Palaeogeography, Palaeoclimatology, Palaeoecology 496 (2018) 192–204

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Late Pleistocene mammoth trackway from Fossil Lake, Oregon

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ARTICLE INFO

Keywords:
Proboscipeda
Ichnology
Mammoth steppe
Paleosol
Fossil Lake Formation

ABSTRACT

Behavior of Columbian mammoths (*Mammuthus columbi*) is revealed by a newly discovered trackway at the Pleistocene locality of Fossil Lake, Oregon. Our 8 by 20 m excavation of the mammoth trackway found 117 tracks, including one 20-m-long adult trail, partial trackways of 3 additional adults, a yearling and a baby all heading generally west. The tracks are in the Marble Bluff biotite tuff (43.2 cal ka), which forms a surface horizon to the Pogani silty clay loam paleosol (Natrargid), with a cracked surface and a columnar-structured, subsurface (Bn) horizon, like soils under desert soda pans with alkali shrubland. Directly below is the Yada silty clay paleosol (Xeroll) with crumb textured surface (A) horizon like grassland soils. The Pasiwa loam (Psamment) is a thin brown siltstone, with sparse roots and burrows of lake-margin early successional vegetation. The Pui sandy loam (Aquent) is well-bedded tuff and sand (A) with subhorizontal calcareous rhizomes and adventitious roots, like those of lake-margin tule reeds (*Schoenoplectus acutus*). Columbian mammoths may have moved like modern elephants with infants in matriarchal groups through landscapes of sagebrush and grassland, and this trackway includes a limping female attended by concerned juveniles. Grassland paleosols common in the Fossil Lake Formation, are now rare in the same region, perhaps related to extinction of proboscidean and equine grazers.

1. Introduction

As recently as 11,500 years ago elephants roamed North America: woolly mammoths (*Mammuthus primigenius*) in Canada and Alaska, and Columbian mammoths (*Mammuthus columbi*) in Washington to South Dakota and south into Mexico, with persistence of isolated Arctic island populations of woolly mammoth until 4000 years ago (MacDonald et al., 2012). Mammoth extinction on the mainland has been blamed on climatic change, human overkill, and indirect effects of human land use (Emery-Wetherell et al., 2017). Elephants create grasslands by trampling of herds, voracious grazing, destruction of trees, and fertilization by large amounts of dung (Owen-Smith, 1987; Kohi, 2013). Mammoths have been viewed as grazers creating a unique Beringian grassland that has been dubbed the "mammoth steppe" (Walker et al., 2001; Guthrie, 2013). The building of soil carbon by such activity has led to calls for rewilding of semiarid to subhumid regions using elephants and horses (Donlan, 2005). Much can be learned about mammoth biology from the form of their bones (Agenbroad, 1994), their DNA (Debruyne et al., 2008), and their isotopic composition (Koch et al., 1989; Fisher et al., 2003), but for ecological and behavioral information a different kind of information is needed. For example, polished surfaces of cliffs in central Oregon, USA, have been interpreted as ancient mammoth rubs (Zancanella, 2016). A copious source of behavioral data on fossil elephants is their trackways (Johnston, 1937; Robertson and Sternberg, 1942; Danson, 1960; Panin, 1961; Panin and Avram, 1962; Vialov, 1966; Gibbard and Dreimanis, 1978; Scrivner and Bottjer, 1986; Kordos, 1987; Kinahan et al., 1991; Fisher, 1994; Williamson and Morgan, 1995; Okamura et al., 1995; Lea, 1996; Pérez-Lorente et al., 1999; Reynolds, 1999a, 1999b; Hills et al., 1999; McNeil et al., 1999, 2000, 2005, 2007; Hubbard et al., 2000; Cabral-Perdomo, 2000; Nagamori and Masakazu, 2001; Okamura, 2001; Lucas et al., 2002; Morgan et al., 2002; Higgs et al., 2003; Rodríguez-de la Rosa et al., 2004; Kim and Kim, 2004; Milàn, 2005; Remeika, 2006; Hunt and Lucas, 2007; Bibi et al., 2012). This paper outlines evidence for the ecology and behavior of Columbian mammoths in central Oregon from a newly discovered trackway.

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https://doi.org/10.1016/j.palaeo.2018.01.037
Received 5 December 2017; Received in revised form 24 January 2018; Accepted 25 January 2018
Available online 31 January 2018
0031-0182/

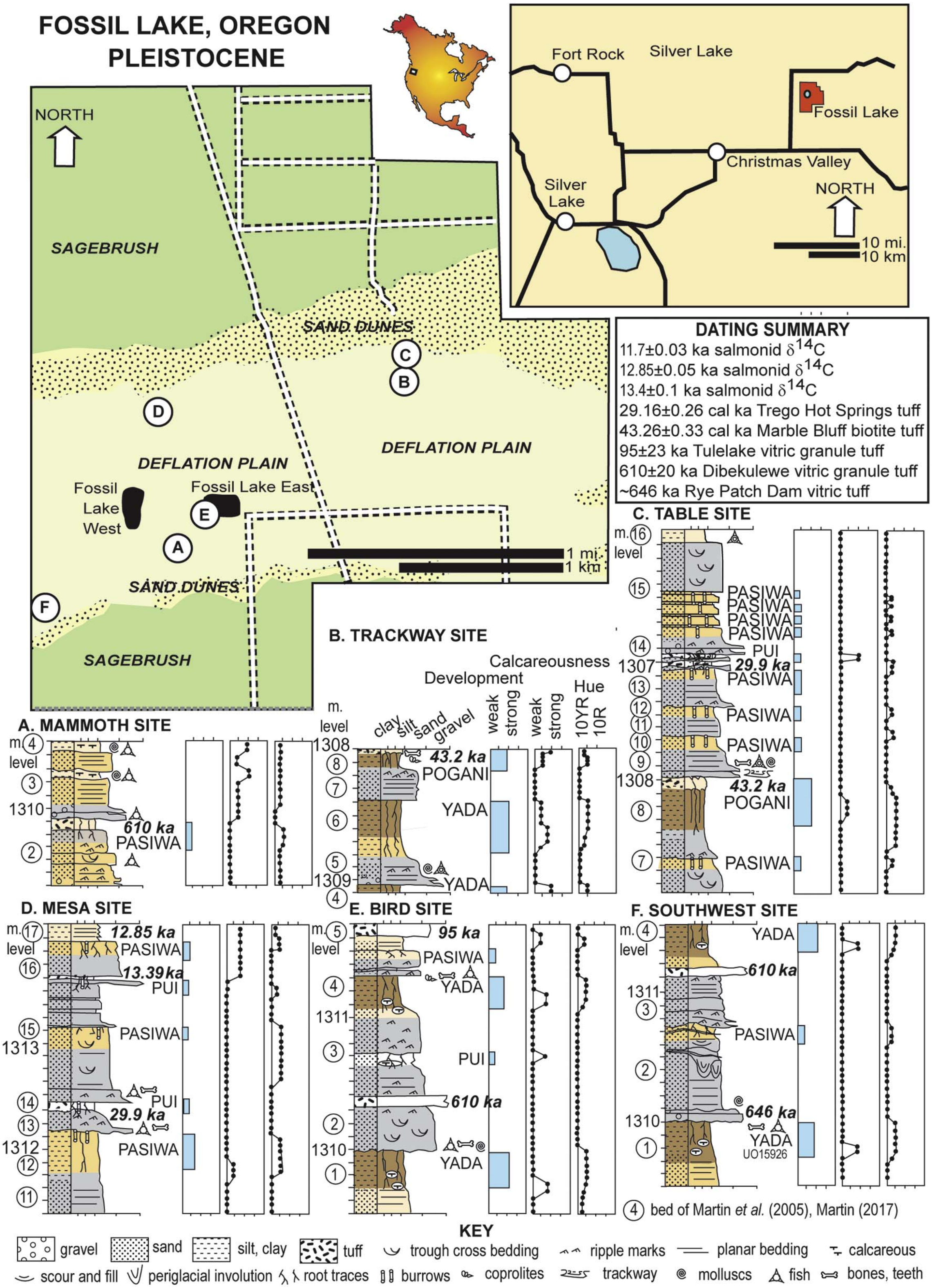

Fig. 1. Location and measured sections of Pleistocene sediments of Fossil Lake, Oregon.

Trace fossils, such as trackways, are evidence of behavior, such as herding, unobtainable in other ways (Lockley, 1999; Bibi et al., 2012). Not all paleosols are bare enough to preserve trackways, which are limited to fresh sedimentary surfaces, or partly bare soils very early in ecological succession (Retallack, 1996). Paleosol chemical composition provides quantitative paleoclimatic information, such as mean annual precipitation and mean annual temperature (Sheldon and Tabor, 2009). Paleoclimatic limits are also useful for understanding former vegetation of paleosols, but more information can be gained from root traces and soil structure. Tabular root systems are evidence of soils with high water table, and crumb ped structure and fine root meshes are formed by sod grasslands (Retallack, 1988).

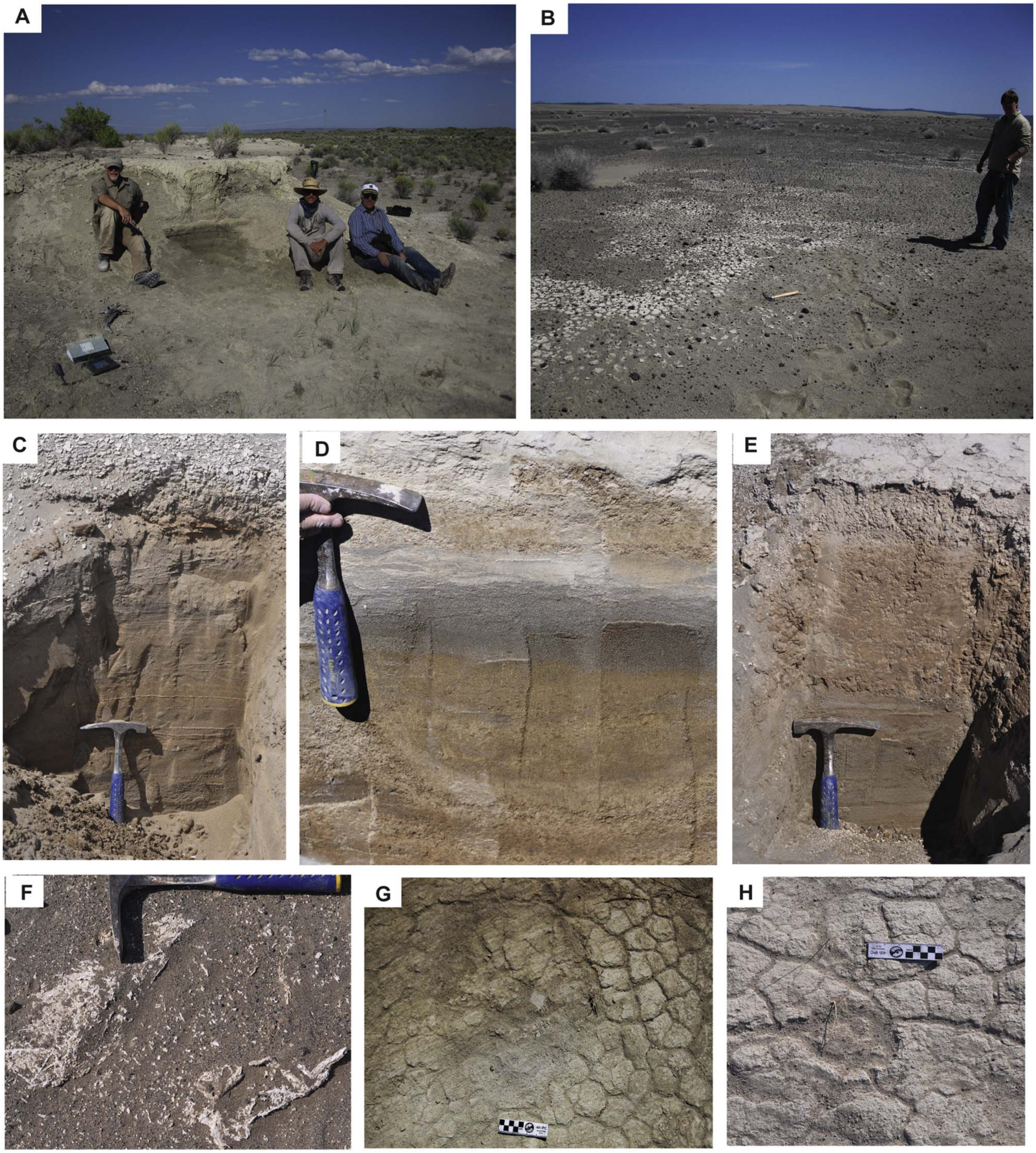

Fig. 2. Paleosol profiles of the Pleistocene Fossil Lake beds: A, section of Pasiwa paleosols above 43.2 ka Marble Bluff tuff at the quarry of Allison (1966) for a Columbian mammoth hind leg; B, Surface of 43.2 ka Marble Bluff tuff at trackway site before excavation showing proboscidean tracks filled with gray sand; C, Pasiwa (below) and Pui (above) paleosols north of the trackway site; D, truncated Pogani (above) and type Yada (below) paleosols at the trackway site; E, type Pogani paleosol north of trackway site; F, Subhorizontal calcareous rhizo-concretions in type Pui paleosol north of trackway site; G, Single proboscidean track (*Proboscipeda panfamilia*) and tessellated surface of Pogani paleosol at trackway site; H, Single equine track (*Hippipeda cardstoni*) and tessellated surface of Pogani paleosol north of trackway site.

2. Geological background

Fossil Lake is a famous locality for Pleistocene fossils in Lake County, eastern Oregon (Figs. 1, 2), first collected in 1876 by John Whiteaker and Thomas Condon, and then in 1879 by E.D. Cope (Cope, 1889; Allison, 1966). Fossils from Fossil Lake include a surprising diversity of fossil birds (Shufeldt, 1913; Howard, 1946, 1964; Jehl, 1967; Olson, 1974; Storer, 1989), as well as fish (Uyeno and Miller, 1963; Miller and Smith, 1981; Allison and Bond, 1983), rodents (Martin, 1996; Moses and Martin, 2014), and large mammals (Elftman, 1931; Allison, 1966; Martin, 2014, 2017; McHorse et al., 2016). Tephrostratigraphy and new radiocarbon dates of the Fossil Lake Formation (Smith and Young, 1926) show that the fossils range in age from 12 to 646 ka, thus Rancholabrean to Irvingtonian North American Land-Mammal “age” (Martin et al., 2005; Benson et al., 2013; Martin, 2014, 2017). The newly discovered trackway is on the upper surface of the

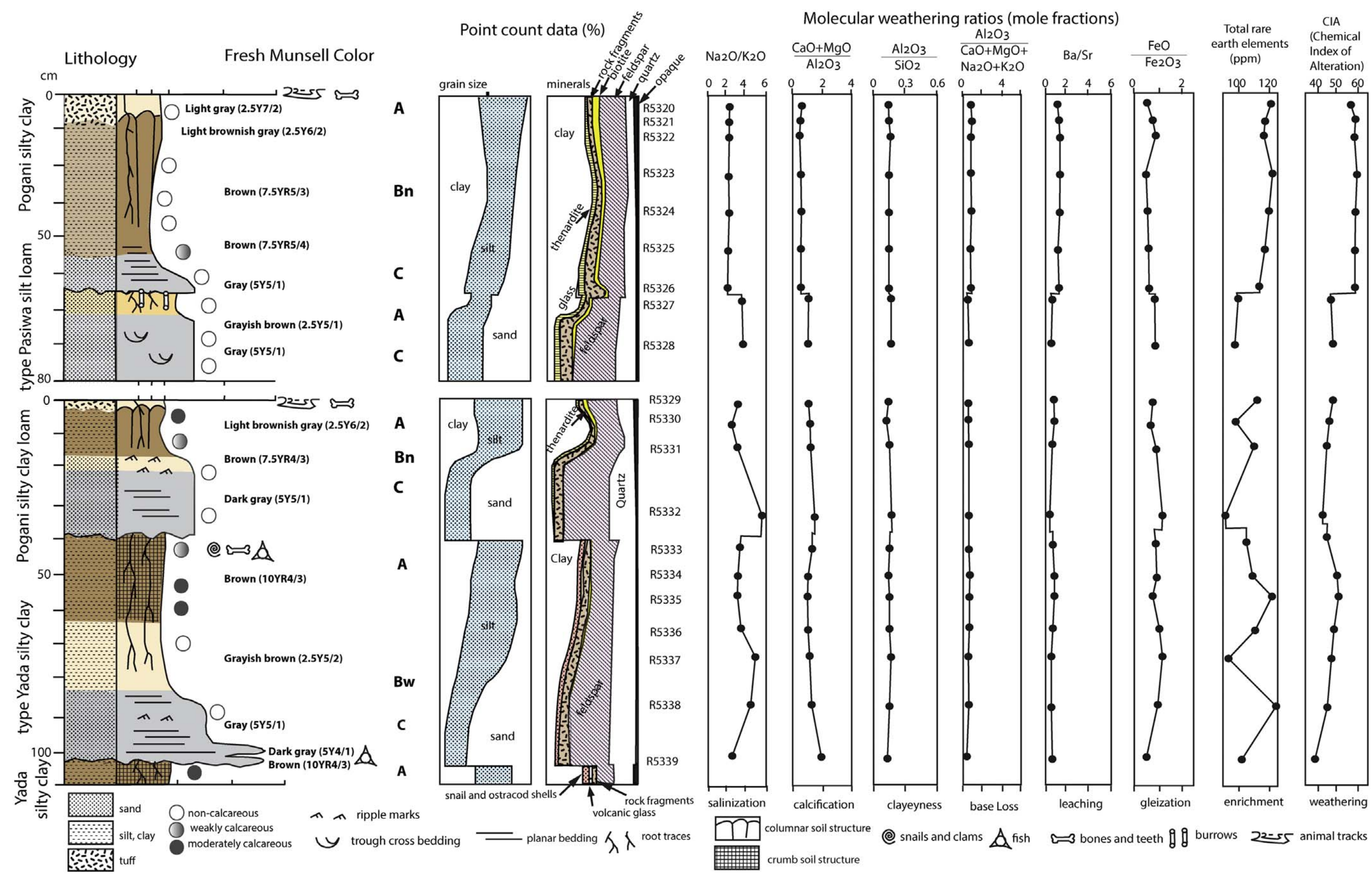

Fig. 3. Geochemical and petrographic data on paleosols of the Pleistocene (43.2 ka) Fossil Lake beds, Oregon.

Rancholabrean Marble Bluff biotite tuff, dated at 43.26 ± 0.33 cal ka elsewhere (Martin et al., 2005; Benson et al., 2013). This biotite tuff has been traced from Fossil Lake to 2.6 km east, past our trackway, and also in Ana River drainage into Summer Lake 50 km southeast of Fossil Lake (Allison, 1966; Kuehn and Foit, 2006; Benson et al., 2013). It can also be recognized from a characteristic fine tessellation that is a surface reflection of columnar structure in the paleosol below (Fig. 2G–H). In contrast, the 29.16 ± 0.26 cal ka Trego Springs tuff is a white silty vitric tuff, and the 95 ± 23 ka Tulelake tuff, 610 ± 20 ka Dibekulewe, and ca. 646 ka Rye Patch Dam tuffs are light gray pumice granule tuffs (Martin et al., 2005; Benson et al., 2013). None of these tuffs show hydrovolcanic surge bedforms or coarse grain size (Bestland, 1985) supportive of the maar lake hypothesis of McCarville (2010), and instead appear to be airfall tuffs from distant rhyodacitic volcanic eruptions (Martin et al., 2005). Remarkably few vertebrate trace fossils have been reported previously from Oregon: Eocene carnivore tracks (Hunt and Lucas, 2007), and Plio-Pleistocene bear tracks (Packard et al., 1951: Packard and Allison, 1980).

3. Materials and methods

The tracks were discovered by GJR during a class field trip, April 20, 2014 (Fig. 2B), and studied under permit OR-50954 from the Bureau of Land Management by a team including most of the authors from July 16–21, 2017. The tracks were uncovered using large stiff haired brooms (Fig. 2G). Only 20 by 8 m was exposed, but additional local outcrops suggest a total tracked area of 1300 by 600 m. Stratigraphic sections were measured by GJR and APB to the east of the excavated track and also in the terrace 100 m to the north (Fig. 1). Other sections were also visited and described, including the quarry where Allison (1966) excavated an articulated left hind leg of a Columbian mammoth (*Mammuthus columbi*). Also documented was reaction with acid and Munsell color.

A Nikon D5100 with a zoom lens set to 18 mm was used for supplemental imagery, and aerial survey photography was flown by DPW using a DJI phantom drone with FC220 camera. Systematic stereoscopic coverage was conducted of the cleaned, track-bearing surface by NAM and BHB using a Nikon D800 with a 28 mm prime lens mounted on a monopod and remotely triggered using a CamRanger and iPad. The focal distance was calculated and fixed for imaging from a height of 2.25 m above the track surface. Eleven imagery transects with approximately 30 images per transect were taken with a stereoscopic overlap of 66% within transects and a sidelap of 66% between transects. Six crossing transects were also taken (with the same focal distance) at 90 degrees for the purpose of camera calibration and to aid in alignment (Matthews, 2008). Selected tracks and track areas were photogrammetrically imaged at a height of approximately 1.3 m. Drone imagery was taken at a height of 6.5 m above the track surface. Calibrated photogrammetric targets were distributed around the perimeter of the exposed track surface and included in the photogrammetric imaging of the area.

Photogrammetric processing was conducted in Agisoft Photoscan Professional Edition, Version 1.3.2 Build 4205 (64 bit), an image-based 3D modeling/photogrammetric software package. All three levels of imagery were aligned together in a single “chunk.” Agisoft Photoscan utilizes the term “chunk” to denote a grouping of images upon which the same structure from motion (SfM) and alignment algorithms, as well as other processing functions, may be applied. All images (800) successfully aligned together on “high,” resulting in a point cloud of over 9 million points. An error reduction and camera optimization workflow was followed (Matthews et al., 2016). The automatic coded target detection algorithm within Photoscan was used to mark the calibrated photogrammetric targets and for assignment of scale bars of appropriate length. The units of the Photoscan project were set to meters. At the conclusion of the error reduction and optimization phase a reprojection error of 0.433 pixels was reached. Factoring in an average image resolution of 0.501 mm per pixel and a scale bar error of 0.0002 mm, a total photogrammetric project error of one millimeter was achieved. Dense point clouds, meshes, digital elevation models (DEM), topographic contours, and digital orthorectified image mosaics (orthomosaics) were generated for the entire track-bearing surface and for selected individual tracks.

Samples of paleosols above and below the trackway level were impregnated with epoxy, and prepared as petrographic thin sections by GJR. Thin sections were used to calculate percent mineral composition and grain size categories (Fig. 3) by counting 500 points in a systematic grid using a Swift automated microscope stage and Hacker electronic counting box by GJR (Supplemental Tables S1–S2). Standard error on such counts are ± 2% for common components (Murphy, 1983). The same samples also were analyzed for major elements (Table S3) and trace elements including REE (Tables S4–5) by inductively coupled plasma atomic emission spectroscopy on glass beads, with Bancroft granodiorite as a standard by ALS Minerals of North Vancouver, British Columbia. Ferrous iron was determined by dichromate titration. These are the basis for calculating molecular weathering ratios (Fig. 3). REE of the paleosols were normalized to North American Shale for comparison with REE analyses of fossils from the same paleosols (Martin et al., 2005). Fossils are enriched in total REE and especially heavy REE compared with the paleosols (Fig. 4).

4. Animal tracks

4.1. Description

The excavated area of 20 by 8 m revealed 117 tracks that are large and nearly round (Figs. 2G, 5, 6), as well as a single heart-shaped track on the same surface as the trackways (Fig. 6C), and a U-shaped track from a small outcrop of the same tuff at the Table site to the north (Fig. 2H). The large round prints vary considerably in length, width, and area (Fig. 7).

A prominent line of large round footprints heading west (magnetic azimuth 276°), has 39 prints 338 ± 56 mm wide, 301 ± 52 mm long, and 304,823 ± 99,985 mm^2 in area. As in modern elephants (Platt et al., 2012), the wide prints were identified as manus, and the narrower ones as pes (Fig. 6B, D). Not all prints were as clear with indications of nails: some were broadly circular with concentric bedding, and may be undertracks impressed on moister ground near the ends of our excavation (Fig. 6A). A particularly unusual feature of this trackway is the differential depth, with the right manus and pes imprints much deeper than the left pes, and left manus intermediate depth, in the middle of the trackway (Fig. 6B, D). Another unusual feature is that the tracks are closely spaced in a sinuous path, unlike the near-linear arcs and well-spaced large spherical tracks of elephants elsewhere (Scrivner and Bottjer, 1986; McNeil et al., 2005; Bibi et al., 2012).

Other large tracks in the northeast side of our excavation are confusingly superimposed and form a trample-ground, as known elsewhere (McNeil et al., 2007). These 17 prints average 345 ± 39 mm wide, 308 ± 37 mm long, and 312,871 ± 70,252 mm^2 in area. A minimum of three individuals are needed to create our excavated portion of the trample ground.

Other lines of proboscidean foot prints are both smaller and less deeply impressed, and at an acute angle to the large main trackway, which obliterated them later (Fig. 6B,D). The smallest two trackways are to the west of our excavation, and these 22 prints average 181 ± 23 mm wide, 159 ± 22 mm long, and 83,853 ± 20,762 mm^2 in area. Three intermediate size trackways include 12 prints to the west averaging 200 ± 49 mm wide, 169 ± 27 mm long, and 97,244 ± 37,148 mm^2 in area, 12 prints in the middle averaging 253 ± 47 mm wide, 213 ± 40 mm long, and 152,762 ± 49,386 mm^2 in area, and 9 prints to the east averaging 255 ± 36 mm wide, 229 ± 50 mm long, and 177,031 ± 79,706 mm^2 in area.

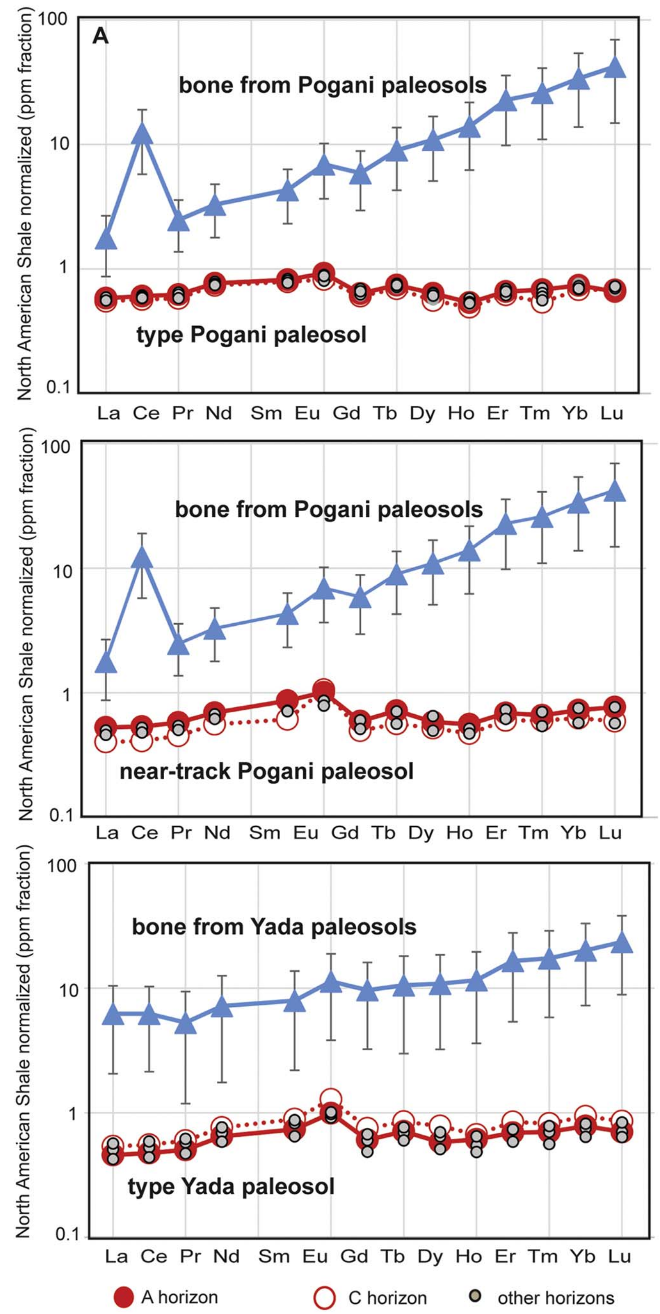

Fig. 4. Rare-earth element composition of paleosols and bones of the Fossil Lake Beds, Oregon. Data on bones are averaged with one standard deviation from Martin et al. (2005).

4.2. Classification and attribution

The large round tracks agree with the ichnospecies *Proboscipeda panfamilia* (Figs. 5–6). One cloven track is ichnospecies *Lamaichnum sarjeanti* (Fig. 6C), and a single U-shaped track from a small outcrop of the same tuff to the north is *Hippipeda cardstoni* (Fig. 2H). Each of these ichnospecies were named by McNeil et al. (2007) for comparable tracks from late Pleistocene (11.0–11.3 ka) silts of Wallys Beach, southern Alberta, and attributed to woolly mammoth (*Mammuthus primigenius*), western camel (*Camelops hesternus*), and horse (*Equus conversidens*), respectively. *Camelops hesternus* bones have been found at Fossil Lake (Allison, 1966), but not that particular horse or mammoth species, so

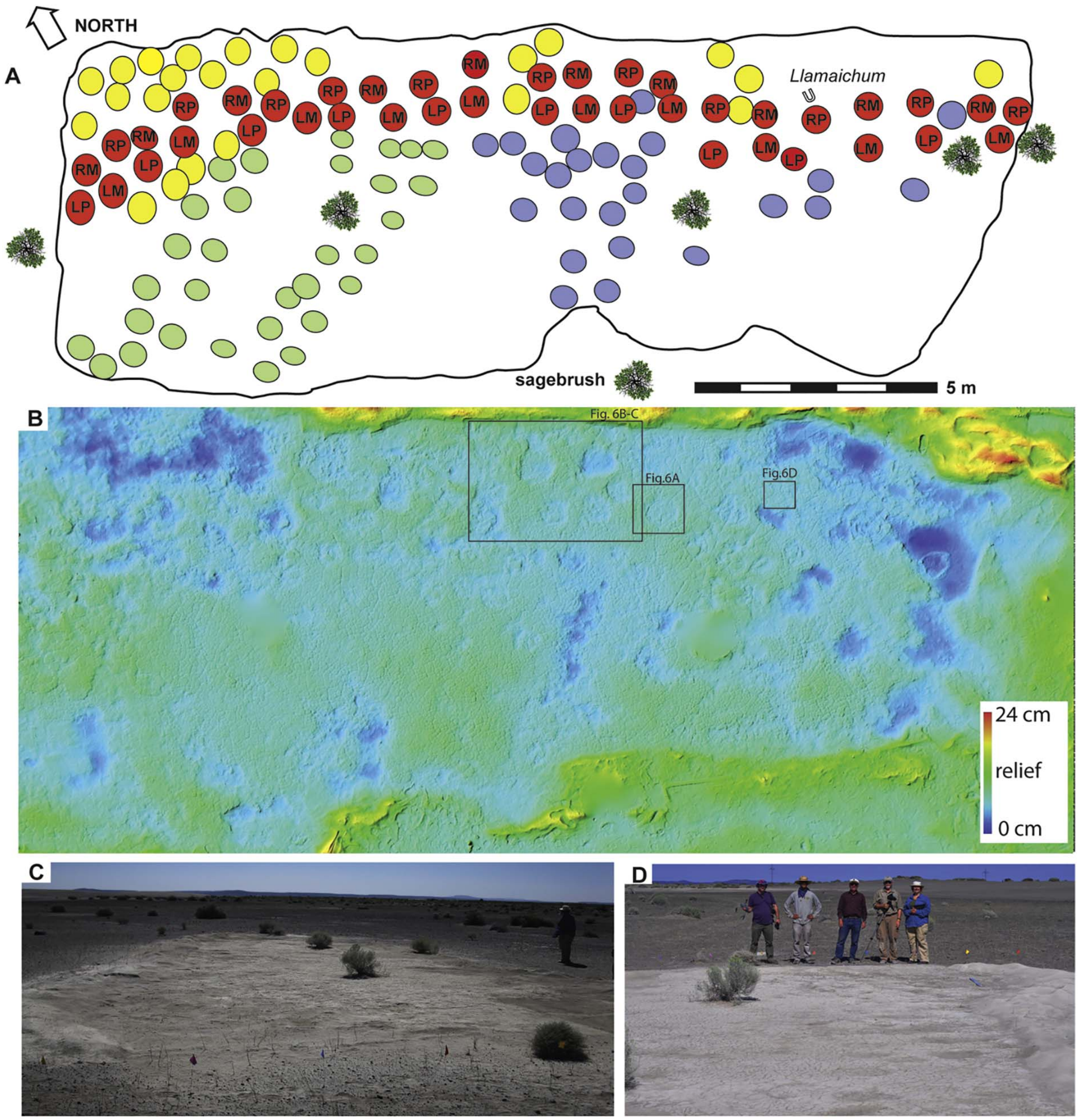

Fig. 5. Maps and overview of excavated proboscidean tracks in the Pleistocene (43.2 ka) Fossil Lake beds, Oregon: A, Schematic diagram of main trackway track with left manus (LM), right manus (RM), left pes (LP) and right pes (RP) marked, as well as other subadult and juvenile tracks; B, False color digital elevation model from photogrammetry of whole trackway, with sagebrush for registration; C, Ground view of whole excavated trackway from west; D, Ground view of west half of trackway from east.

that these same ichnospecies were more likely made in Fossil Lake by locally demonstrated *Equus scotti* (McHorse et al., 2016) and *Mammuthus columbi*, respectively (Elftman, 1931; Allison, 1966). Small *Proboscipeda panfamilia* footprints have been attributed to Sardinian dwarf mammoth, *Mammuthus lamarmorai* (Pillola and Zoboli, 2017). Ichnospecies are commonly more broadly defined than biological species.

Other elephant-like tracks have been referred to trace fossils *Stegomastodonichnum australis* (Aramayo and Manera de Bianco, 1987; Aramayo, 2004) and *S. garbani* (Remeika, 2006), *Proboscipeda enigmatica* (Panin and Avram, 1962; Brustur, 2003) and *Mammuthichnum* (Remeika, 2006). This diversity has been revised by Lucas et al. (2007) who assign all large (200–700 mm diameter) circular tracks with 3–5 toe impressions to the ichnogenus *Proboscipeda*, and recognize only two species, circular *P. panfamilia* and ovoid *P. enigmatica*. Other camel-like tracks include *Camelipeda turkomenica* (Vialov, 1966), *Megalamaichnum tulipensis* (Aramayo and Manera de Bianco, 1996), *M. album* (Remeika, 2001), and *Lamaichnum guanacoe* (Aramayo, 2004), *L. macropodum*, *L. alfi*, *L. obliquiclavum*, *L. enteromorphum* (Sarjeant and Reynolds, 1999), and *L. borregoensis* (Remeika, 2001, 2006). A comprehensive revision of camel tracks by Lucas and Hunt (2007) describes paired teardrop-impressions with modest curvature as camel tracks, and has reduced both generic and specific diversity to two species: *Lamaichnum guanacoe* 40–150 mm long and *L. macropodum* 160–260 mm long. *Lamaichnum sarjeanti* is also a large track (200–260 mm), but lacks the claw impressions seen in *L. macropodum* (McNeil et al., 2007). Other horse tracks include *Hippipeda aurelianus* (Vialov, 1966), *H. parva* (Kulchitskij, 1980), *H. absidata*, *H. gyripeza*, *H. araculata* (Sarjeant and Reynolds, 1999), and *H. downsi* (Reimeka, 1999, 2001). *Hippipeda* is widely used for hemiellipsoidal to hemispherical tracks, but *H. cardstoni* is 90–120 mm long, and more hemispherical than other species (McNeil et al., 2007).

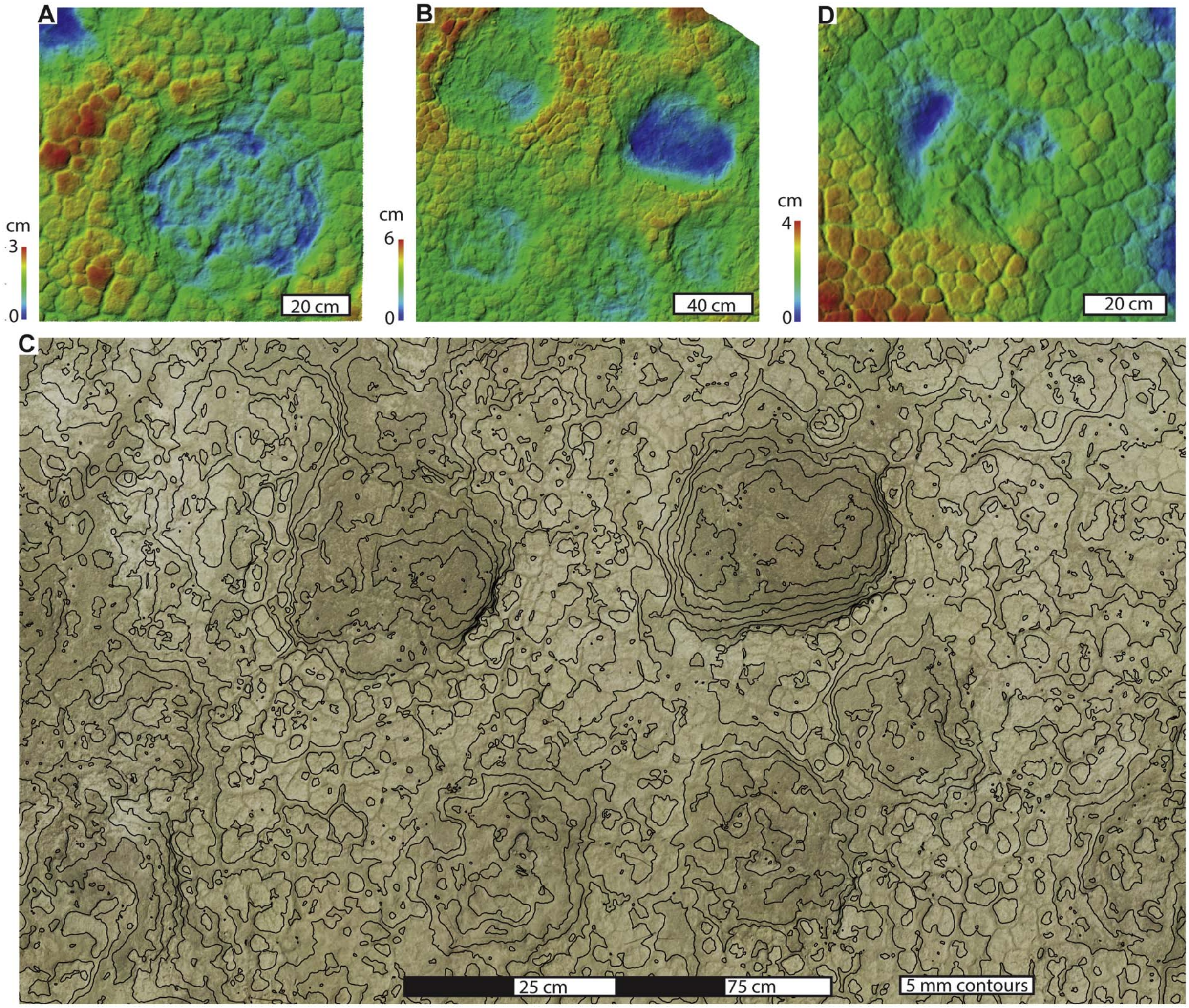

Fig. 6. Photogrammetric images of individual proboscidean tracks of *Proboscipeda panfamilia* (A–C) and camel track of *Lamaichnum sarjeanti* (D); A, large circular track with concentric lamination; B–D, different depths of right pes and manus (top) compared with left pes and manus (bottom), and an additional track of a smaller animal behind as a false color digital elevation model and contoured with interval of 5 mm; D, false color digital elevation model of small track.

4.3. Interpreted animal behavior

Little can be gleaned from a single equid and camelid print, but the assemblage of proboscidean tracks offers a variety of information on Columbian mammoth behavior, such as herd age-distribution and gait. The main trackway and at least 3 individuals of the trample ground are of a size found in 11 ± 2 year old African elephants, using a scale devised to predict ages of animals from the size of mammoth footprints (McNeil et al., 2005). Age of female sexual maturity can be as early as 7 (Whitehouse and Hall-Martin, 2000) and as late as 15 years (Moss, 2001), so that if these largest tracks were female, they were early mature individuals. Male African elephants reach testes and seminal vesical maturity at 15 years (Hanks, 1972), but are successful fathers by 26–59 years (Hollister-Smith et al., 2007), so that if these tracks were male, they would have been immature. The smallest trackway was from a baby less than a year old, and the three other tracks of intermediate size were between 1 and 3 years old, judging from the age scale of McNeil et al. (2005). Thus the herd included at least 4 adults, a baby, and at least one subadult.

The main adult trackway in our excavation appears to have been a limping animal for the following reasons: close spacing of manus and pes, overall sinuous path (Fig. 5A), and deeply impressed prints on one side compared with the other (Fig. 6B–C). The deepest prints of right limbs show scalloping from toes on the western edge of both manus and pes (Fig. 6C), so were heading west. The left pes is especially lightly impressed compared with the left manus (Fig. 6C). An alternative explanation is that the left and right tracks were two separate animals striding out at different times and thus different substrate consistency. This explanation does not account for the 20 pairs of tracks following the same sinuous course with the same lateral spacing. The baby track and subadult tracks also have closely spaced manus and pes, as if diverging slowly out and returning slowly to the adult that later overprinted the small prints. Comparable behavior is known around injured modern elephants (Dublin, 1983; Fowler and Mikota, 2006). Inflections in the paths of the main large trackway correspond to these smaller animals approaching and retreating, as if they were interacting. An adult animal limping to ease its left side may have been attended by concerned juveniles slowly diverging and returning. For this reason the main trackway is likely to have been a female mammoth, though perhaps not the large matriarch of the group, and perhaps an individual fated for early death. Matriarchal herds known from modern African and Asian elephants (Rasmussen and Schulte, 1998) can be inferred as long ago as late Miocene from elephant trackways (Bibi et al., 2012).

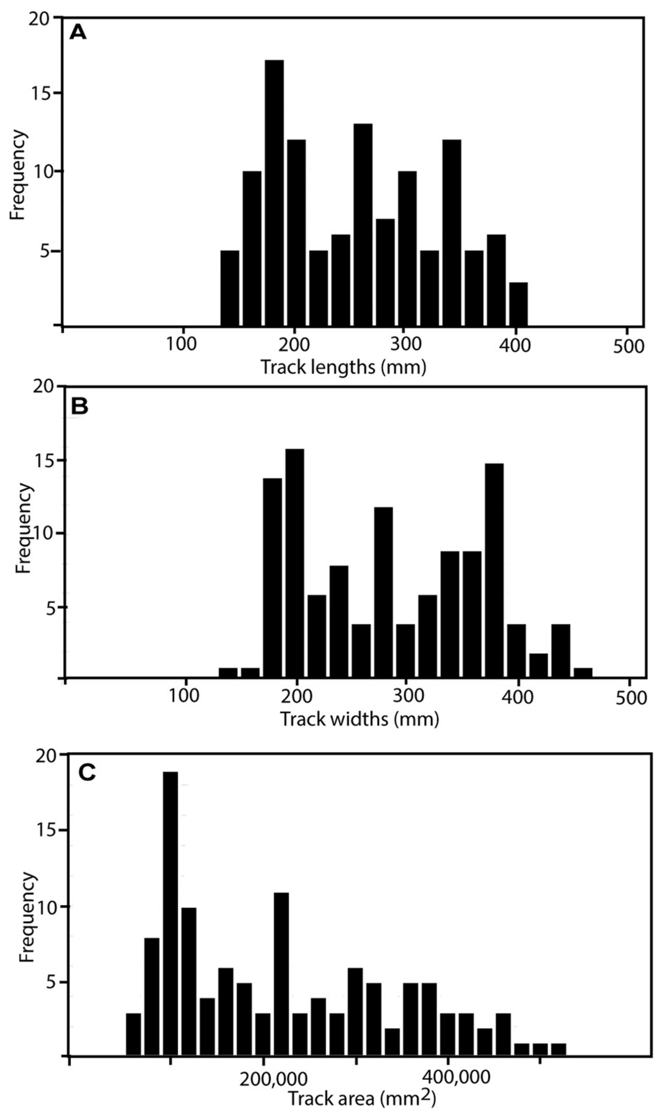

Fig. 7. Histograms of track length, width, and areas, each approximated as an ellipse from length and width measured in the field.

5. Paleosols

5.1. Description

A variety of paleosols were recognized in excavated sections, starting with the trackway, which was a land surface itself, with a very distinctive pattern of surface tessellation (Fig. 2G–H, 6A–B, D). Excavation below the trackway revealed that the tessellation was a surface expression of columnar structure, in a brown, non-calcareous clayey subsurface (Figs. 1B, 2D), and a more complete profile was excavated nearby (Fig. 1C, 2E). This profile was given the descriptive pedotype name Pogani, from the Great Basin Paiute word for "to be cracked up" (Liljeblad et al., 2012).

Immediately below the Pogani paleosol near the trackway was another kind of paleosol (Fig. 1A), with brown, crumb structure over moderately calcareous nodules and mottles, called here the Yada pedotype from Paiute for "winnowing basket" (Liljeblad et al., 2012). Yada paleosols were also seen at lower stratigraphic horizons below the 95 ka Tulelake tuff and 610 ka Dibekulewe tuff near the Bird and Southwest Sites (Fig. 1E–F). Descriptive pedotype names are not stratigraphic markers like geosols, but reflect paleoenvironments independent of age (Retallack, 1994).

A third pedotype is represented by subhorizontal networks of calcareous rhizoconcretions (Fig. 2F) diagnostic of the paleosols here called Pui, Paiute for "root" (Liljeblad et al., 2012). These paleosols, again on different stratigraphic levels (Fig. 1C, D, E), are very weakly developed with clear ripple marks and interbedded tuffs and sandstones undisrupted within the profile. Another weakly developed pedotype is Pasiwa, or "sandy" (Liljeblad et al., 2012), which is a bedded sand with some brown stain, vertical root traces, and vertical insect burrows, but little soil clay, or soil structure.

5.2. Classification

Soil classification of paleosols is a first step to interpreting their paleoenvironment and is summarized in Tables 1 and 2. Thenardite in thin section and soda excess from chemical analysis (Fig. 3) mark the Pogani pedotype as an Aridisol, and more specifically a Natrargid (Soil Survey Staff, 2014). The crumb structure and dark color of the surface 22 cm of the Yada pedotype marks it as a Mollisol. Summer dry climate regime is indicated by common siliceous rhizoliths and coprolites in Yada paleosols (Retallack, 2004), which therefore had a xeric soil moisture regime as in Xerolls of Soil Survey Staff (2014). Both Pasiwa and Pui paleosols are Entisols. Tabular rhizoconcretions in the Pui paleosols are evidence of waterlogging and high water table as in an Aquent, and red color and sandy texture of the Pasiwa pedotype is evidence of free drainage as in Psamment of Soil Survey Staff (2014).

In the classification of the Food and Agriculture Organization (1974) a soilscape of the pedotypes recognized on the 43.2 ka Marble Bluff tuff near Fossil Lake would be mainly Orthic Solonetz (map symbol So) with local Calcic Kastanozems (Kk), Eutric Fluvisols (Je) and Calcaric Gleysols (Gc). A close match is map unit So4-2a with associated Mollic Gleysols (Gm) and Luvic Yermosols (Yl) around Christmas, Malheur, and Alvord Lakes of eastern Oregon (Food and Agriculture Organization, 1975). In other words, the Pleistocene Solonetz paleosols are no different from the soils around Fossil Lake today. Malheur Field Station has 10.6 °C mean annual temperature, 252 mm mean annual precipitation, and is summer dry with 35 mm mean annual range of precipitation (Ruffner, 1980). The natural vegetation of these region is sagebrush (Anderson et al., 1998), and the parent materials of the soils are volcanic ash and basaltic sands of late Pleistocene lakes (Allison, 1966; Kuehn and Foit, 2006). Another soilscape match in North America is map unit So5-2a with associated Mollic Gleysols (Gm) and inclusions of Eutric Fluvisols (Je) on lacustrine sediments in central California along the eastern side of the Great Valley from Bakersfield north to Fresno (Food and Agriculture Organization, 1975). Fresno has 16.8 °C mean annual temperature, 261 mm mean annual precipitation,

Table 1
Summary of Fossil Lake paleosol definition and classification.

Pedotype	Paiute meaning	Diagnosis	US taxonomy	FAO map unit
Pogani	To be cracked	Silty, tan, granular-structured surface (A) borazon, over clayey, brown, columnar subsurface (Bn) horizon	Natrargid	Orthic Solonetz
Yada	Winnowing basket	Clayey, brown, crumb-structured surface (A) horizon over granular mottled (Bw) horizon	Xeroll	Calcic Kastanozem
Pui	Root	Subhorizontal calcareous rhizoconcretions (A horizon) over megarippled sand and tuff (C horizon)	Aquent	Eutric Gleysol
Pasiwa	Sandy	Brown mottled sandy surface (A) horizon over gray bedded sand (C horizon).	Psamment	Eutric Fluvisol

Great Basin Paiute definitions are from Liljeblad et al. (2012).

Table 2
Summary of Fossil Lake paleosol interpretation.

Pedotype	Paleoclimate	Organisms	Topography	Parent material	Soil duration
Pogani	Semiarid temperate	Halophytic shrubland, large mammals including Columbian mammoth, horse, and camel	Low alluvial terrace	Tuffaceous silt	1000–2000 years
Yada	Subhumid temperate	Sod grassland	Low floodplain	Tuffaceous silt	500–1000 years
Pui	Not informative	Tule reed fen	Lake margin	Crsrtal tuff and basaltic sand	50–100 years
Pasiwa	Not informative	Early succession grasses, shrubs and burrowing beetles	Streamside levees	Basaltic to quarztofeldspathic sand	500–100 years

and is summer-dry with 47 mm mean annual range of precipitation (Ruffner, 1980). The natural vegetation of this region is California annual grassland, now extensively grazed and cultivated (Bartolome et al., 2007), and the parent materials of the soils are quartzofelspathic Pleistocene alluvium (Harden, 1982).

5.3. Paleoclimate

A variety of chemical indicators of paleoclimate have been quantified from large chemical datasets of North American soils (Sheldon and Tabor, 2009). Alkali index [$S = (mK_2O + mNa_2O) / mAl_2O_3$, where m is moles] of soil B horizons is a proxy for mean annual temperature (T in °C, with coefficient of determination $r^2 = 0.37$; standard error S.E. = ± 4.4 °C; probability $p < 0.00001$; number of soils $n = 147$), according to the following equation derived from large databases for modern soils (Sheldon et al., 2002).

$$T = -18.5S + 17.3 \quad (1)$$

Sodium is the most reactive of alkalies, and chemical reactions are promoted by increased temperature, so that the alkali index declines with increasing temperature. This proxy yields a mean annual temperature of 9.8 ± 4.4 °C and 8.2 ± 4.4 °C for the type Pogani silty clay and Pogani silty clay loam, respectively, and 9.1 ± 4.4 °C for type Yada silty clay paleosol. These estimates are comparable with 10° C mean annual temperature estimated from oxygen isotopic composition of fossil bone in this region since 3.2 million years ago (Kohn and Law, 2006).

Paleoprecipitation can be estimated from paleosols using chemical index of alteration without potash or CIA-K ($I = 100mAl_2O_3 / (mAl_2O_3 + mCaO + mNa_2O)$, in moles), which increases with mean annual precipitation (P in mm) in modern soils ($r^2 = 0.72$; S.E. = ± 182 mm; $p < 0.00001$; n = 147), as follows.

$$R = 221e^{0.0197.I} \quad (2)$$

This formulation is based on the hydrolysis equation of weathering, which enriches alumina at the expense of lime, magnesia, potash and soda. Magnesia is ignored because it is not significant for most sedimentary rocks, and potash was left out because it can be enriched during burial alteration of sediments (Maynard, 1992). This proxy is not suitable for samples with free carbonate, but can be applied to carbonate-free soil above carbonate horizons. This proxy yields a mean annual precipitation of 794 ± 182 mm and 590 ± 182 mm for the type Pogani silty clay and Pogani silty clay loam, respectively, and 611 ± 182 mm for type Yada silty clay paleosol.

A second paleohyetometer can be applied to calcareous soils, such as the Yada pedotype, from a global database of 674 soils of postglacial age in unconsolidated sediments of low lying terrane under grasslands and shrublands (Retallack, 2005). Mean annual precipitation (P in mm) is related to depth to calcareous nodules (D in cm) given by the following formula, with standard error of ± 147 mm and coefficient of determination ($r^2 = 0.52$; $p < 0.00001$; $n = 674$).

$$P = 137.24 + 6.45D - 0.013D^2 \quad (3)$$

The distribution of carbonate nodules in modern soils reflects soil respiration levels as a source of CO_2 and carbonic acid, and these in turn are related to primary productivity of vegetation and mean annual precipitation. By this metric the type Yada silty clay with carbonate mottles at a depth of 27 cm had mean annual precipitation of 301 ± 147 mm. It is not appropriate to apply this function to paleosols like the basal Yada paleosols at the Bird and Southwest site, which have been eroded by basaltic conglomerate, but the ash-mantled upper Yada paleosols at those sites have depth to nodules comparable with semiarid soils (mean annual precipitation 261 ± 147 mm and 255 ± 147 mm, respectively).

Seasonality of precipitation in soils, defined as difference in mean monthly precipitation of the driest versus wettest month (M in mm) has been shown by Retallack (2005) to be related to thickness of soil with carbonate, or distance between lowest and highest nodule in the profile (H_o in cm), by Eq. (4) ($R^2 = 0.58$; $p < 0.00001$; n = 674; S.E. = ± 22 mm).

$$M = 0.79H_o + 13.71 \quad (4)$$

In highly seasonal monsoonal climates, soil respiration levels vary greatly with precipitation levels through the year, and nodules thus form at various levels within the soil, rather than focused in a narrow horizon in less seasonal climates (Retallack, 2005). Application of this proxy to the type Yada silty clay did not correct for compaction because it is so shallowly buried, and gives seasonal monthly precipitation range of 31 ± 22 mm. For the upper Yada profiles of the Bird and Southwest sites, mean annual range of precipitation was 23 ± 22 mm and 24 ± 22 mm, respectively. Siliceous rhizoconcretions and coprolites are evidence that the dry season was in summer, as it is now (Retallack, 2004).

In conclusion, the paleosols examined reveal a paleoclimate comparable with modern climate at Fossil Lake, and also summer dry. Snowfall may be have been more significant, and lakes larger than currently at Fossil Lake during accumulation of the Fossil Lake Formation (Allison, 1966).

5.4. Paleoecology

The type Pogani silty clay and Pogani silty clay loam have siliceous rhizoconcretions up to 3 cm in diameter, yet had enough bare ground to take the footprints of at least 5 elephants. Thus, sparse vegetation of sagebrush and desert ephemerals is envisaged, similar to the modern vegetation (Fig. 2B, 5C–D). Wind-sculpted and desert varnished rocks that litter the surface of the modern deflation plain are unlikely to have covered the ancient soil surface, because none were driven into the soil by the footprints (Fig. 5B).

Animal life of Pogani paleosols included footprints here attributed to camel (*Camelops hesternus*), horse (*Equus scotti*), and Columbian mammoth (*Mammuthus columbi*). Identifiable bones and teeth found in Pogani paleosols as part of this work (localities UO15909, UO15910, UO15912, UO15913) include horse (*Equus scotti*, 1 specimen) and mustelid (3). Also found were birds such as avocet (*Recurvirostra americana*, 1) and Canada goose (*Branta canadensis*, 1), and carnivore coprolites (*Hyaenacoprus bucklandi*, 7: Hunt et al., 2012). Pogani paleosols also yielded aquatic snails such as keeled ramshorn (*Carinifex newberryi*, 4) and pond snail (*Lymnea stagnalis*, 4), and fish including sucker (*Chasmistes batrachops*, 44), chub (*Gila altarcus*, 5), and salmon (*Oncorhynchus mykiss*, 10), but these aquatic elements are more common in Pui and Pasiwa paleosols. A more comprehensive collection

(29 specimens) of the Pogani paleosol (Unit 9 of Martin, 2017) had 47% Leporidae, 13% Camelidae, 11% Bovidae and 8% Canidae, and can be characterized as a camel community.

Yada paleosols are calcareous at depth with crumb-structure and abundant fine root traces characteristic of sod grassland. This sod does not preserve footprints, but Yada paleosols (UO15915, UO15916, UO15919, UO15926, OU15923, UO15924) yielded Columbian mammoth (*Mammuthus columbi*, 3), horse (*Equus scotti*, 11), western camel (*Camelops hesternus*, 1), and bear (*Ursus*, 1). Trace fossils in Yada paleosols include carnivore coprolites (*Hyaenacoprus bucklandi*, 10: Hunt et al., 2012), insect burrows (*Planolites montanus*, *Scaphichnium hamatum*, 3: Bown and Kraus, 1983; Seilacher, 2007), weevil cocoon (*Rebuffoichnus casmiqueli*, 1: Tilley et al., 1997; Genise, 2016), dung beetle boli (*Coprinisphaera murguai*, 5: Genise, 2016), and crustacean burrow (*Thalassinoides suevicus*, 4: Seilacher, 2007). Two units of Martin (2017) are Yada paleosols: unit 6 has 25% Leporidae, 22% Equidae, 16% Camelidae and 9% Geomyidae, and unit 4 has 23% Equidae, 23% Geomyidae, 10% Leporidae and 9% Camelidae. Also from the Yada paleosol atop unit 4 (Martin, 2017) are 2 skeletons of pocket gopher (*Thomomys townsendi*), 5 limbs of horse (*Equus scotti*), a camel dentary (*Camelops hesternus*), and a mammoth tooth (*Mammuthus columbi*). The mammal fauna of Yada paleosols can be characterized as a horse community.

Birds from Yada paleosols include grebe (*Podilymbus podiceps*, 1) and pygmy goose (*Anabernicula oregonensis*, 1). Fish from Yada paleosols include sucker (*Chasmistes batrachops*, 16), chub (*Gila altarcus*, 12), and salmon (*Oncorhynchus mykiss*, 30). Aquatic molluscs include keeled ramshorn (*Carinifex newberryi*, 34), ramshorn snail (*Vorticifex effusa*, 1), and pond snail (*Lymnea stagnalis*, 3). Molluscs and fish were seen in thin section in the parent material of the type Yada silty clay paleosol (Fig. 3). These paleosols formed on lake sediment but were generally well drained, and may also have been seasonally inundated grasslands.

Grassland paleosols of the Yada pedotype are common in the Fossil Lake Formation (Fig. 1), but grasslands are < 10% of the area of the shrub steppe region of eastern Oregon, mainly around upland seeps (Franklin and Dyrness, 1988; Anderson et al., 1998). Grasslands are returning to this area of Oregon, which is near the grassland-shrubland ecotone, with global climatic temperature and precipitation increases (Retallack et al., 2016). Grasslands uncommon now, but common in the Fossil Lake Formation, may have been related to late Pleistocene extinction of obligate grazers, such as horses and mammoths, due to their unique regime of disturbance and fertilization (Owen-Smith, 1987; Kohi, 2013).

Pasiwa paleosols (UO15918) have yielded mainly aquatic molluscs such as keeled ramshorn (*Carinifex newberryi*, 4), pond snail (*Lymnea stagnalis*, 4), and pea clam (*Pisidium variabile*, 1), and fish such as sucker (*Chasmistes batrachops*, 4), and chub (*Gila altarcus*, 1). Mammals found in Pasiwa paleosols include the hind limb of a Columbian mammoth (*Mammuthus columbi*) excavated by Allison (1966). The Pasiwa paleosol of unit 2 of Martin (2017) had 26% Cricetidae (mainly voles, *Microtus*), 20% Leporidae, 18% Geomyidae and 12% Equidae. Pasiwa paleosols on trough cross bedded sand supported early successional riparian or shoreface vegetation that is dominated by willow (*Salix scouleriana*) and aspen (*Populus tremuloides*) in the sagebrush (*Artemisia tridentata*) steppe of eastern Oregon today (Franklin and Dyrness, 1988).

Pui paleosols (UO11542, UO11543; UO11544; UO15911, UO15914, UO15924) have yielded mainly fish such as sucker (*Chasmistes batrachops*, 25), chub (*Gila altarcus*, 11), and salmon (*Oncorhynchus mykiss*, 2), and the aquatic molluscs, keeled ramshorn (*Carinifex newberryi*, 26), Dall ramshorn (*Vorticifex effusa*, 24), flat ramshorn (*Planorbella trivolvis*, 18), pond snail (*Lymnea stagnalis*, 10), and pea clam (*Pisidium variabile*, 1). Also in Pui paleosols are worm burrows (*Planolites montanus*, 1: Seilacher, 2007) and insect burrows (*Scaphichnium hamatum*, 1: Bown and Kraus, 1983). Unit 14 of Martin (2017) is mainly a Pui paleosol with Leporidae (7), Sciuridae (2), pocket gopher (*Thomomys*, 1), horse (*Equus scotti* 2), and Camelidae (4). The large calcareous rhizoconcretions of Pui paleosols include both rhizomes and mats of branching rootlets which do not penetrate the paleosol (Fig. 2F), as is usual in waterlogged soils (Retallack, 1988). They are on bedded sand and tuffs with lamination comparable with lacustrine facies. The rhizomes are similar in morphology to those of tule reeds (*Schoenoplectus acutus*) common around lakes of the Klamath Basin of Oregon today (Tilley, 2012).

5.5. Paleorelief

The Fossil Lake Formation includes several distinct facies that are evidence of a low relief sedimentary basin of lake margins (Martin et al., 2005). Basaltic sands and granule gravels with trough cross bedding and ripple marks (Fig. 2D) represent deposits of shallow streams (Allison, 1966). Laminated marls with aquatic ostracods, snails and clams and tuffs (Fig. 2A) represent eutrophic lakes (Allison, 1966). A distinctive feature of bone from the Pogani paleosol is a strong positive cerium anomaly as well as pronounced overall rare earth enrichment (Fig. 4A–B). Blackening of bones at Fossil Lake comes from enrichment in iron, manganese, and rare earth elements (Martin et al., 2005), but a positive cerium anomaly is produced by reducing formation water over durations of 10–30 ka (Wright et al., 1987; Patrick et al., 2002; Metzger et al., 2004). The positive cerium anomaly is thus evidence of high water table that was chemically reducing after burial of the Pogani paleosol. In contrast, bones from Yada paleosols lack the cerium anomaly (Fig. 4C), and thus were buried in oxidized groundwater. Water table was permanently high within Pui profiles to prevent downward penetration of root traces (Fig. 2F). Pasiwa paleosols also have limited oxidation in the surface only (Fig. 1). Paleotopography was not very different from today, but for intermittent streams delivering coarse debris to the lake between intervals of soil stability (Fig. 8).

5.6. Parent materials

Parent materials to Yada paleosols in the Fossil Lake beds are rhyodacitic airfall tuffs mixed with other quartzofeldspathic silt of eolian origin, but the basal beds of these units are basaltic sands and granule conglomerates (Dole, 1942; Martin et al., 2005). The Pogani paleosol has similar silts in its subsurface, but its upper part is the biotite tuff of Marble Bluff. Parent materials of Pasiwa paleosols are basaltic and quarztofeldspathic sands of fluvial or shoreface origin. Pui paleosols also had mixed parent materials including basaltic sands and rhyodacitic tuff.

5.7. Paleotiming

Time over which a paleosol formed can be inferred from the size of carbonate nodules (Retallack, 2005). In modern soils the diameter of nodules (S) is related to soil age (A in ka) by Eq. (5) (with $r^2 = 0.57$; $p < 0.01$; $n = 10$; S.E. = $\pm$ 1.8 kyr from Retallack, 2005).

$$A = 3.92S0.34 \tag{5}$$

Burial compaction can compromise this calculation for deeply buried paleosols (Sheldon and Retallack, 2001), but is not an issue for paleosols like these within 2 m of the land surface. The results of these calculations show soil durations of 5.0 ± 1.8 kyr for carbonate for the type Yada silty clay paleosol, and 5.7 ± 1.8 kyr and 6.3 ± 1.8 kyr for the upper Yada paleosols at the Bird and Southwest sites, respectively. The Pogani paleosol is developed to comparable thickness and destruction of original bedding, and so represents a comparable time for formation. On the other hand, development of both Pui and Pasiwa paleosols has been minimal, with original bedding preserved. Comparable weakly developed soils in the San Joaquin Valley of California represent only a century or less of soil formation (Harden, 1982).

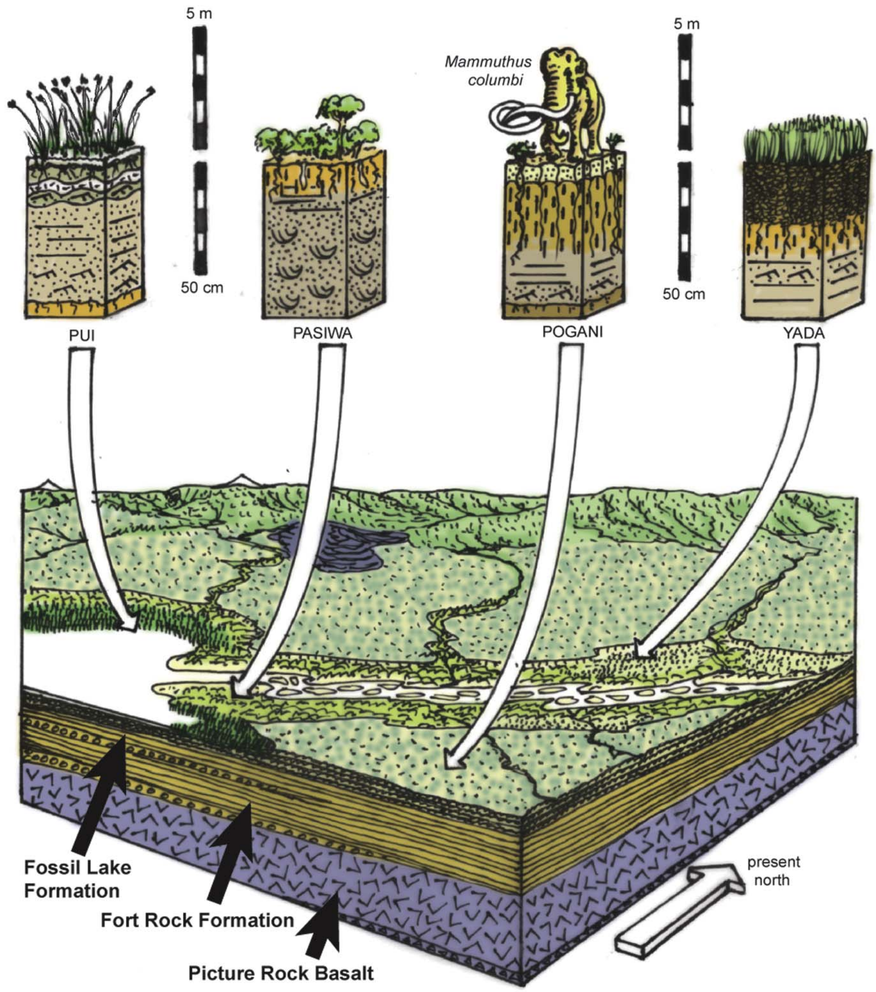

Fig. 8. Reconstruction of paleosols of the Pleistocene Fossil Lake beds, Oregon.

6. Conclusions

Paleosols associated with the mammoth trackway at Fossil Lake are evidence of a paleoclimate and environment not much different from today, but with more lowland grassland (Yada pedotype) than currently in this part of eastern Oregon. These grasslands supported both horses (*Equus scotti*) and Columbian mammoths (*Mammuthus columbi*) that have been extinct on the North American mainland for 11,500 years. Large grazing animals promote grassland by producing copious liquid manure, and a regime of trampling and grazing that is difficult for plants other than grasses to tolerate. Grassland paleosols of the Fossil Lake beds lend some support to the idea that Holocene desertification of some lake basins of eastern Oregon was a consequence of megafaunal extinction.

Alkali shrubland paleosols (Pogani pedotype) also were found in the Fossil Lake Formation, and had sufficient bare soil to preserve tracks of proboscidians (*Proboscipeda panfamilia*), as well as horse (*Hippipeda cardstoni*) and camel (*Lamaichnum sarjeanti*). These ichnospecies represent tracks of Columbian mammoth (*Mammuthus columbi*), western camel (*Camelops hesternus*) and horse (*Equus scotti*), represented by bones at Fossil Lake. The main mammoth trackway excavated for this study was made by a limping animal easing weight on the left leg, and appears to have been very seriously injured. Baby and subadult tracks diverging and returning to this limping track suggest it was made by a female, and the track size is comparable with a young sexually mature adult (11 ± 2 years old). The excavated trackway had at least 4 adults, a baby, and a subadult, all heading generally west toward lake marls. Like African and Asian elephants, Columbian mammoths may have lived in matriarchal herds.

Acknowledgments

We thank H.G. McDonald, K.J. Stangl, G. Shine, K. Martine of the Bureau of Land Management for permit OR-50594 to collect and expose the trackway. J. Hargrave and T. Stidham aided bird identifications. Work was funded by a Sandal Society grant from the Museum of Natural and Cultural History of the University of Oregon.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2018.01.037.

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