



## **Following their footsteps: Report of vertebrate fossil tracks from John Day Fossil Beds National Monument, Oregon, USA**

**Conner J. Bennett, Nicholas A. Famoso, and Daniel I. Hembree**

### **ABSTRACT**

John Day Fossil Beds National Monument (JODA) preserves an exceptional geologic record stretching from the upper Eocene to the upper Miocene (50–6 Ma) of Oregon. These strata contain countless well-preserved vertebrate body fossils for which JODA is famous. While great emphasis has been placed on the study of the body fossils of JODA, comparatively little work has been done on vertebrate and invertebrate tracks recovered from the area. Four specimens with vertebrate tracks are known from JODA, which detail the behaviors of at least four separate types of trackmaker. These include avian and possible lacertiform reptile tracks from the Eocene upper Clarno Formation (50–39 Ma) and superimposed feliform tracks and a tridactyl ungulate track from the Oligocene Turtle Cove Member of the John Day Formation (31–26 Ma). We used commercially available software (Agisoft Metashape Professional) to produce 3-dimensional and digital elevation models (DEMs) of each track surface. The models allow digital preservation and remote study of the specimens, enable an enhanced resolution of surface features, and provide the means to acquire more accurate measurement of the tracks and trackways. The Clarno Formation tracks are the only evidence to suggest that both birds and lizards were present in the John Day Basin during the Eocene, providing a greater knowledge of faunal diversity at this time. The John Day Formation tracks bear resemblance to animals already known from the Turtle Cove Member from body fossils, such as false sabertooth cats (nimravids) and odd-toed ungulates (perissodactyls). Combined with the body fossil record, the JODA tracks provide important insights into the fauna, environment, and behaviors of taxa through the Eocene and Oligocene of Oregon.

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## INTRODUCTION

John Day Fossil Beds National Monument (JODA) in central and eastern Oregon is known for body fossils of upper Eocene to upper Miocene mammals which comprise a nearly continuous, 50 million-year record of mammalian evolution (Bestland et al., 1999; Hunt and Stepleton, 2004; Albright et al., 2008; Fremd, 2010; Samuels and Cavin, 2013; Maguire et al., 2018). This abundance of body fossils has caused other fossil types within the monument to remain relatively understudied. Among those are fossil tracks from the Eocene upper Clarno Formation (50–39 Ma) and the Oligocene Turtle Cove Member of the John Day Formation (31–26 Ma). While not prevalent in the John Day basin, fossil tracks provide data on trackmaker behaviors made during the life of the living organism, which cannot be defined in detail by using body fossils alone (Lockley and Hunt, 1995). When used in tandem with the body fossil record, tracks can also improve interpretations of faunal diversity, often providing evidence of ancient organisms in strata where body fossils are rare (Irmis, 2005). Key aspects of fossil tracks and associated trace fossils also provide information on ancient habitats (Hogue, 2018).

Fossil tracks similar to those at JODA have previously been described from the Eocene deposits of the Chuckanut Formation (49.9 Ma) of Washington (Mustoe, 2002) and the Green River Formation (56–38 Ma) of Utah, Wyoming, and Colorado (Moussa, 1968; Scott and Smith, 2015; Hogue, 2018; Lockley et al., 2021). The Chuckanut Formation contains very few body fossils, but a relative abundance of diverse fossil tracks which record the occurrence of several types of birds, turtles, plantigrade and digitigrade perissodactyl mammals. The Green River Formation is also well known for a diverse and abundant supply of fossil tracks (Scott and Smith, 2015) while also preserving numerous, well-preserved body fossils. By using the body fossil record and the fossil track record within the Green River Formation, further conclusions can be drawn concerning the overall diversity of organisms of the Eocene. While work has been done to describe the fossil tracks from both the Chuckanut and Green River formations, the JODA tracks have only been mentioned twice

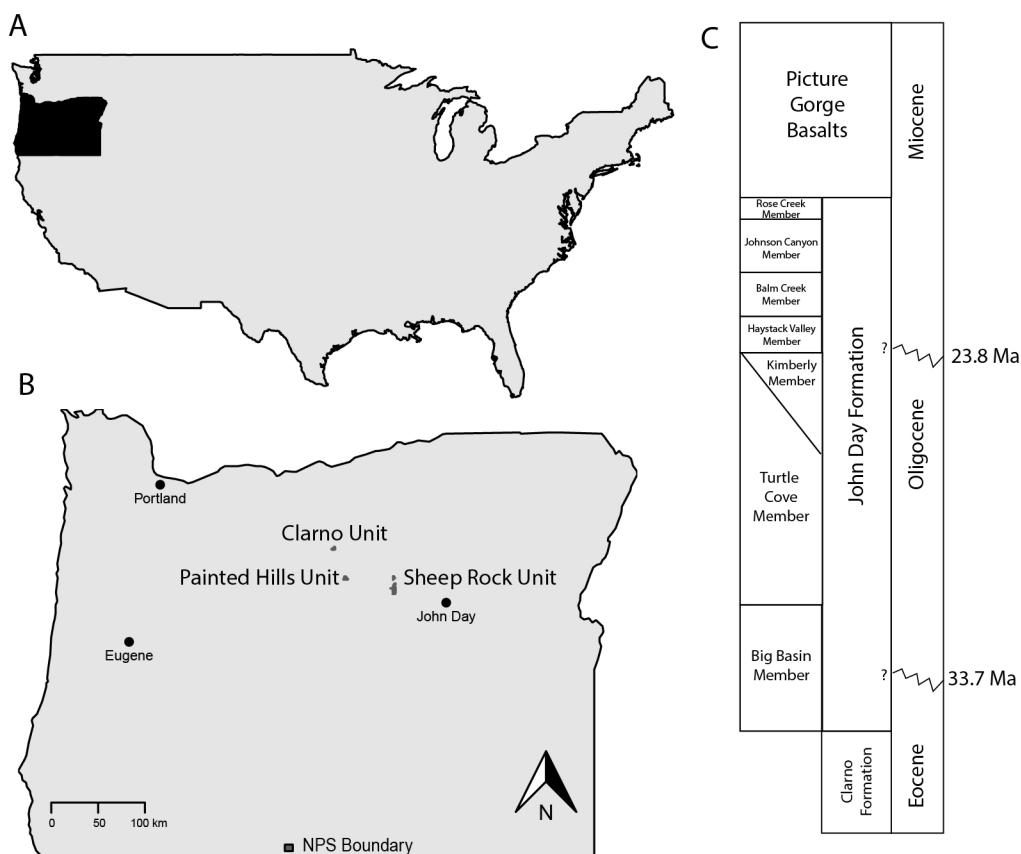
before, with both instances wrongly attributing the John Day Formation tracks to the Clarno Formation and neglecting to mention the actual Clarno Formation tracks entirely (Lockley and Hunt, 1995; Santucci et al., 1998). Due to this inaccurate attribution, it is necessary to properly describe the JODA tracks and attribute them to their proper formations.

In order to describe the JODA tracks, each was rendered as a photogrammetric model to identify surface features which are difficult to discern through visual study alone. Rendered models help to describe each sample and any possible behaviors they preserve, while also digitizing fossil track specimens for remote study (Lallensack et al., 2020). This provides easy access to the data each specimen holds while also assisting in monitoring the condition of the fossil tracks in the future (Lockley et al., 2022).

## GEOLOGIC SETTING

Four formations are recognized within JODA: Clarno (50–39 Ma), John Day (31–25 Ma), Mascall (16–12 Ma), and Rattlesnake (8–6 Ma) (Dillhoff et al., 2009). However, the only tracks recovered have come from the Clarno and John Day formations (Figure 1). The apparent absence of tracks from the Rattlesnake and Mascall formations is likely a result of either the lithology or the depositional environment of each formation. The Rattlesnake Formation is dominated by matrix-rich conglomerates and gravel deposits (Merriam et al., 1925; Samuels and Zancanella, 2011; Samuels and Cavin, 2013), which are not conducive to preservation of fossil tracks. The Mascall Formation possesses layered tuff beds and lacustrine deposits (Maguire et al., 2018), which may be conducive to the preservation of tracks. The apparent absence of tracks within the Mascall Formation may be due to either collection bias or the lacustrine environment represented by these deposits may have been too deep for terrestrial vertebrate tracks to be preserved.

The upper section of the Clarno Formation is composed of mudstones capped by the Member A welded tuff of the Big Basin Member of the John Day Formation, whereas the lower section is composed of lahar deposits with interbedded shales



**FIGURE 1.** Locality maps and stratigraphic column from JODA. A. The state of Oregon shaded in black in relation to the continental United States. B. The three sections of JODA in relation to major cities within Oregon. C. Simplified stratigraphic column of JODA, including the Clarno and John Day formations.

and mudstones (Bestland et al., 1999; Wheeler and Manchester, 2002). The Clarno tracks, JODA 1535 and 1536, were found on pieces of interbedded shales from the lower section. These shales are stratigraphically below lahars, which causes deformation in these beds making it difficult to locate and identify tracks.

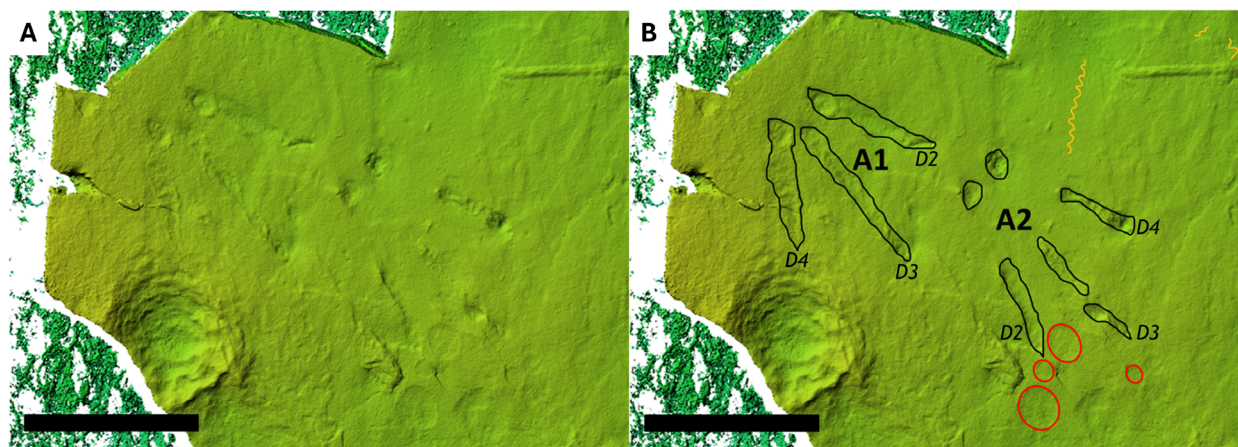
The John Day Formation is currently subdivided into seven members: Big Basin, Turtle Cove, Kimberly, Haystack Valley, Balm Creek, Johnson Canyon, and Rose Creek (Retallack et al., 2000; Hunt and Stoppelton, 2004; Albright et al., 2008). Two of the specimens described in this study, JODA 251 and 283, are likely from the A/B Tuff of the Turtle Cove Member (29.75 Ma) (Albright et al., 2008). The exact locality of JODA 251 and 283 was not properly documented, leading to their stratigraphic context being inferred as the A/B Tuff. The Turtle Cove Member consists of about 400 m of predominantly volcanoclastic mudstones and volcanic tuffs that Albright et al. (2008) divided into 14 lithostratigraphic subunits (A–K2) with 10 dated tuffs including the Picture Gorge ignimbrite (PGI) –

a super-volcanic event bed related to the Yellowstone Hotspot (Seligman et al., 2014). The PGI is between subunits F and G. The Turtle Cove fauna is assigned to the Whitneyan (Wh2) and Arikarean (Ar1 and Ar2) North American Land Mammal Ages (NALMAs).

## METHODS

Vertebrate tracks were found within the monument on specimens JODA 1535, 1536, 251 and 283. JODA 1535 and 1536 were found in the Clarno Formation (50–39 Ma). JODA 251 and 283 were found in the Turtle Cove Member of the John Day Formation (31–25 Ma). The Clarno Formation tracks were collected through a Bureau of Land Management funded survey in 1987, and the Turtle Cove Member samples were donated to JODA by Larry McGraw in 1979, shortly after JODA was established in 1975.

Each JODA specimen was documented through rendered photogrammetric models using Agisoft Metashape Professional (version 1.7). Photographs were taken using a Nikon D810 digital



**FIGURE 2.** DEM models of avian tracks from JODA 1536. A. Tracks and associated features without highlighting. B. A1 and A2 highlighted in black, beak impressions highlighted in red, and *Cochlichnus* highlighted in yellow. Digits indicated by D2-D4. Black scale bar measures approximately 20 mm.

camera and Nikon AF Micro NIKKOR 60 mm lens. Models were rendered from photographs taken of each specimen, using standard techniques outlined by Lallensack et al. (2022). Adequate image overlap, having roughly 60–70% overlap between images, is essential to provide Metashape with enough data to link together the entire model. In addition, tracks and tracksites require images to be captured perpendicular to the surface. Shadows within photographs will not register in the model, creating holes in the final product. Because of this, proper lighting of a surface is essential to capture as much detail as possible. Proper positioning and full capture of scale bars within images is required to ensure proper scaling information.

Model types used in this study include 3-Dimensional Mesh and Digital Elevation Models (DEMs). Each surface was rendered as a 3D Mesh model for remote study and accurate measurement. DEM models helped to visualize subtle shifts in surface elevation through color change, allowing small details to be observed. Screenshots taken from photogrammetric models were then measured in ImageJ (version 1.53t) to provide interdigital angle measurements using the techniques from Sarjeant et al. (2002). Pace data were measured using the ruler tool through Agisoft Metashape (version 1.8).

**Institutional Abbreviations.** JODA = John Day Fossil Beds National Monument, Kimberly, OR, USA; JDNM = Locality number for John Day Fossil Beds National Monument.

## RESULTS

### JODA 1536

**Material.** JODA 1536 preserves two tracks (A1 and A2) from the Clarno Formation (JDNM-66, Hanson's Bird Tracks) in the Clarno Unit (Wheeler County) of JODA (Figure 2; Tables 1–3). Also present are four ovoid impressions clustered below A2, as well as several well-preserved sinusoidal trails (Figure 2B). 3D mesh models of JODA 1536 (A) part (<https://doi.org/10.17602/M2/M454455>) and JODA 1536 (B) counterpart (<https://doi.org/10.17602/M2/M454460>) are available through MorphoSource.

**TABLE 1.** Length and width dimensions for fossil track specimens JODA 1535, 1536, 251, and 283. -- = measurement could not be taken.

Track #	Track Type	Length (mm)	Width (mm)
JODA 1535 (L1)	Lacertiform	20.7	19.3
JODA 1535 (L2)	Lacertiform	--	--
JODA 1535 (L3)	Lacertiform	--	29
JODA 1536 (A1)	Avian	20	16.9
JODA 1536 (A2)	Avian	22.2	15.1
JODA-251 (F5)	Feliform	29.9	29.3
JODA-251 (F6)	Feliform	--	26.5
JODA 251 (P1)	Perissodactyl	--	119
JODA 283 (F1)	Feliform	--	--
JODA 283 (F2)	Feliform	24.9	30.6
JODA 283 (F3)	Feliform	23.6	29.4
JODA 283 (F4)	Feliform	24.6	30

**TABLE 2.** Interdigital angles for fossil tracks specimens JODA 1535, 1536, 251, and 283. -- = measurement could not be taken.

Track #	Track Type	Inter Angle	Inter-Angle	Inter-Angle	Inter-Angle
		I–II	II–III	III–IV	IV–V
JODA 1535 (L1)	Lacertiform	34.9	32.4	29.4	49.8
JODA 1535 (L2)	Lacertiform	--	--	--	--
JODA 1535 (L3)	Lacertiform	--	--	--	--
JODA 1536 (A1)	Avian	--	36.5	34.7	--
JODA 1536 (A2)	Avian	--	21.3	25.8	--
JODA-251 (F5)	Feliform	--	18.9	23.4	34.4
JODA-251 (F6)	Feliform	--	--	--	23.2
JODA 251 (P1)	Perissodactyl	--	24.1	18.6	--
JODA 283 (F1)	Feliform	--	--	--	--
JODA 283 (F2)	Feliform	--	19.5	29.9	35.2
JODA 283 (F3)	Feliform	--	--	--	--
JODA 283 (F4)	Feliform	--	19.9	20.5	29.1

**Description.** The tracks are small, with a mean length of 21.2 mm and a mean width of 15.8 mm. The mean angles between digits II–III, III–IV, and II–IV are 28.9°, 30.5°, and 62.2° respectively. The distance between the two tracks is approximately 40.2 mm. Both A1 and A2 lack webbing between digits. Digit claw impressions on A1 are pointed and slightly oblique to the digit direction. A1 is more detailed than A2 because digit claws and pads are difficult to discern in A2.

The ovoid impressions have a short axis between 2–3.5 mm in diameter and a long axis between 2–5 mm in diameter, of which the long axis is parallel to the orientation of A1 and A2 (Figure 2B). Three of the ovoid impressions are clustered roughly 5 mm from digit II of A2, with the smallest of the ovoid impressions outlying this concentration, approximately 18.3 mm from digit II of A2.

The trails have smooth surfaces, possess a meandering sinusoidal morphology, have very shallow depths, and lengths ranging from 1.60–5.25 cm (Figure 2B). The trails are abundant along the margins of the specimen, and less common toward the center.

### JODA 1535

**Material.** JODA 1535 preserves three possible tracks (L1, L2, L3) from the Clarno Formation (JDNM-66, Hansen’s Bird Tracks) in the Clarno Unit (Wheeler County) of JODA (Figure 3; Tables 1–3). 3D mesh models of JODA 1535 (A) part (<https://doi.org/10.17602/M2/M454449>) and JODA

1535 (B) counterpart (<https://doi.org/10.17602/M2/M454444>) are available on MorphSource.

**Description.** L1 preserves the most detail of the three tracks, with five claw-like impressions. Digit V of L1 is significantly smaller and located distally to digits I–IV; digit III is the longest of the impressions (Tables 1–3). Digit V is oriented almost perpendicular to the long axis of L1, while the remaining digits are roughly parallel to the long axis of L1. The toe claw impressions of L1 curve proximally toward the trackmaker, showing drag marks from motion of the foot during locomotion.

The remaining two impressions are incomplete; L2 only includes three digit impressions (likely from digits II–IV), while L3 preserves only partial impressions of digits I–V. The morphology of L2 and L3 differs from that of L1, in that each digit impression is roughly equidistant and oriented perpendicular to the long axis of the tracks. It is important to note that both L2 and L3 may represent a different trackmaker. No pace data could be collected from L2 and L3 due to the incomplete nature of these tracks.

### JODA 283

**Material.** JODA 283 preserves four tracks (F1, F2, F3, F4), with F1–F2 and F3–F4 each representing a pair of superimposed impressions, likely from the A/B Tuff of the Turtle Cove Member of the John Day Formation (JDNM-8, Sheep Rock) in the Sheep Rock Unit (Grant County) of JODA (Figure 4, Tables 1–3). A 3D mesh of JODA 283 is available on MorphoSource (<https://doi.org/10.17602/M2/M454313>).

**TABLE 3.** Length and width dimensions for fossil tracks specimens JODA 1535, 1536, 251, and 283. -- = measurement could not be taken.

Track #	Track Type	Digit #	Length (mm)	Width (mm)	Track #	Track Type	Digit #	Length (mm)	Width (mm)
JODA 1535 (L1)	Lacertiform	1	3.89	0.818	JODA-251 (F5)	Feliform	5	7.19	4.56
JODA 1535 (L1)	Lacertiform	2	8.67	1.82	JODA-251 (F6)	Feliform	2	13.4	6.28
JODA 1535 (L1)	Lacertiform	3	7.4	1.69	JODA-251 (F6)	Feliform	3	14.1	6.42
JODA 1535 (L1)	Lacertiform	4	5.02	1.93	JODA-251 (F6)	Feliform	4	12.2	5.35
JODA 1535 (L1)	Lacertiform	5	2.56	1.37	JODA-251 (F6)	Feliform	5	7.18	6.24
JODA 1535 (L2)	Lacertiform	1	--	--	JODA 251 (P1)	Perissodactyl	2	41.5	32.8
JODA 1535 (L2)	Lacertiform	2	--	--	JODA 251 (P1)	Perissodactyl	3	42.4	35.3
JODA 1535 (L2)	Lacertiform	3	--	--	JODA 251 (P1)	Perissodactyl	4	26.3	22.6
JODA 1535 (L2)	Lacertiform	4	--	--	JODA 283 (F1)	Feliform	2	--	--
JODA 1535 (L2)	Lacertiform	5	--	--	JODA 283 (F1)	Feliform	3	--	--
JODA 1535 (L3)	Lacertiform	1	1.96	1.3	JODA 283 (F1)	Feliform	4	11.2	4.41
JODA 1535 (L3)	Lacertiform	2	4.62	1.26	JODA 283 (F1)	Feliform	5	10.5	4.3
JODA 1535 (L3)	Lacertiform	3	8.23	0.775	JODA 283 (F2)	Feliform	2	10.6	5.19
JODA 1535 (L3)	Lacertiform	4	8.17	1.44	JODA 283 (F2)	Feliform	3	11.5	6.14
JODA 1535 (L3)	Lacertiform	5	4.82	1.42	JODA 283 (F2)	Feliform	4	11.4	5.89
JODA 1536 (A1)	Avian	2	13.8	1.53	JODA 283 (F2)	Feliform	5	6.34	5.23
JODA 1536 (A1)	Avian	3	17.7	1.81	JODA 283 (F3)	Feliform	2	--	--
JODA 1536 (A1)	Avian	4	13	2.2	JODA 283 (F3)	Feliform	3	--	--
JODA 1536 (A2)	Avian	2	13.2	1.25	JODA 283 (F3)	Feliform	4	7.11	4.35
JODA 1536 (A2)	Avian	3	17	1.01	JODA 283 (F3)	Feliform	5	6.19	4.17
JODA 1536 (A2)	Avian	4	13.7	1.64	JODA 283 (F4)	Feliform	2	9.38	5.63
JODA-251 (F5)	Feliform	2	--	--	JODA 283 (F4)	Feliform	3	10.6	5.74
JODA-251 (F5)	Feliform	3	9.99	5.1	JODA 283 (F4)	Feliform	4	11.3	5.64
JODA-251 (F5)	Feliform	4	12.3	5.44	JODA 283 (F4)	Feliform	5	6.68	5.05

**Description.** The tracks have a mean length of 24.5 mm and a mean width of 30 mm. Mean interdigital angles for digits II–III are 19.7°, III–IV 25.2°, and IV–V 32.2°. Pace data between F1 and F3 is 94.4 mm, while F2 and F4 is 95.3 mm. Each track is composed of one center pad impression and four ovoid digit impressions forming a semicircle in front of the center pad. The long axis of the digital pads points outward away from the center of the track and the ends of each digital pad lack digit claw impressions. The digital pads of F1 and F3 are slightly obscured due to the overprinting from F2 and F4.

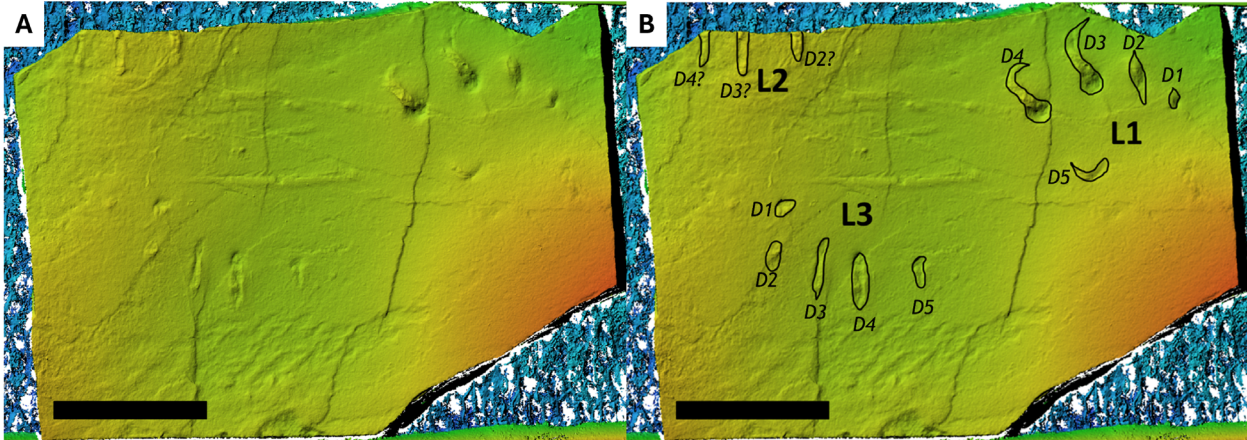
#### JODA 251

**Material.** JODA 251 preserves two overlapping tracks, one of which (F5) is superimposed over the other (F6), as well as a single partial track (P1) (Figures 5-6; Tables 1–3). This slab is likely from

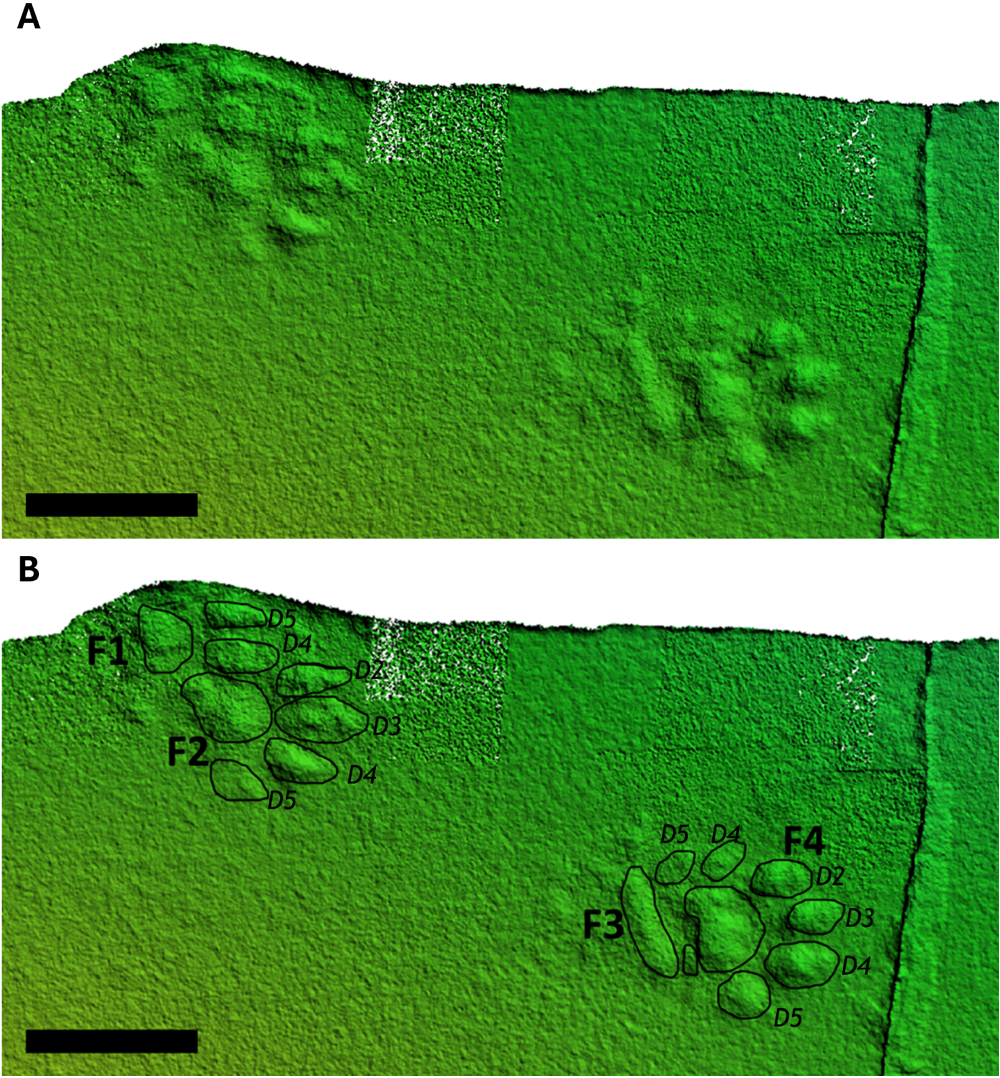
the A/B Tuff of the Turtle Cove Member of the John Day Formation (JDNM-8, Sheep Rock) in the Sheep Rock Unit (Grant County) of JODA. A 3D mesh of JODA 251 is available on MorphoSource (<https://doi.org/10.17602/M2/M454308>).

**Description.** The morphology and size of F5 and F6 are similar to the tracks (F1–F4) from JODA 283. F5 has a length of 29.9 mm and a width of 29.3 mm. The width of F6 is 26.5 mm, however, the length cannot be accurately determined due to overprinting by F5. Interdigital angles for F5 are distorted; the only measurable angle is 23.2° between digits IV–V. In F6 the interdigital angles between digits II–III is 18.9°, III–IV is 23.4°, and IV–V is 34.4°.

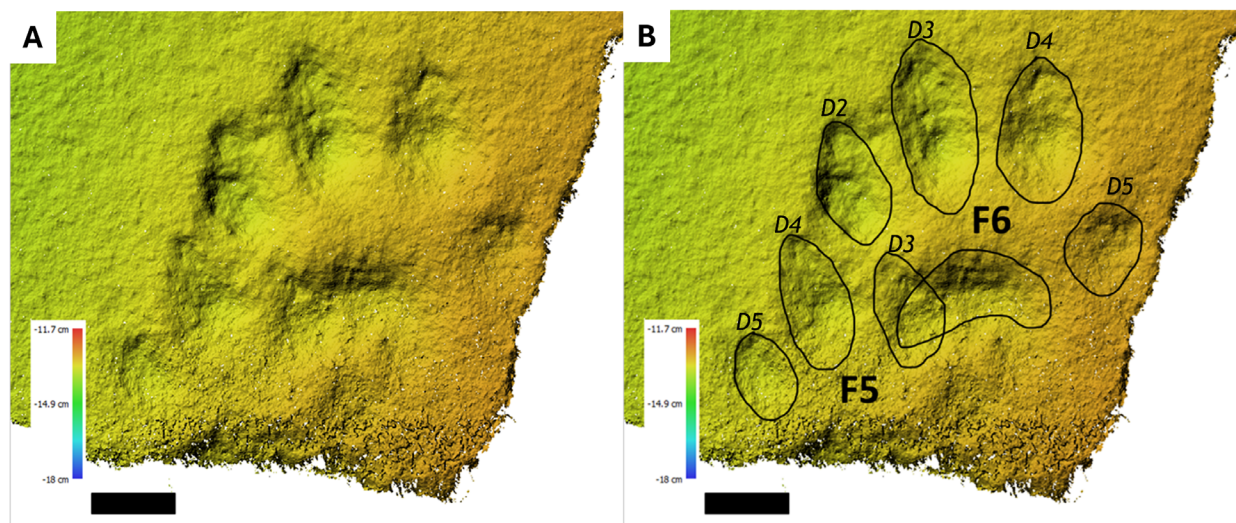
P1 consists of three ovoid pad impressions lacking a central pad. The width of P1 is approximately 119 mm, however, the length of the track cannot be determined due to the absence of an



**FIGURE 3.** DEM models of reptile tracks from JODA 1535. A. Tracks and associated features without highlighting. B. L1, L2, and L3 highlighted in black. Digits indicated by D1-D5. Black scale bar measures approximately 20 mm.



**FIGURE 4.** DEM models of feliform tracks on JODA 283. A. Tracks and associated features without highlighting. B. F1, F2, F3, and F4 highlighted in black. Digits indicated by D2-D5. Black scale bar measures approximately 30 mm.



**FIGURE 5.** DEM models of feliform tracks on JODA 251. A. Tracks and associated features without highlighting. B. F5 and F6 highlighted in black. Digits indicated by D2-D5. Black scale bar measures approximately 7 mm.

impression of the back of the foot. The interdigital angles between digits II–III is  $24.1^\circ$  and between digits III–IV is  $18.6^\circ$ . The three digits are rounded and ovoid, with no digit claw impressions evident. Digit II and III are noticeably larger than digit IV. Digit IV is also spaced farther from III than digit II is from III.

## DISCUSSION

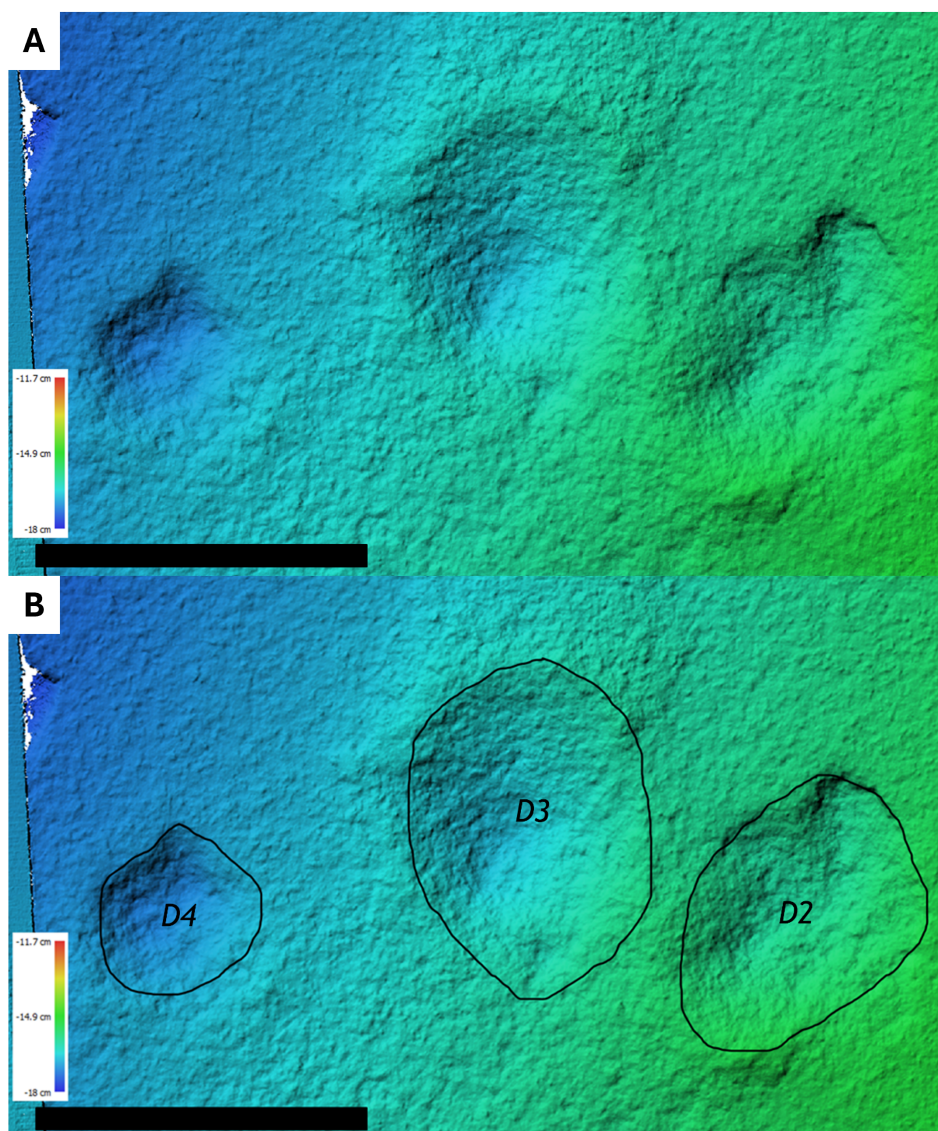
### Avian Tracks and Feeding Behavior (JODA 1536)

The tracks present on JODA 1536 are interpreted as the first avian fossils from the Eocene of JODA. In order to better understand the possible ichnotype, the divarication angles of A1 and A2 were compared to those of similar ichnotypes including *Aviadactyla vialovi*, *Aviadactyla* sp., *Avipeda gryponyx*, *Avipeda phoenix*, *Avipeda thrinax*, and *Avipedidae* (WWU Site RU-1; Mustoe, 2002) (Figure 7). Of these, A1 and A2 are most similar to the ichnogenus *Avipeda* because of the absence of webbing within the tracks, the narrow digit divarication angles, and the apparent absence of digit I (Sarjeant and Langston, 1994). However, the lack of further avian track material from JODA, coupled with the incomplete nature of A2, makes it impossible to definitively attribute the ichnogenus of these avian tracks. JODA 1536 is not attributed to ichnotaxa such as *Rivavipes*, *Fuscinapeda*, and *Charadriipeda*, because JODA 1536 possesses slender digits and no evidence of webbing (Sarjeant and Langston, 1994; Mustoe 2002; Mustoe, 2012). The absence of hallux impressions does not

allow for JODA 1536 to be attributed to ichnotaxa such as *Gruipeda* and *Ardeipeda*.

Originally, the ovoid impressions on JODA 1536 were considered raindrop impressions. Raindrop impressions are found widely dispersed over a bedding surface, oftentimes with impressions occurring within each other (Metz, 1981). The JODA 1536 ovoid impressions are localized to the region near A2 and do not occur within each other. Because the JODA 1536 ovoid impressions lack these general aspects of raindrop impressions, we interpret the numerous ovoid impressions near A2 as beak impressions of the avian trackmaker. This feeding behavior is shared between numerous modern shorebird species which consume various worms, insects, crustaceans, and molluscs on and within the substrate (Van de Kam, 2017). Invertebrate traces attributed to *Cochlichnus* (Figure 2) occurring on JODA 1536 provide evidence of possible prey for the trackmaker and suggest the tracks were made along a lakeshore environment likely in very shallow water (Hogue, 2018). Previously described “foot-stirring” and beak-probing behaviors have been identified from the Cretaceous (Lockley et al., 2009; Falk et al., 2010). Erickson (1967) also described a bird feeding trace from the Eocene of Utah from a larger, web-footed bird. Zonneveld et. al. (2024) also recently described numerous circular to ovoid impressions in proximity to avian trackways from the Eocene Tanjung Formation of Indonesia. Due to the commonality between modern shorebird feeding behavior and that inferred from JODA 1536, this feeding process is successful in sourcing a variety





**FIGURE 6.** DEM models of the odd toed ungulate track on JODA 251. A. P1 without highlighting. B shows P1 highlighted in black. Digits indicated by *D2-D4*. Black scale bar measures approximately 50 mm.

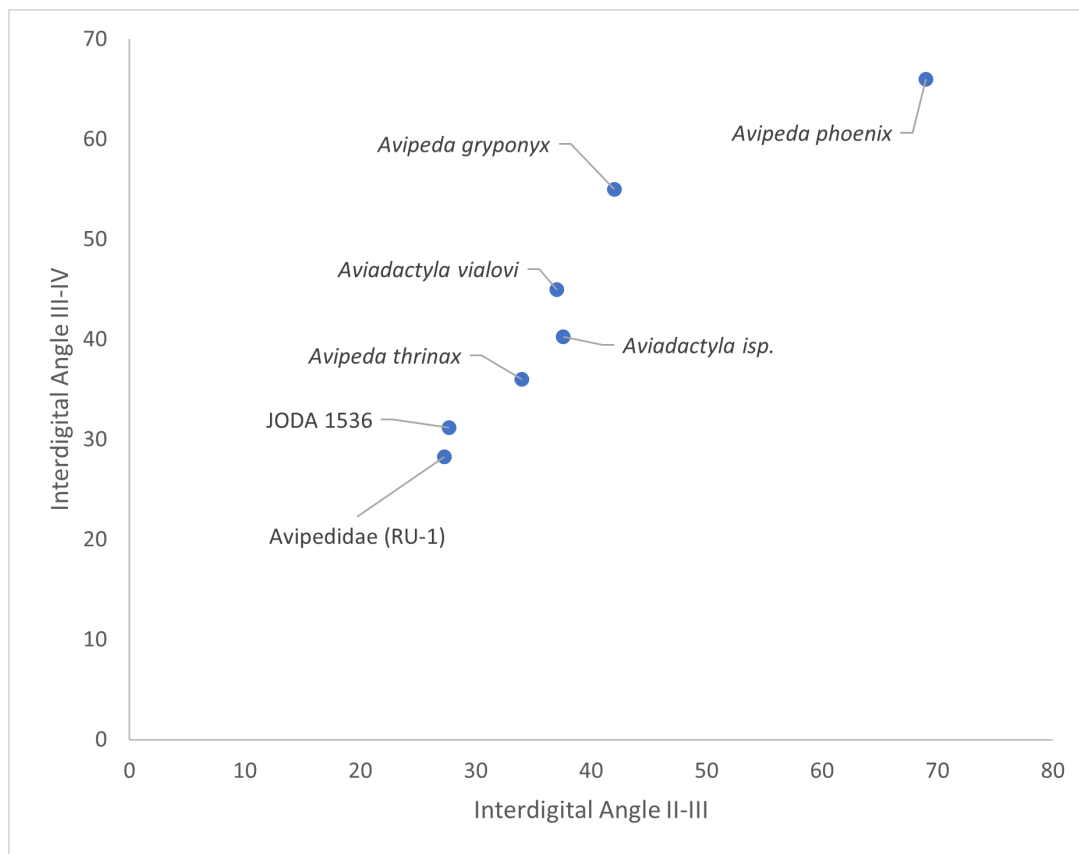
of food types and has been utilized by shorebirds for millions of years. As there are few examples of feeding traces of birds from the Eocene, JODA 1536 provides an important understanding of Eocene shorebird feeding behaviors.

Avian and invertebrate traces are likely to occur within a near-shore, lacustrine environment. The lithology of the JODA 1536 sample slab supports this assumption, as it has been classified as a section of interbedded shale within the otherwise lahar-rich geology of the Clarno Formation (Wheeler and Manchester, 2002). Because shale deposits are not dominant within the Clarno, JODA 1536 is therefore important in possessing traces, which would have otherwise been impossible to

preserve within the more dominant lahar deposits. Therefore, the lithology and fossil traces of the JODA 1536 slab provide a greater understanding of this Eocene ecosystem, suggesting interaction between avian and invertebrate taxa along a near-shore, lacustrine environment.

#### **Reptile Tracks (JODA 1535)**

The morphology of L1 in JODA 1535 is similar to tracks produced by reptiles, especially those of extant lizards (Kubo, 2010). This is significant because few Eocene reptilian ichnotaxa have been described. Unfortunately, the incomplete preservation of the JODA 1535 tracks prevents attribution to any specific ichnotaxon.



**FIGURE 7.** Graph comparing interdigital angles of known avian ichnotaxa against JODA 1536.

Sarjeant and Langston (1994) described a trackway from the Chadronian (Late Eocene) of Texas, which they attributed to the ichnogenus *Chelonipus* and interpreted as being produced by an amphibious turtle. Mustoe (2019) described similar *Chelonipus* trackways from the Lower Eocene of Washington as well as the new ichnogenus *Anticusuchipes* which they attributed to a crocodylian trackmaker. Lizard-like tracks are also known from Eocene deposits but have not been described in any detail. For example, the Green River Formation of Utah, Colorado, and Wyoming has one documented trackway (Curry, 1957) and one isolated track (Lockley et al., 2021) with morphologies similar to L1.

Track L1 in JODA 1535 possesses thin digits with pronounced, sharp digit claw impressions. This eliminates dactyloidiform, helodermatiform, iguaniform, and crocodyliform traces from attribution to JODA 1535. The claw marks, thin digits, and digit orientation (I-V) of L1 are more similar to *Neosauroides* which are interpreted as lacertiform tracks from the Lower Cretaceous of Korea (Kim et al., 2017, 2019). These features have also been

described from tracks produced by various extant lizards in neoichnological experiments (Kubo 2010). The absence of similar Eocene track descriptions makes JODA 1535 an essential sample to base future research into Eocene lacertiform fossil tracks. If correctly attributed, JODA 1535 would be the first lacertiform fossil from JODA.

#### Feliform Tracks (JODA 283, 251)

We attribute JODA 283 and 251 (F5–F6) to a feliform trackmaker because of the presence of four spheroid to ovoid digits with a semicircular center pad and the absence of claw impressions, a trait primarily possessed in felids which discerns them from canid tracks (Remeika, 2001). Feliform body fossils are well known from the John Day Formation and include the nimravids *Dinaelurus*, *Dinictis*, *Hoplophoneus* (= *Eusmilus*), *Nimravus*, and *Pogonodon*, and the palaeogalid *Palaeogale* (Fremd, 2010; Barrett, 2016; Barrett et al., 2021; Famoso and Orcutt, 2022; Barrett and Hopkins, 2024). While matching the JODA feliform tracks to any one of these taxa is impossible, the small size of the tracks compares well with the nimravid *Hop-*

*lophoneus* (= *Eusmilus*) *cerebralis*, a small, bobcat-sized nimravid of the Oligocene John Day Formation (Barrett, 2016).

Currently, four ichnogenera belong to the morphofamily Felipedidae: *Felipeda* (Panin and Avram, 1962), *Mitsupes* (Rodríguez-de la Rosa and Guzmán-Gutiérrez, 2012), *Pantheraichnus* (Diedrich, 2011), and *Pycnodactylopus* (Sarjeant et al., 2002). JODA 283 and JODA 251 (F5–F6) tracks closely resemble the ichnogenus *Felipeda* based on the symmetrical nature of the center pad, the overall “U” shape of the center pad, and the ratio of digit width to length exhibited in the JODA feliform tracks (specifically digits III and IV) (Anton et al., 2004; Agnolin et al., 2018). The ichnogenus *Mitsupes* is characterized by large center pads in the shape of a “U”, but asymmetrically oriented to the digits, a trait not shared with the symmetrical center pads from the JODA feliform tracks. The ichnogenus *Pantheraichnus* possess center pads more plantigrade than those of the JODA tracks, in some cases being partially or completely ovoid in shape, as opposed to the “U” shape exhibited by the JODA feliform tracks (Diedrich, 2011). The ichnogenus *Pycnodactylopus* is a broad, overall ovoid track with digits having widths two-thirds their length, much thicker than the digit width ratio of the JODA tracks (approximately one-third).

To better understand how JODA 283 and JODA 251 (F5–F6) compared to other feliform ichnotaxa, we compared the interdigital angles of the JODA impressions to the ichnospecies *Felipeda parvula*, *Felipeda scrivneri*, and *Pycnodactylopus achras* (Figure 8 A–B) (Sarjeant et al., 2002). Of the ichnospecies compared, JODA 283 and JODA 251 (F5–F6) are most similar to *Felipeda parvula*. However, while similar to the ichnogenus *Felipeda*, the superimposition of the feliform tracks in JODA 283 and JODA 251 (F5–F6) makes this attribution difficult, and therefore assignment to a single ichnogenus is provisional.

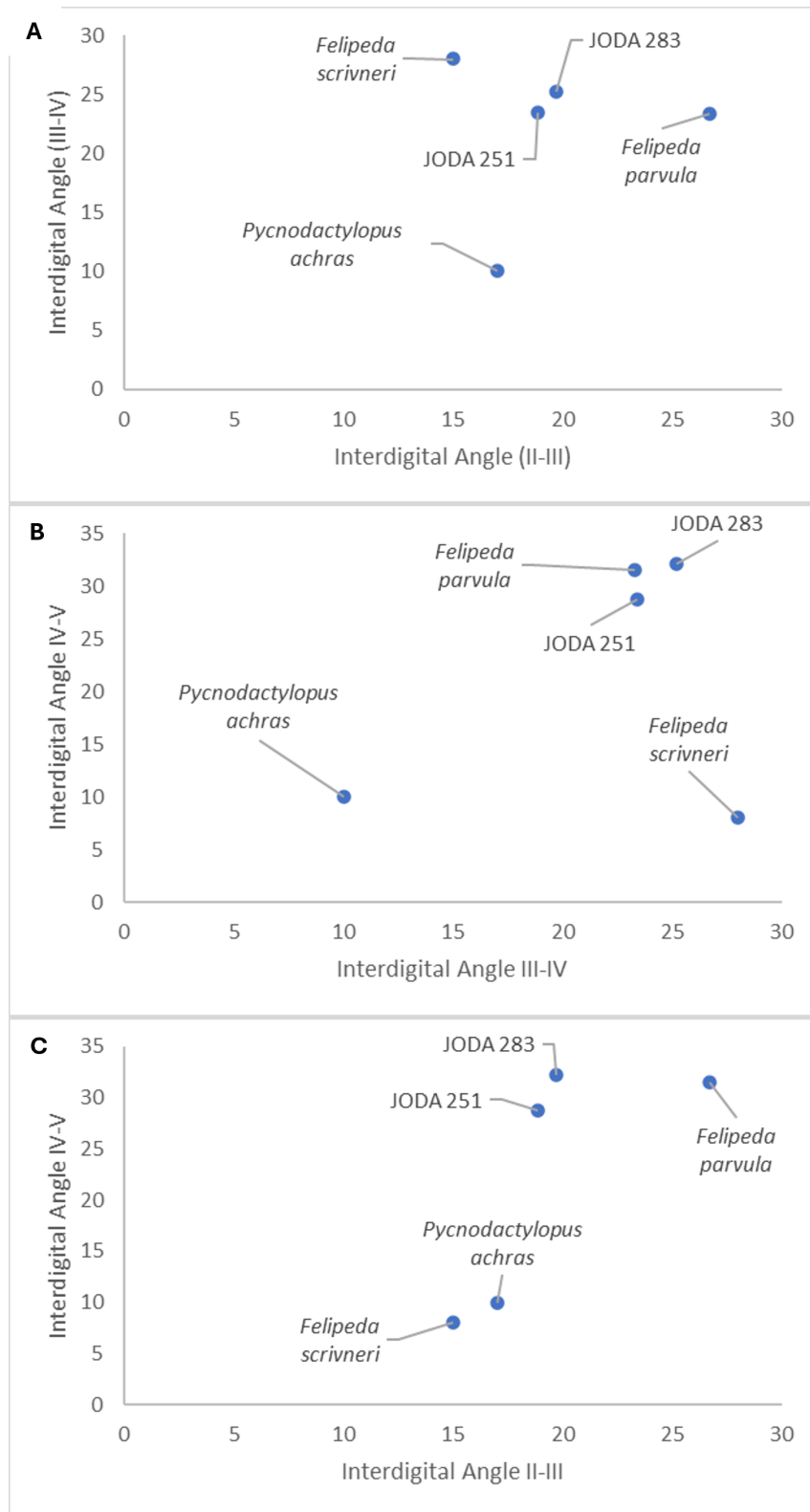
### Odd-Toed Ungulate Track (JODA 251)

The three round impressions on JODA 251 (P1) resemble known Miocene perissodactyl track types (Vyalov, 1966; Sarjeant and Langston, 1994; Mustoe and Hopkins, 2012; Vera and Krapovickas, 2022). Numerous perissodactyl trackmakers are known from the John Day Formation, including equids such as *Miohippus annectens* and *Mesohippus* sp. (Fremd, 2010; Famoso, 2017), rhinocerotids such as *Diceratherium* (Albright et al., 2008) and tapirids such as *Nexuotapirus* (Dingus, 1990; Fremd, 2010).

Ichnotaxa likely made by rhinocerotids include *Rhinoceripeda* (Vyalov, 1966), *Palaeotheriipus* (Ellenberger, 1980), and *Dicerotinichnus* (Guerin and Demathieu, 1993). The primary components of rhinocerotid tracks include three small, rounded digit impressions with occasional preservation of a large central pad that corresponds to the sole of the foot (Sarjeant and Langston, 1994). The absence of a center pad within P1 of JODA 251 does not affect determination of the possible ichnotaxon, as some rhinocerotid tracks can lack this feature (Costeur et al., 2009). This absence may suggest that P1 is an undertrack, causing only the front digits to be preserved. However, the digit impressions from P1 include an overall greater length to width ratio in digits II and III, an aspect which is not shared in rhinocerotid impressions (Vyalov, 1966; Ellenberger, 1980; Guerin and Demathieu, 1993).

An ichnogenus associated with equids includes *Hippipeda* (Vyalov, 1966). This ichnogenus was attributed to hoofed ungulates after Vyalov (1965) amended the ichnogenus from the previous name, *Hippichnis*. These equid tracks lack digit impressions, composed solely of a convexly arched center pad similar to the hoof of the trackmaker (Lucas, 2007). *Miohippus*, a functionally three-toed taxon with a center pad, is smaller than a rhino or tapir (Famoso, 2017; McHorse et al., 2017; Janis and Bernor, 2019; McHorse et al., 2019). The presence of only digit impressions from P1 does not conclusively rule out equid ichnotaxa, but this track does not match the described morphology of known ichnotaxa, as *Hippichnis* does not possess digit impressions.

Tapirid ichnogenera include *Apoxyopus* (Sarjeant and Langston, 1994) and *Oplidctylapes* (Mustoe and Hopkins, 2012). Each of these ichnotaxa have four-digit manus and three-digit pes impressions; pes digit impressions have overall greater length to width ratios, as do digits II and III of P1. This similar ratio suggests a tapirid trackmaker is more likely than other perissodactyls. It is important to note, however, that P1 is likely an undertrack, causing distortion of the digits and absence of the center section of the track. If attributed as tapiriform, JODA 251 (P1) would be one of only three tapirid fossils from the John Day Formation. However, the incomplete nature of P1 and the lack of similar tracks in the region provides insufficient evidence to attribute this track to a known ichnogenus.



**FIGURE 8.** Graphs showing the interdigital angles of known feliform ichnotaxa compared against JODA 283 and 251.

## CONCLUSIONS

Fossil tracks found within JODA detail significant data in helping to understand the fauna of both the Eocene and Oligocene of Oregon. While most of the JODA samples are incomplete and can be impossible to accurately assign to known ichnogenera, these trace fossils aid in understanding the behaviors and diversity of fauna during their respective periods. JODA 1536 is especially significant, as it records the behavior of Eocene lacustrine shorebirds. In addition, the presence of possible lacertiform traces from JODA 1535 adds to our understanding of known fauna within the Eocene of Oregon. Environmental conditions from the Clarno shales can be inferred from JODA 1535 and 1536, which suggest a nearshore, lacustrine area with low flow velocity. The presence of many invertebrate traces, small shorebird feeding traces, and potential small lizard traces all are suggestive of organisms which would likely inhabit such an environment. For these reasons, the JODA traces can serve to identify aspects of the upper Eocene environment of Oregon. The traces from JODA 283 and 251 (F5–F6) provide a link between feliform

trace and body fossil taxa within JODA. In addition, JODA 251 (P1) may further support the presence of tridactyl trackmaker within the Oligocene of Oregon. While future study of the formations within JODA may present further fossil track material, the current JODA tracks provide important insights into the fauna, environment, and behaviors of taxa through the Eocene and Oligocene of Oregon.

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