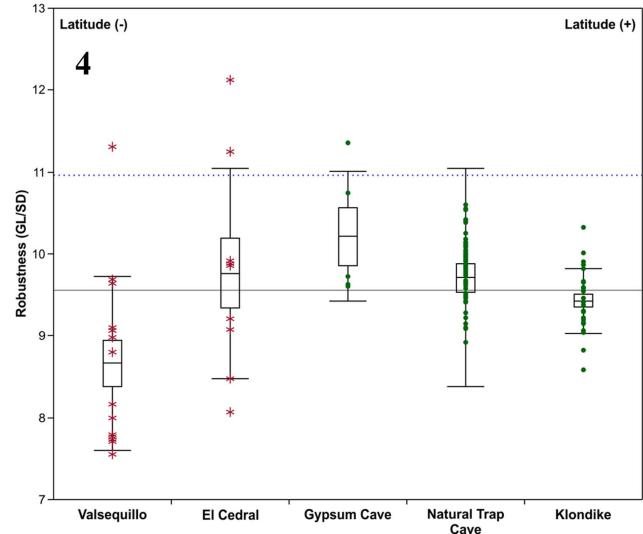
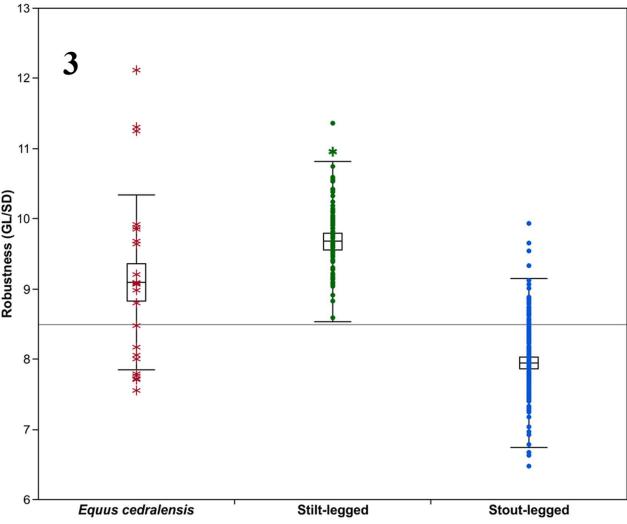
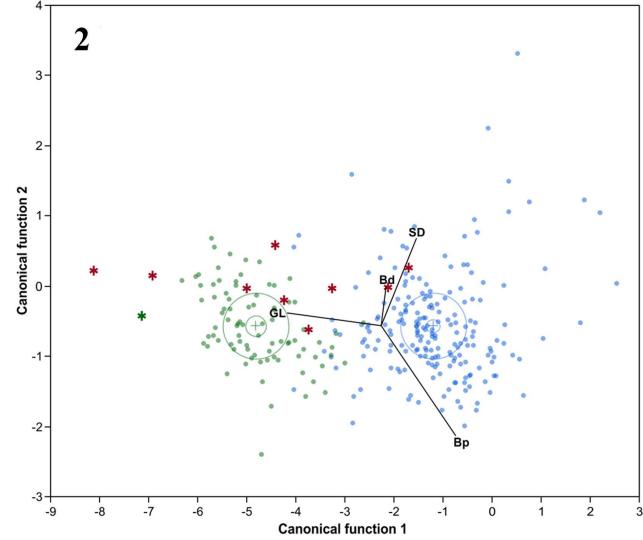
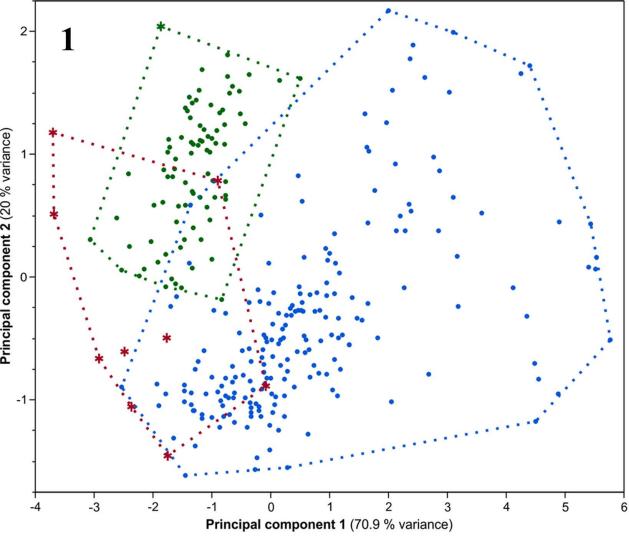
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## Figure Captions

**Figure 1.** Fossil localities of the samples analyzed in this work. The star indicates the type locality of *Equus cedralensis* (El Cedral, San Luis Potosí), and the triangle, the type locality of *Haringtonhippus francisci* (Lissie Formation, Texas). **He**, Herschel Island (Yukon), **K**, Klondike area (Yukon), **Wh**, White River area (Yukon), **Ca**, Carmacks (Yukon), **Gl**, Glacier Creek (Alaska), **Na**, Natural Trap Cave (Wyoming), **Gy**, Gypsum Cave (Nevada), **Sl**, Slaton local fauna (Texas), **Dr**, Dry Cave (New Mexico), **Cd**, Cedazo local fauna (Aguascalientes), **Va**, Valsequillo local fauna (Puebla).

**Figure 2. 1**, Two main components of the Principal Component Analysis (cumulative variance= 90.931%). The dotted lines represent metatarsal morphospaces. **2**, Results of the Discriminant Analysis, the crosses represent the multivariate centroid of the groups, the inner circles correspond to a 95% confidence limit of the groups's mean, and the outer circles are the 50% of the points of that group. Variables abbreviations are the same as in the Table 1. **3**, Univariate analysis of the robustness index among North American Pleistocene horses classified as stilt-legged and stout-legged, including the *E. cedralensis* sample (including the Valsequillo site sample). **4**, Geographical variation of the robustness index of stilt-legged horses (*E. cedralensis* included). The dotted blue line represents the robustness index of the *Haringtonhippus francisci* holotype. For figures 3 and 4, the box plots show the means and standard deviation of each group. The middle line shows the great mean. Blue dots represent the stout-legged horses, green dots stilt-legged horses, red asterisks *E. cedralensis*, and green asterisk *Haringtonhippus francisci* holotype.





**TABLE 1 - Eigenvector values for each principal component (PC) of the PCA. The highest values employed for the robustness index are in bold.**

Variable	PC1	PC2	PC3	PC4
Greatest length (Gl)	0.31437	<b>0.94811</b>	0.01243	0.04584
Proximal breadth (Bp)	0.55436	-0.14616	-0.51146	-0.64010
Smallest breadth of the diaphysis (SD)	<b>0.55730</b>	-0.21756	-0.27549	0.75246
Distal breadth (Bd)	0.53223	-0.17997	0.81385	-0.14826



**TABLE 2 - Results of the Tukey-Kramer test of different stilt-legged horse localities, including the Mexican sites. The statistically significant value is in bold**

<b>Site A</b>	<b>Site B</b>	<b>Difference</b>	<b>Std. Err. Dif.</b>	<b>p-Value</b>
<i>Gypsum Cave</i>	<i>Valsequillo</i>	1.549932	0.5937468	0.0756
<i>El Cedral</i>	<i>Valsequillo</i>	1.097405	0.4869139	0.1683
<i>Natural Trap Cave</i>	<i>Valsequillo</i>	1.045295	0.3382593	<b>0.021</b>
<i>Gypsum Cave</i>	<i>Klondike</i>	0.786412	0.56025	0.6267
<i>Klondike</i>	<i>Valsequillo</i>	0.76352	0.3832619	0.2769
<i>Gypsum Cave</i>	<i>Natural Trap Cave</i>	0.504637	0.5304807	0.876
<i>Gypsum Cave</i>	<i>El Cedral</i>	0.452527	0.6356693	0.9534
<i>El Cedral</i>	<i>Klondike</i>	0.333884	0.4454548	0.9441
<i>Natural Trap Cave</i>	<i>Klondike</i>	0.281775	0.2752529	0.8439
<i>El Cedral</i>	<i>Natural Trap Cave</i>	0.05211	0.4073814	0.9999

Taxon	Robustness MV	ID	Institution	Collection number	Site	Region	Greatest length (GL)	Proximal breadth (bp)	Smallest breadth of the diaphysis (SD)	Distal breadth (Bd)	Reference	Robustness index
Haringtonippus francisci	stilt-legged	NWSL equids	YG	160.8 Irish Gulch	Klondike	262.59	40.12	28.65	30.48	Heintzman et al., 2017	9.16544506	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	76.2 Hester Creek	Klondike	255.42	42.2	25.52	31.42	Heintzman et al., 2017	10.00862069	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	130.6 Quartz Creek	Klondike	258.04	37.4	27.04	27.05	Heintzman et al., 2017	9.6398949408	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	404.40 Hunter Creek - Altom Placer	Klondike	253.67	40.14	26.28	30.46	Heintzman et al., 2017	9.63587519	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	413.19 Tureka Creek	Klondike	253.28	41.96	26.77	31.42	Heintzman et al., 2017	9.63167318	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	109.7 Quartz Creek	Klondike	250.93	42.58	27.05	32.16	Heintzman et al., 2017	8.96302151	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	404.205 Hunter Creek - Altom Placer	Klondike	254.78	41.69	27.65	30.44	Heintzman et al., 2017	9.21446564	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	404.662 Hunter Creek - Altom Placer	Klondike	254.49	42.36	27.69	30.49	Heintzman et al., 2017	9.19065057	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	29.169 Hunter Creek - T&C Holdings	Klondike	260.58	44.32	28.83	31.79	Heintzman et al., 2017	9.03850151	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	303.371 Eldorado Creek	Klondike	257.69	40.56	26.03	26.03	Heintzman et al., 2017	8.89973108	
Haringtonippus francisci	stilt-legged	NWSL equids	YG	401.268 Quartz Creek	Klondike	262.36	40.24	26.71	20.61	Heintzman et al., 2017	8.93258375	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	25922 Natural Trap Cave	Wyoming	267.36	41.56	28.38	32.35	Heintzman et al., 2017	9.42071881	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	26002 Natural Trap Cave	Wyoming	276.91	42.33	27.95	33.04	Heintzman et al., 2017	9.90733452	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	25919 Natural Trap Cave	Wyoming	279.81	40.97	29	31.37	Heintzman et al., 2017	9.64862069	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	25916 Natural Trap Cave	Wyoming	268.29	39.56	28.92	31.2	Heintzman et al., 2017	9.276970954	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	33141 Natural Trap Cave	Wyoming	280.19	41.77	26.44	32.6	Heintzman et al., 2017	10.59720121	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	25918 Natural Trap Cave	Wyoming	281.3	41.43	29.88	34.15	Heintzman et al., 2017	9.414323963	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	32288 Natural Trap Cave	Wyoming	270.18	39.67	27.42	31.43	Heintzman et al., 2017	9.853391685	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	32776 Natural Trap Cave	Wyoming	273.04	43.98	30.03	31.33	Heintzman et al., 2017	9.092241092	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	32327 Natural Trap Cave	Wyoming	268.52	41.14	26.62	31.01	Heintzman et al., 2017	10.08715252	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	32326 Natural Trap Cave	Wyoming	282.65	42.35	28.15	33.82	Heintzman et al., 2017	9.91636098	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	33440 Natural Trap Cave	Wyoming	270.32	38.97	27.26	31.02	Heintzman et al., 2017	9.09955827	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	33718 Natural Trap Cave	Wyoming	267.8	40.1	29.43	30.9	Heintzman et al., 2017	9.67654157	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	33421 Natural Trap Cave	Wyoming	275.04	43.6	27.9	31.88	Heintzman et al., 2017	10.42049883	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	33420 Natural Trap Cave	Wyoming	275.79	43.65	28.69	31.81	Heintzman et al., 2017	9.612757058	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	33419 Natural Trap Cave	Wyoming	270.88	41.38	27.81	34.1	Heintzman et al., 2017	9.740381158	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	33333 Natural Trap Cave	Wyoming	283.58	43.54	28.74	31.72	Heintzman et al., 2017	8.967804203	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	41435 Natural Trap Cave	Wyoming	284.67	41.05	28.58	33.87	Heintzman et al., 2017	9.960461861	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	39778 Natural Trap Cave	Wyoming	272.41	42.34	27.9	31.31	Heintzman et al., 2017	9.763799283	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	41750 Natural Trap Cave	Wyoming	276.21	41.07	27.65	32.34	Heintzman et al., 2017	9.989511754	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	43812 Natural Trap Cave	Wyoming	273.75	41.67	28.29	32.7	Heintzman et al., 2017	10.42049883	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	43380 Natural Trap Cave	Wyoming	267.39	40.52	25.66	31.73	Heintzman et al., 2017	10.42058717	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	43626 Natural Trap Cave	Wyoming	271.94	41.13	27.07	32.62	Heintzman et al., 2017	9.1425634	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	42262 Natural Trap Cave	Wyoming	266.78	41.97	29.18	31.82	Heintzman et al., 2017	9.45584652	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	44670 Natural Trap Cave	Wyoming	279.75	40.24	29.38	33.13	Heintzman et al., 2017	9.52178352	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	42150 Natural Trap Cave	Wyoming	273.43	40.53	27.82	31.71	Heintzman et al., 2017	9.828560168	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	47164 Natural Trap Cave	Wyoming	286.85	42.86	27.17	33.59	Heintzman et al., 2017	10.55670029	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	45644 Natural Trap Cave	Wyoming	271.44	42.52	28.57	34.45	Heintzman et al., 2017	9.50085044	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	45421 Natural Trap Cave	Wyoming	284.22	40.96	28.33	32.34	Heintzman et al., 2017	10.03247441	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	45207 Natural Trap Cave	Wyoming	270.69	41.57	29.36	32.54	Heintzman et al., 2017	10.19387368	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	41007 Natural Trap Cave	Wyoming	290.03	47	29.66	36.52	Heintzman et al., 2017	10.40217824	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	50784 Natural Trap Cave	Wyoming	276.52	43.23	26.20	30.82	Heintzman et al., 2017	10.52090378	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	50564 Natural Trap Cave	Wyoming	268.31	43.07	29.0	33.35	Heintzman et al., 2017	10.49337538	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	50438 Natural Trap Cave	Wyoming	275.19	42.97	27.25	32.28	Heintzman et al., 2017	10.09897156	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	52025 Natural Trap Cave	Wyoming	266.81	41.17	25.63	31.77	Heintzman et al., 2017	9.63759577	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	52020 Natural Trap Cave	Wyoming	267.29	41.08	26.25	31.62	Heintzman et al., 2017	10.18347619	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	52034 Natural Trap Cave	Wyoming	270.74	40.35	25.68	32.35	Heintzman et al., 2017	10.54283489	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	52030 Natural Trap Cave	Wyoming	271.6	40.16	25.78	31.98	Heintzman et al., 2017	9.53529886	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	53055 Natural Trap Cave	Wyoming	264.95	41.74	26.42	32.38	Heintzman et al., 2017	10.02838759	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	53054 Natural Trap Cave	Wyoming	278.26	40.29	27.34	31.95	Heintzman et al., 2017	10.17766152	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	51843 Natural Trap Cave	Wyoming	275.41	43.1	27.46	32.48	Heintzman et al., 2017	10.947297293	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	50716 Natural Trap Cave	Wyoming	276.41	40.39	27.83	31.11	Heintzman et al., 2017	9.63795577	
Haringtonippus francisci	stilt-legged	NWSL equids	KU	52203 Natural Trap Cave	Wyoming	288.07	46.07	28.81	35.8	Heintzman et al., 2017	9.99858695	
Haringtonippus francisci	stilt-legged	NWSL equids	LACM(CIT)	109 / 149291 Gypsum Cave	Nevada	268.38	43.07	27.87	33.64	Heintzman et al., 2017	9.625079365	
Haringtonippus francisci	stilt-legged	NWSL equids	LACM(CIT)	109 / 160129 Gypsum Cave	Nevada	254.81	40.73	23.72	31.25	Heintzman et al., 2017	10.74241147	
Haringtonippus francisci	stilt-legged	NWSL equids	LACM(CIT)	109 / 160130 Gypsum Cave	Nevada	2						

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