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JQS Journal of Quaternary Science QRA Quaternary Research Association

First reported fossil occurrences of *Phrynosoma* sp. from the Columbia Plateau (Washington State, USA) dated to the Late Pleistocene

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ABSTRACT: Reptiles, squamates in particular, can be extremely valuable as indicator species due to their commonly small fundamental niche ranges. Yet these taxa are often overlooked in North American Cenozoic palaeoecological studies in favour of mammalian specimens. At the Coyote Canyon Mammoth Site (CCMS) on the Columbia Plateau (eastern Washington State, USA) excavation has focused on the collection and subsequent identification of all diagnostic fossil specimens, whether associated directly with the mammoth remains or not, including small non-mammalian vertebrates and invertebrates. Here we show that with appropriate excavation techniques, microvertebrate fossils are recoverable and can be identified to at least the genus level. We place the identification of two fossils of *Phrynosoma* at the CCMS, dated to ~13 and 15 ka, in the context of all recorded fossils identified to this genus in North America since the Middle Miocene. These specimens represent the first fossils of *Phrynosoma* adequately described and reported from the Columbia Plateau and the greater Pacific Northwest.
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KEYWORDS: horned lizard; palaeoecology; palaeontology; reptile; squamate

Introduction

There is a growing appreciation of the value of using palaeoecological proxies to aid in modern conservation efforts for various species (Jackson, 2007; Gillson, 2015, 2021; Jackson and McClenachan, 2017; Gillson and Ekblom, 2020; Djamali and Segarra-Moragues, 2021; Dirk, 2022). It is now widely recognized that the current global biodiversity crisis is a direct result of anthropic influences (Begum et al., 2022). However, conservation efforts typically rely on ecological studies encompassing a few decades (Foster et al., 1990; Birks, 2012; Meadows, 2012; Seddon et al., 2013) to determine the impact these alterations have on an ecosystem (Foster et al., 1990; Birks, 2012).

The melding of ecological conservation and palaeoecology provides the opportunity to study species abundance, composition and richness in assemblages over temporal scales ranging from 100 years to over 100 000 years in regions exhibiting the absence of modern anthropic influence. Such data provide the opportunity to study dynamic fluctuations in species composition at specific locations and biological responses to climatic shifts over varying spatial, temporal and taxonomic scales (Gillson and Ekblom, 2020; Blanco et al., 2021; Djamali and Segarra-Moragues, 2021; Gillson, 2021; Goodenough and Webb, 2022). Although the practical use of palaeoecological data in modern conservation biology is sound (Foster et al., 1990; Bennington et al., 2009; Willis et al., 2010; Gillson, 2015; Jackson and McClenachan, 2017), the link between the two is currently weak. One reason for this lies in the temporal, spatial and taxonomic resolution being too coarse (Birks, 2012), with certain taxonomic groups (e.g. mammals) being the focus of study and others often ignored or overlooked. For example, in the Pacific Northwest, reptile fossil remains from the Pleistocene have received little attention compared to their mammalian counterparts (Martin et al., 1983; Rensberger et al., 1984; Spencer, 1989; MacEachern and Roberts, 2013; Bader et al., 2016).

Late Pleistocene reptile responses to climate change in North America

The Late Pleistocene (126–12 ka) experienced both glacial and interglacial periods (Rasmussen et al., 2014; Ehlers et al., 2016). Such temperature fluctuations would have put pressure on existing biota requiring them to disperse and/or adapt to these changes (Hewitt, 2003) or risk extirpation (Hadly and Barnosky, 2017).

Holman (1995) researched reptile species' responses to Pleistocene climate changes by studying 170 Pleistocene sites in the USA, distributed within eight regions; however, none were within the Pacific Northwest.

Southeastern Washington palaeontolgical studies

A commonality amongst palaeontological research sites located in the Columbia Plateau region, southeastern Washington State, USA, is the focus on the identification of mammalian fossils to the level of genus or species using recovered skeletal (Martin et al., 1983; Rensberger et al., 1984; Spencer, 1989; Bader et al., 2016; Last et al., 2022) and ichnological trace (MacEachern and Roberts, 2013) material, along with invertebrates (O'Geen and Busacca, 2001), and vegetation (Blinnikov et al., 2002). If reptile fossils were recovered, taxonomic identification would only go as far as placing them within Reptilia (Bader et al., 2016), Serpentes or Squamata (Rensberger et al., 1984).

Taxonomic classification beyond class is not a common practice due to a scarcity of reptile remains in museums and universities for comparative purposes (Olsen, 1968), and the personal collection

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of comparative specimens poses an ethical dilemma due to the sensitive nature of reptile conservation efforts (Olsen, 1968; Holman, 1995; Broughton and Miller, 2016). Additionally, the under-representation of such animals in North American archaeological sites does not lend itself to collections of reptiles compared to mammals (Lyman, 1994; Broughton and Miller, 2016); however, we note that the latter may be a consequence of inadequate or inappropriate sampling techniques or research focus rather than a true absence of reptile faunal material.

For various reasons, the methods of excavation and recovery are rarely standardized across palaeontological sites. For example, the volume of bulk sample excavation is often arbitrary unless a concerted effort is made to sample to the point at which recovery leads to redundancy (Lyman, 2008). A common practice in the recovery of organics relies on surface prospecting (Martin et al., 1983; Barnosky et al., 2004; Rogers et al., 2010) and, possibly, filtering excavated material using a mesh screen of a specific size (Barnosky et al., 2004; Rogers et al., 2010). By its very nature, the screen mesh size results in a bias towards recovering organics too large to pass through the screen (Nagaoka, 1994; Shaffer and Sanchez, 1994; Nagaoka, 2005). Hence, if no or minimal search effort is expended on checking the material that passed through the smallest mesh size, the remains of organisms in these smaller size categories will not be recovered. Depending on the taphonomic processes, the number of skeletal bone elements available for identification may be limited (Nagaoka, 2005; Su and Croft, 2018). Additionally, some taxonomic groups (e.g. reptiles and amphibians) only have a few diagnostic skeletal elements that can be used for identification to the species level (Lyman, 2008). Therefore, the screen mesh size may prove crucial for recovering rare species and skeletal remains that allow for precise taxonomic identification. Greater precision in identification allows for the interpretation of ecological characteristics such as relative abundance, modes of life, feeding types, population dynamics and trophic interactions (Kowalewski, 2017), which are valuable metrics for conservation purposes (Hadly and Barnosky, 2017; Diele-Viegas and Rocha, 2018).

The value of palaeo-reptile proxies for modern conservation

Reptiles are useful indicators of environmental change because they commonly have low individual body mass (e.g. mean body mass for North American lizards $\leq$200 g; Olalla-Tárraga et al., 2006) and small home ranges coupled with high reproductive efficiency. These factors also make them important components of modern and palaeo food webs (Valencia-Aguilar et al., 2013; Hocking and Babbitt, 2014). In present-day ecosystems, reptiles provide a range of direct and indirect ecosystem services that impact human well-being on a global scale, including food consumption, medicines, control of disease-carrying invertebrates and agricultural pests, and cultural relevance. Despite their ecological importance and utility as indicators of ecosystem change, the impact of glacial cycles on reptiles has received relatively little attention.

In this study we focused on the identification of reptile remains recovered from a fossil site on the Columbia Plateau (Washington State, USA) dated to the Late Pleistocene. Our primary objective was to determine whether sufficiently detailed excavation techniques would generate reptile fossil material that could be identified beyond class or order, and preferably to genus and/or species level. If this objective was met we would follow up by placing the fossils within the wider context of other published North American specimens at the same level, thus providing valuable palaeontological data for reptile conservationists in their efforts to better understand these responses to current and predicted climate drivers.

Materials and Methods

Excavation and recovery of microvertebrates

In 2008, the discovery of mammoth bones provided an opportunity for researchers to investigate a locale that might otherwise have been ignored due to its atypical characteristics. The site was very dry and sloping, not a catchment environment or a cave shelter environment, and typically there would have been little attention devoted to examining any microelements. In fact, the site was only explored due to community interest in the megafauna remains. A purposeful decision was made (by B.R.B.) to excavate with a focus on the collection of provenience data to provide the palaeoenvironmental context of microfossils and macrofossils for the site versus merely quarrying for the mammoth elements for museum display purposes.

This location is now known as the Coyote Canyon Mammoth Site (CCMS) located in Benton County, Washington (46°9′31″N, 119°15′53″W), at an elevation of ~315–319 m asl (211 m above the Columbia River; Last and Rittenour, 2021). Starting in 2010, a palaeoecological excavation and site reconstruction was initiated using a blend of palaeontological and archaeological methodologies. This time and labour-intensive systematic methodology occurs in three major stages: recovery, preparation/conservation and analysis. Recovery involves modified standard archaeological excavation techniques, preparation utilizes wet screening and quick drying techniques, followed by descriptive analysis using sample sorting and picking, microscopy, taxonomic and taphonomic analyses (Richter et al., 2020; Supporting Information Figure S1).

A grid system at CCMS was established resulting in 13 excavation units (henceforth referred to as XUs). Each XU's maximum surface area measures 2 × 2 m and is divided vertically into 10-cm spits (levels). The total volume of matrix excavated from XU1, the unit of interest here, totalled ~4.25 m^3.

Chronology of the Coyote Canyon Mammoth Site

A chronology of the CCMS sediments and finds was generated with the analysis of four optically stimulated luminescence (OSL) ages and two accelerator mass spectrometry (AMS) ^{14}C dates (Figure 1; Barton et al., 2012; Last and Rittenour, 2021). The ages of each OSL sample are as follows [mean ± 95% confidence interval (CI)], with depth calculated below the maximum elevation of 319 m asl: OSL-1 (slackwater flood deposit) collected at a depth of 4 m is 20.87 ± 1.12 ka; OSL-2 (slackwater flood deposit) at a depth of 3.65 is 16.77 ± 1.32 ka; OSL-3 (loess deposit) at a depth of 2.2 m is 14.01 ± 1.02 ka; and OSL-4 (loess deposit) at a depth of 1.8 m is 10.88 ± 1.03 ka (Figure 1). These data were plotted to generate a polynomial regression line of mean age to provide a numerical dating approximation for bone elements recovered from levels 1–35 with a maximum depth of 3.5 m (Figure 2).

Taxonomic analysis

In October 2010, XU1 level 15 was excavated and processed following the CCMS methodologies described in Figure S1. A year later, in April 2011, XU1 level 20 was completed. During initial analysis of organics from these levels, one of the authors (B.R.B.), spotted the presence of a lizard maxilla (CCMS XU1 L15 FS021 1a), later noting its striking resemblance to a fragmented maxilla belonging to *Phrynosoma* sp. in the faunal analysis of herpetofauna recovered from the Porcupine Cave, in Colorado, USA (Bell et al., 2004). The authors contacted Dr Christopher Bell at the University of Texas at Austin for verification that the

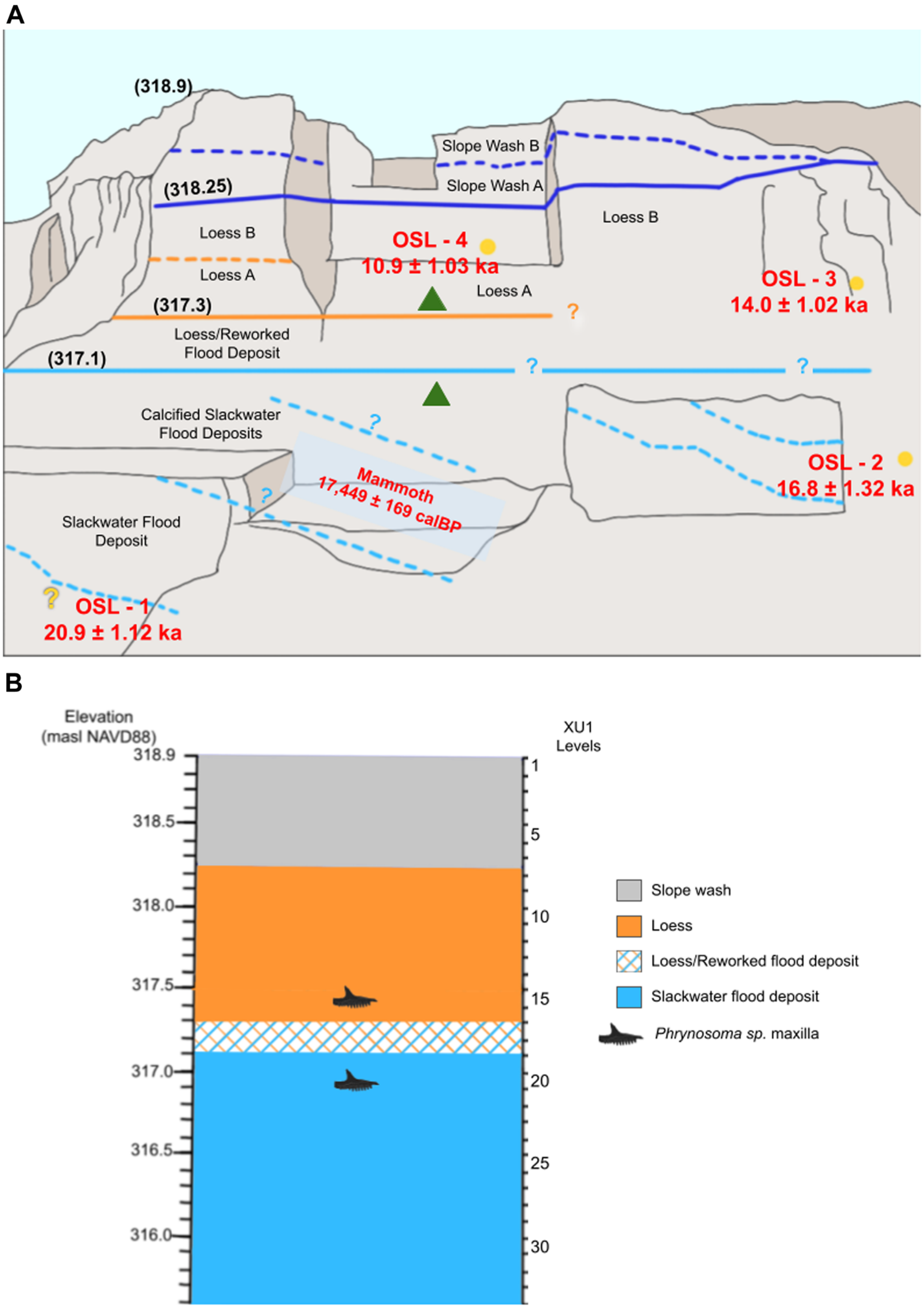


Figure 1. (A) Elevation view of the Coyote Canyon Mammoth Site excavation (adapted from an image provided by G. V. Last, personal correspondence, 30 August 2018). Four OSL sample ages (mean ± 95% CI) are indicated by yellow dots and yellow '?' (Last and Rittenour, 2021) and radiocarbon dating of *in situ* mammoth bones (Barton et al., 2012). Elevations are measured in metres (asl NAVD88) bracketed in parentheses. Green triangles represent the elevation from which each *Phrynosoma* maxilla element was recovered. (B) Stratigraphy of XU1 showing elevations and corresponding levels along with the substrate composition and levels/elevations from which each fossil maxilla was recovered. [Color figure can be viewed at wileyonlinelibrary.com]

specimen is from *Phrynosoma*. Further analysis (by A.J.R.) of the digital specimen files resulted in the preliminary identification of a second similar lizard maxilla (XU1 L20 FS038 1c). This led to the more robust quantitative and qualitative analyses of the two maxilla specimens (by A.J.R.) described below.

Results

Lizard maxillae temporal resolution

The first lizard maxilla (CCMS XU1 L15 FS021 1a) was excavated from level 15 (elevation 317.4 m asl), which is found in 'loess' (Figure 1). The CCMS OSL polynomial regression curve suggests an approximate age (mean ± 95% CI) of this bone of ~13.2 ± 1.14 ka (Figure 2). The second maxilla (CCMS XU1 L20 FS 038 1c) was recovered from level 20 (elevation 316.9 m asl), found within flood deposits, which were a result of the multiple glacial outburst floods known as the late Wisconsinan Missoula Floods occurring between 20 and 14 ka (Figure 1; O'Connor et al., 2020) and has been similarly plotted and dated to ~15.4 ± 1.14 ka (Figure 2).

Taxonomic identification

Morphological variables for each lizard maxilla were identified and coded (Figures 3 and 4) similarly to Meyers et al.'s

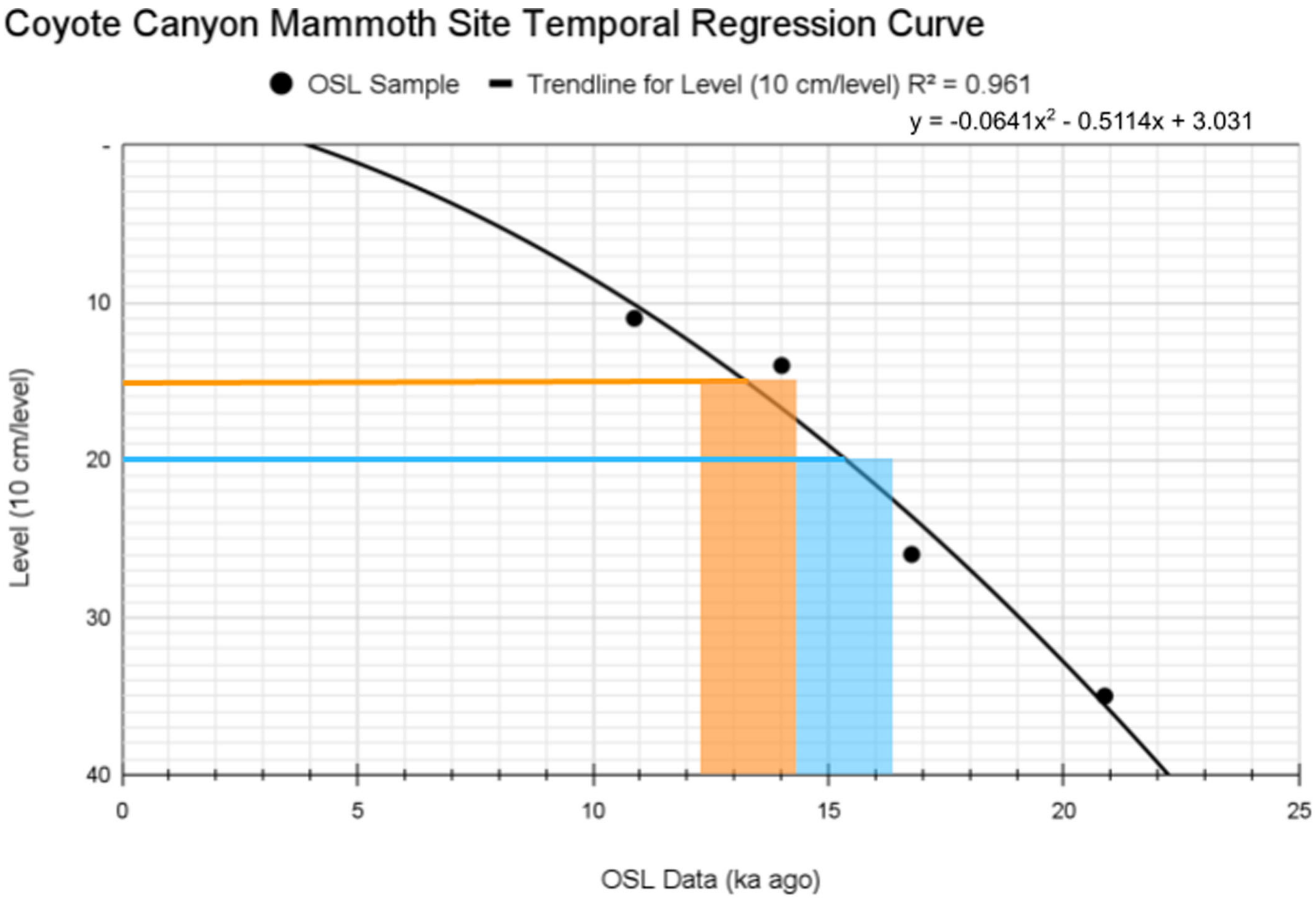


Figure 2. Polynomial regression of OSL data at the CCMS locale placing *Phrynosoma* maxillae within the temporal context of the site. The *Phrynosoma* maxillae were recovered from levels 15 (CCMS XU1 L15 FS021 1a) and 20 (CCMS XU1 L20 FS038 1c), dating to a mean ± 95% CI of ~13.2 ± 1.14 ka (orange horizontal line and orange shaded vertical area) and ~15.4 ± 1.14 ka (light blue horizontal line and light blue shaded vertical area), respectively. [Color figure can be viewed at wileyonlinelibrary.com]

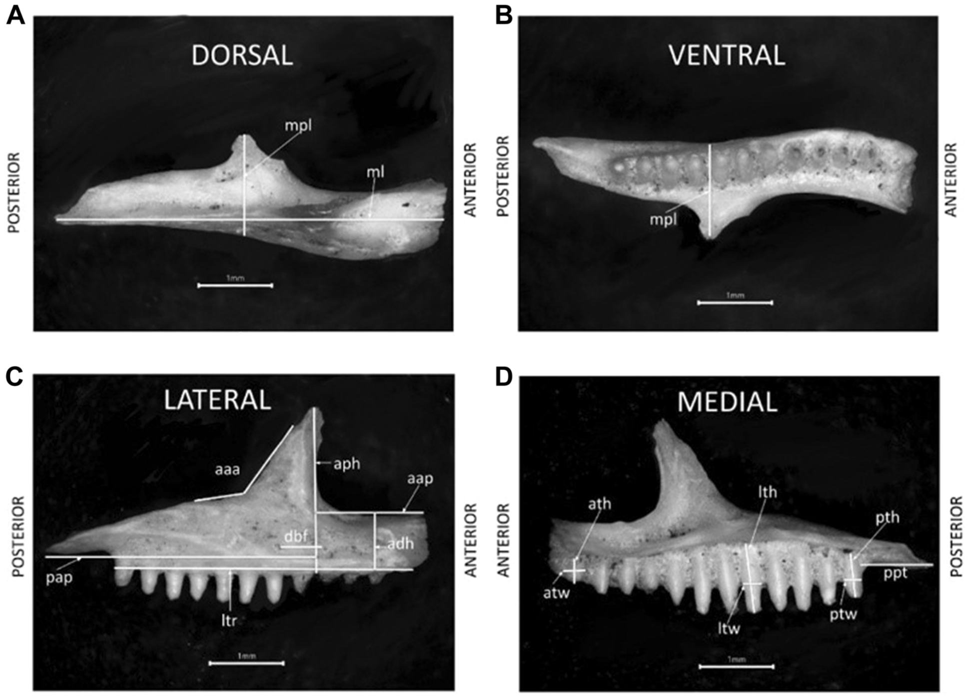


Figure 3. Morphological variables measured for XU1 L15 FS021 1a. (A), maxilla length (ml), medial process length (mpl). (B), medial process length (mpl). (C), anterior ascending process angle (aaa), distance between anterior and ascending process (aap), height of dentary at the most anterior tooth (adh), ascending process height (aph), distance between foramina (dbf), length of tooth row (ltr), distance between posterior and ascending process (pap). (D), anterior-most tooth height (ath), anterior-most tooth width (atw), longest tooth height (lth), longest tooth width (ltw), distance between posterior and posterior-most tooth (ppt), posterior-most tooth height (pth), and posterior-most tooth width (ptw).

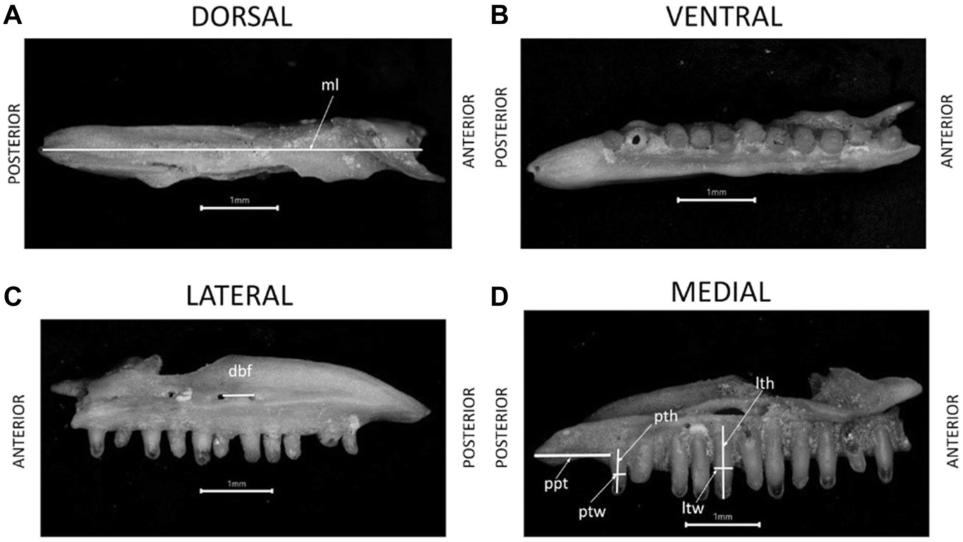


Figure 4. Morphological variables measured for XU1 L20 FS038 1c. (A), maxilla length (ml). (B), ventral side of maxilla showing the conical shape of the teeth at the parapet. (C), distance between foramina (dbf). (D), longest tooth height (lth), longest tooth width (ltw), distance between posterior and posterior-most tooth (ppt), posterior-most tooth height (pth), and posterior-most tooth width (ptw).

Table 1. Morphometric measurements for XU1 L15 FS021 1a

Code	Description	Measurement
aaa	Anterior ascending process angle	135 mm
aap	Distance between the anterior and ascending process	1.53 mm
aat	Distance between anterior and anterior-most tooth	1.0 mm
adh	Height of dentary at the most anterior tooth	0.76 mm
aph	Ascending process height	2.35 mm
ath	Anterior-most tooth height	0.35 mm
atw	Anterior-most tooth width	0.29 mm
chr	Crown height range (distance between labial edge/parapet and apex of tooth)	0.18–0.41 mm
dbf	Distance between foramen	0.6 mm
lth	Longest tooth height	1.0 mm
ltr	Length of the tooth row	4.24 mm
ltw	Longest tooth width	0.24 mm
ml	Maxilla length	5.5 mm
mpl	Medial process length	1.4 mm
nf	Number of foramina	2?
nt	Number of teeth	12
pap	Distance between the posterior and ascending process	1.75
pth	Posterior-most tooth height	0.6 mm
ptw	Posterior-most tooth width	0.24 mm
ts	Tooth shape	Non-cuspate, conical, peg-like and blunt

Table 2. Morphometric measurements for XU1 L20 FS038 1c

Code	Description	Measurement
aaa	Anterior ascending process angle	No data
aap	Distance between anterior and ascending process	No data
adh	Height of dentary at the most anterior tooth	No data
aph	Ascending process height	No data (fractured)
ath	Anterior-most tooth height	No data
atw	Anterior-most tooth width	No data
chr	Crown height range (distance between labial edge/parapet and apex of tooth)	0.25–0.5 mm
dbf	Distance between foramen	0.38 mm
lth	Longest tooth height	1.0 mm
ltr	Length of tooth row	No data
ltw	Longest tooth width	0.29 mm
ml	Maxilla length	5.11 mm (apparent)
mpl	Medial process length	No data (fractured)
nf	Number of foramina	4
nt	Number of teeth	11
pap	Distance between posterior and ascending process	No data
ppt	Distance between posterior and posterior-most tooth	1.06 mm
pth	Posterior-most tooth height	0.65 mm
ptw	Posterior-most tooth width	0.24
ts	Tooth shape	Non-cuspate, conical, peg-like with some bulbous ends

(2006) work on morphological characteristics of *Phrynosoma* lizards. Morphometric measurements were recorded in millimetres (Tables 1 and 2).

Specimen CCMS XU1 L15 FS021 1a

Compared to Hotton's (1955) survey on the morphological relationships of teeth for three species of *Phrynosoma* (*P. platyrhinos*, *P. cornutum* and *P. douglassii* subsp. *ornatissimum*) and species belonging to the genera *Sceloporus*, *Uta*, *Crotaphytus*, *Gambelia*, *Holbrookia*, *Callisaurus*, *Dipsosaurus*, *Sauromalus* and *Ctenosaura*, XU1 L15 FS021 1a is identified as belonging to the genus *Phrynosoma*. In addition, all the teeth of the maxilla are non-cuspate with crowns being blunt, rounded and peg-like (Hotton, 1955; Holman, 1995; C. Bell, pers. comm., 12 November 2019), with the tips of the teeth being non-striated (Holman, 1995). The highest teeth are found in the range from tooth number 1 to 6, and the lowest are found in the tooth range from 10 to 12 (Hotton, 1955). Hotton (1955) described all three species of *Phrynosoma* with an 'increase in crown width from anterior to posterior not distinguishable … Teeth set very close together in maxilla' (p. 96), which is evident in Figure 4. Measurements from this maxilla show a slight tooth width increase from 0.24 to 0.30 mm, anterior-most to posterior-most tooth, respectively. Additional diagnostic characteristics include an anteroposteriorly shortened facial process (C. Bell, pers. comm., 12 November 2019) and the synapomorphic characteristic of a 'triangular ascending process that terminates in a sharp dorsal tip' (Bell et al., 2004; p. 119).

Specimen CCMS XU1 L20 FS038 1c

This fossil shows evidence of fractures on the dorsal, medial and anterior sides thus reducing the number of morphometric measurements available. Regardless, CCMS XU1 L20 FS038 1c shows many characteristics consistent with identification to the genus *Phrynosoma*. On the lateral side, there is a large foramen posterior to where the ascending dorsal process may have been with a smaller foramen directly posterior (Robinson and Van Devender, 1973). Additionally, the crowns of the teeth are conical with several being bulbous (Robinson and Van Devender, 1973), and all teeth being non-cuspate, peg-like (Hotton, 1955; Holman, 1995) with no striations (Holman, 1995) and close together (Hotton, 1955). The crown height and the highest crown width are within the range reported for *Phrynosoma*. Finally, there is no distinguishable difference in crown width for any of the teeth (Hotton, 1955).

Discussion

First identification of Phrynosoma *sp. from the Late Pleistocene of the Pacific Northwest*

The two specimens reported in this work are, to our knowledge, the first published accounts of fossil *Phrynosoma* in the Pacific Northwest (specifically the area north of San Francisco Bay, California, and west of Split Rock, Central Wyoming) throughout the Neogene and Quaternary (Figure 5; Table S1; Oelrich, 1954; Etheridge, 1958; Holman, 1968, 1970, 1977, 1980, 1995; Robinson and Van Devender, 1973; Gehlbach and Holman, 1974; Rickart, 1976; Mead et al., 1984; Rogers, 1984; Johnson, 2007; Messing, 1986; Parmley, 1988; Devender et al., 1991; Czaplewski et al., 1999; Mead et al., 1999; Hockett, 2000; Bell et al., 2004; Schap et al., 2023). There are undoubtedly many such specimens awaiting discovery and publication.

After comparing these two elements to maxillae of extant lizard genera within this region, both lack sharply pointed anterior teeth that curve posteriorly, as are common in species of *Elgaria*, *Eumeces*, *Gambelia*, *Sceloporus*, *Uta* and *Crotaphytus*. Furthermore, *Gambelia* and *Sceloporus* have posterior tricuspid teeth (Etheridge 1958; Robinson and Van Devender, 1973; Van Devender and Mead, 1978; Mead et al., 1984). Many *Cnemidophorus* (now *Aspidoscelis*) have unicuspid anterior teeth and tricuspid posterior teeth, with the middle consisting of bicuspid teeth (Hollenshead and Mead, 2006). Although the taxonomic placement for each of these elements is consistent with belonging to the genus *Phrynosoma*, species designation for each is more speculative. Accurate species-level identification of skeletal remains may not always be possible due to insufficient morphometric variation within a

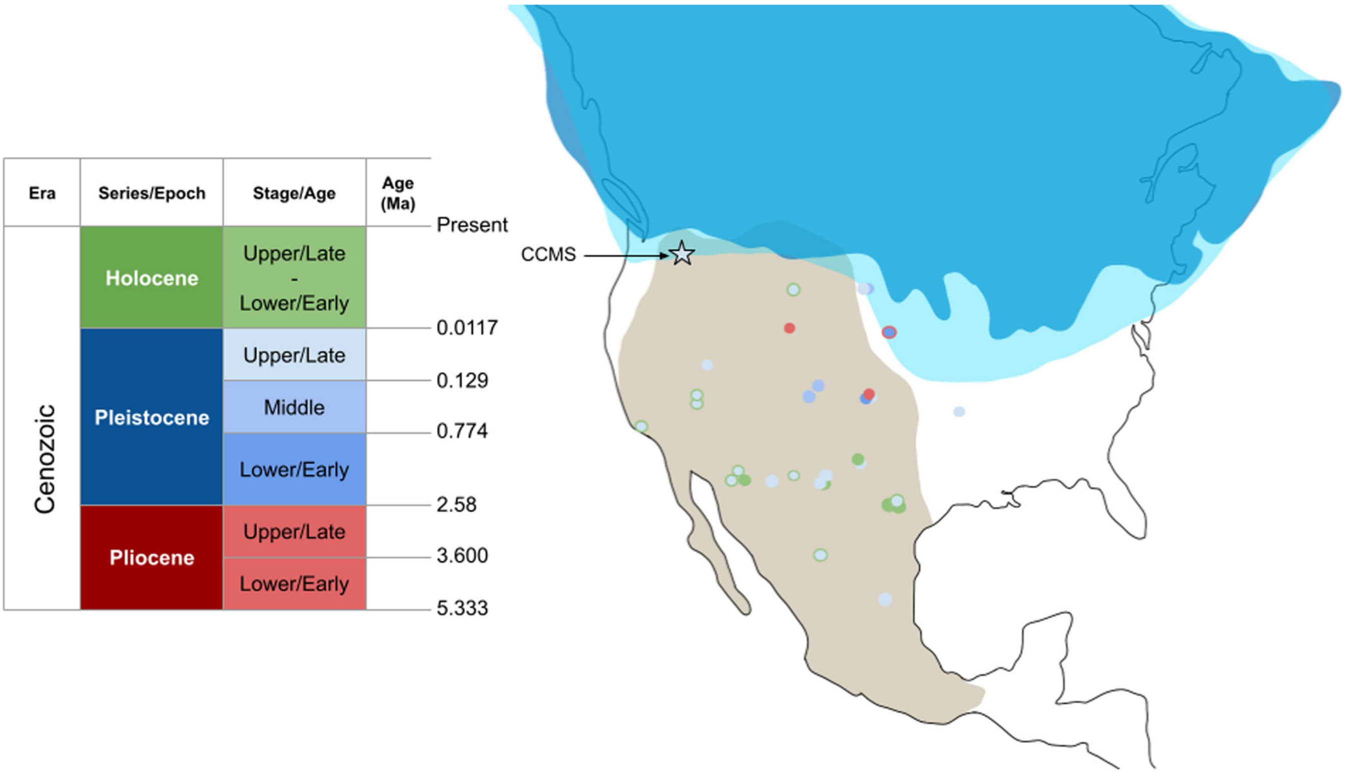
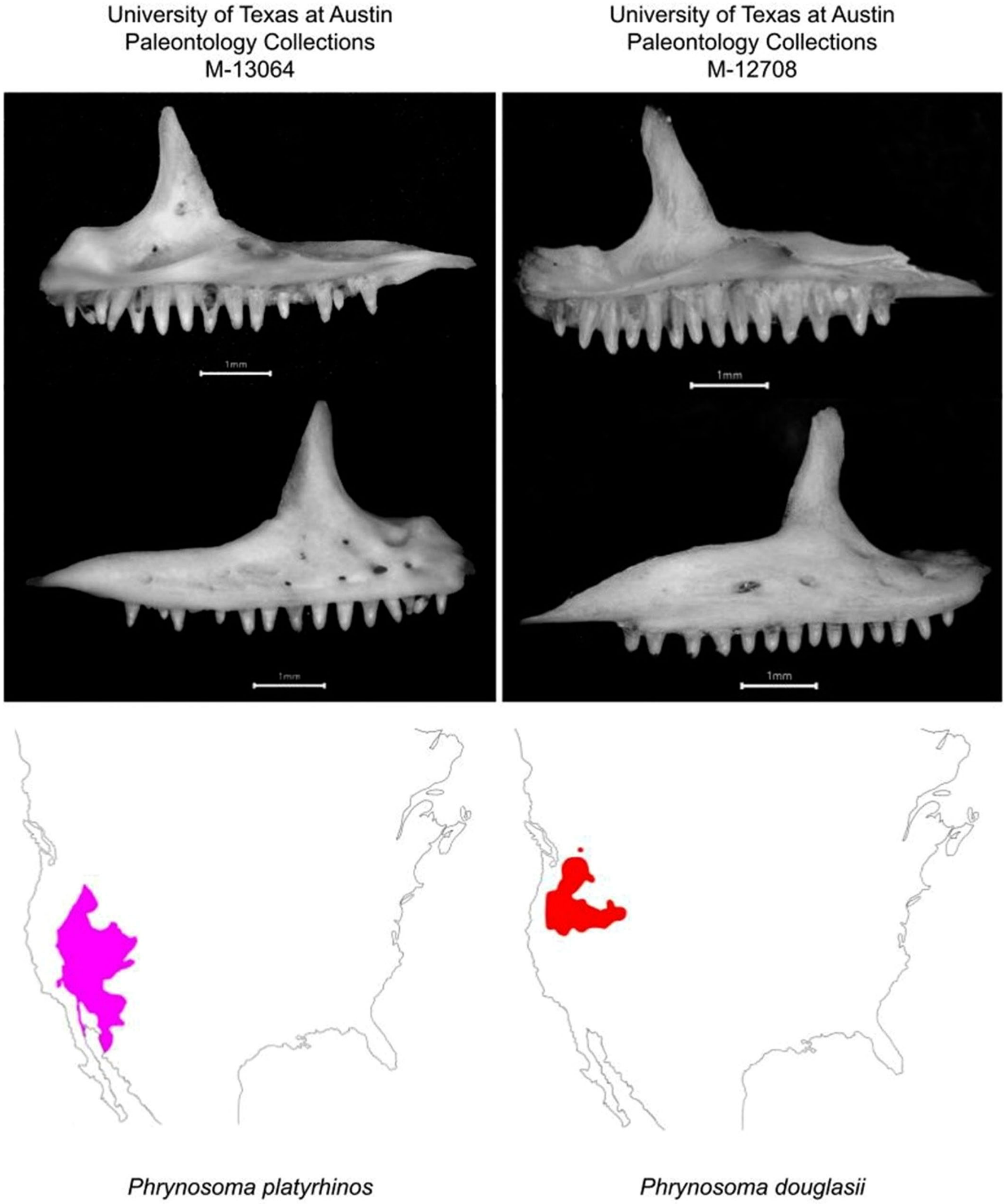


Figure 5. Spatial extent of all published *Phrynosoma* fossil bone elements dating from the Miocene to ~6 ka. The blue-shaded regions covering northern North America represent two glacial events. The darker blue represents the Last Glacial Maximum (LGM) and the lighter blue represents ancient glaciation extent during the Brunhes Chron dating as far back as 781 ka (Ehlers et al., 2016). The timescale table is colour-coded to match the temporal age of the locale where *Phrynosoma* was recovered. Elements dating from the Late Pleistocene to early Holocene are represented by both colours. The geographical range of extant species of *Phrynosoma* is represented by the tan shaded area provided by www.hornedlizards.org accessed on 29 June 2022. The star represents the two maxillae belonging to *Phrynosoma* recovered from CCMS. [Color figure can be viewed at wileyonlinelibrary.com]

genus, and this is often a recognized problem when diagnosing skeletal elements from small reptiles (Bell et al., 2010). Modern reptile geographical locations suggest the most likely species for the CCMS specimens would be *P. douglasii*, whose current range extends from eastern Washington to central and southeastern Oregon, southern Idaho, and the northern tips of California and Nevada (COSEWIC, 2007; Figure 6). A greater number of comparative skeletal specimens of *Phrynosoma*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Paleontology Collections
M-13064

University of Texas at Austin
Paleontology Collections
M-12708

Phrynosoma platyrhinos

Phrynosoma douglasii

Figure 6. Modern geographical ranges for the extant species *P. platyrhinos* and *P. douglasii*. Both comparative specimens are from the University of Texas Vertebrate Paleontology Recent Skeleton Collections (used with permission). Left: *P. platyrhinos* (specimen number M-13064) maxilla in medial (top) and lateral (bottom) views with geographical range shaded pink (http://www.zo.utexas.edu/faculty/pianka/phryno.html). Right: *P. douglasii* (specimen number M-12708) maxilla in medial (top) and lateral (bottom) views with geographical range shaded red (https://fieldguide.mt.gov/speciesDetail.aspx?elcode=ARACF12030). [Color figure can be viewed at wileyonlinelibrary.com]

spp. would need to be analysed to determine whether it is possible to identify these elements at the species level through taxonomic analysis.

Ecological significance of Phrynosoma *spp*

Hotton (1955) and Meyers et al. (2006) argued that the teeth of *Phrynosoma* show significant evidence of the reduction of morphological features, e.g. shape and the number of teeth, compared to two outlying species belonging to the genera *Uma* and *Callisaurus*, which correlates positively with myrmecophagy (a specialist diet of ants). It may be of interest to conduct a wider community analysis of ant species recovered from CCMS to potentially aid in reptile species identification based on dietary preferences. For example, there is evidence that carpenter ants make up a high proportion of *P. douglasii*'s diet in present-day central Washington State (Meyers et al., 2006; Lahti and Beck, 2008) whereas *P. platyrhinos* prefers larger members of a variety of ant species (Newbold and MacMahon, 2009).

Extant species of *Phrynosoma* are located in habitats that range from dry to semi-arid open country, with rocky and sandy soil having low vegetation (Behler and King, 1979; Brown et al., 1995; St. John, 2002; Stebbins, 2003), with certain species found in vegetation ranging from grasses, shrubs, coniferous forests and broadleaf woodland (Brown et al., 1995; St. John, 2002; Stebbins, 2003; Hammerson, 2005). Habitat elevations range from 0 to 3400 m (Behler and King, 1979; Munger, 2002).

Phrynosoma bioclimatic envelope palaeoecological proxies

The *Phrynosoma* maxilla (CCMS XU1 L20 FS038 1c) is dated to ~15.4 ± 1.14 ka, whereas the second specimen (CCMS XU1 L15 FS021 1a) is dated to ~13.2 ± 1.14 ka. Pollen analysis from three sites in proximity to CCMS, Kahlotus-Pasco-1 (KP-1, 96 km, 410 m asl, 46°31′10″N, 118°37′30″W), Wildcat Lake (~145 km, 342 m asl, 47.6045°N, 122.7668°W) and Carp Lake (~204 km, 755 m asl, 47.1513°N, 122.5635°W), provides estimates of the vegetation composition during the period from 21 to 9 ka (Figure 7).

The KP-1 site, which is the site closest to CCMS, and Carp Lake are estimated to have mainly been shrub steppe prior to 16 ka (Blinnikov et al., 2002) with colder and much drier conditions compared to the present (Webb et al., 1993; Blinnikov et al., 2002). From ~16 to 14 ka, there was a warming trend in the northern hemisphere and a decrease in snow accumulation (Alley, 2000). This change in climate was followed at the KP-1 site by a transition to *Festuca–Agropyron* grassland with some *Pinus ponderosa* between 16 and 11 ka (Blinnikov et al., 2002), with a relatively cooler and wetter climate than today (Webb et al., 1993; Alley, 2000; Blinnikov et al., 2002). Whereas the vegetation for the Wildcat Lake site remained conifer dominant, the Carp Lake site habitat transitioned to a *Picea* parkland during this period.

The estimated vegetation communities from the period 15.4–13.2 ka match present-day habitats in which extant *Phrynosoma* are commonly found. The only extant species of *Phrynosoma* found in the Columbia Basin ecoregion is the

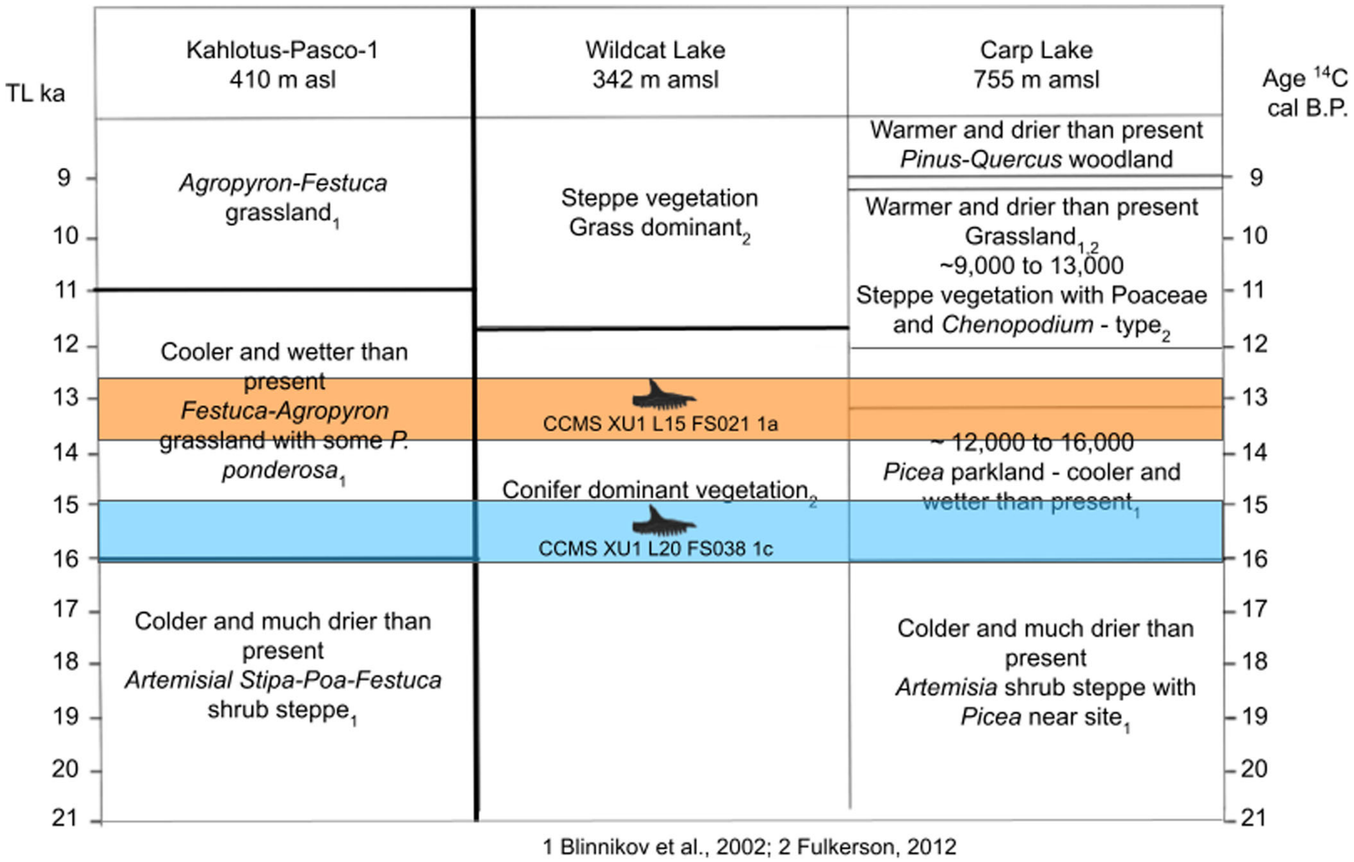

Figure 7. Pollen and phytolith analysis of three sites in proximity to CCMS. Orange and light blue horizontal bars represent the placement of the CCMS XU1 L15 FS021 1a and CCMS XU1 L20 FS038 1c elements, respectively. The KP-1 age is measured in TL ka (column to the left of the thick vertical black line; Blinnikov et al., 2002) and Wildcat Lake and Carp Lake ages in ^{14}C cal BP (columns to the right of the thick vertical black line; Fulkerson, 2012). Image adapted from Alley (2000), Blinnikov et al. (2002) and Fulkerson (2012). [Color figure can be viewed at wileyonlinelibrary.com]

pygmy short-horned lizard *Phrynosoma douglasii* whose current range extends to elevations from 275 to 3400 m with habitats including woodland-mixed, grassland/herbaceous and shrubland-chaparral (Hammerson, 2005). Hence, *Phrynosoma* cf. *douglasii* appears the most likely option, although this remains speculative and more support is needed to refine identification below the genus level. Further analysis of material from extant *Phrynosoma* species using geometric morphometric techniques (Gray et al., 2017) may eventually enable confident placement of our maxillae to the species level.

Conclusions

To our knowledge, no previous fossils of *Phrynosoma* have been recovered and published from the Columbia Plateau or indeed the Pacific Northwest north of San Francisco Bay. Given the specialized nature of *Phrynosoma*'s feeding niche, the site age of ~13–15 ± 1.14 ka, and the vegetation communities estimated for that period, we believe that our identification lends further support to a wider palaeoenvironmental reconstruction of the CCMS locale and the greater Columbia Plateau region.

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Declaration of competing interest

The authors declare that they have no conflict interests.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting information

Additional supporting information can be found in the online version of this article.

Supporting Information.

Abbreviations. AMS, accelerator mass spectrometry; asl, above sea level; CCMS, Coyote Canyon Mammoth Site; COSEWIC, Committee on the Status of Endangered Wildlife in Canada; FS, field specimen; KP-1, Kahlotus-Pasco-1; L, Level; NAVD88, North American Vertical Datum of 1988; OSL, optically stimulated luminescence; PNW, Pacific Northwest; TL, thermoluminescence; WA, Washington State; XU, excavation unit.

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