Eocene Bird, Reptile, and Mammal Tracks from the Chuckanut Formation, Northwest Washington

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The diversity and abundance of bird and animal tracks preserved in Eocene strata of the Chuckanut Formation in Washington contrasts to the scarcity of body fossils. These ichnofossils were made by vertebrates that inhabited river margins, the only depositional environment favorable for track preservation. Three of the four localities described herein contain tracks from at least two different types of animals. Site SM-6 contains approximately 200 shallow circular plantigrade footprints, perhaps made by a type of archaic mammal of the Orders Pantodonta or Dinocerata. Site RU-1 yielded footprints from a small shorebird and tracks from an early equid or tapiroid. The same type of perissodactyl tracks were preserved at Site KC-1, along with a single webbed bird track, and trackways from a large heron-like bird and a turtle. Site SM-9.5 contained multiple bird tracks of a type not found at the other localities. The discovery of tracks only at Chuckanut Formation sites that expose large bedding planes indicates the importance of considering outcrop architecture during the search for vertebrate ichnofossils, and inspires the hope that similar fossils may eventually be found in correlative formations in the Pacific Northwest.

INTRODUCTION

Western Washington contains extensive outcrops of Tertiary sedimentary rock that preserve abundant plant fossils but few animal remains (Mustoe and Gannaway, 1997). The report of an avian trackway (Mustoe, 1993) from the Eocene Chuckanut Formation inspired a search for other vertebrate trace fossils, resulting in the discovery of bird and mammal tracks at four other sites (Fig. 1). The diversity and abundance of ichnofossils comes as a surprise because the Chuckanut Formation was long believed to contain no evidence of vertebrate life (Pabst, 1968). Tracks previously have been reported from only two other Washington localities: Miocene mammal tracks found near Mount Saint Helens (Kaler, 1998), and an undescribed Eocene mammal trackway from a coal mine in King County (Anonymous, 1997).

The tracks described in this paper are important for several reasons. Cenozoic vertebrate tracks have world-wide distribution (Table 1), but few of these occurrences have the ichnofaunal diversity of the Chuckanut Formation. The Chuckanut trace fossils provide a record of Eocene terrestrial faunal communities in western Washington, a region where vertebrate body fossils are extremely rare. These ichnofossils can be used to make a variety of paleoecological interpretations. An avian trackway illustrates how footprints can be used to reconstruct patterns of locomotion and feeding strategies. Bedding planes that preserve several types of tracks document the coexistence of various birds and animals, and mammal footprints that show impressions left by fleshy pads offer anatomical perspectives for the foot architecture of early perissodactyls.

GEOLOGIC SETTING

The Chuckanut Formation consists of beds of conglomerate, arkosic sandstone, siltstone, and coal that unconformably overlie Paleozoic and Mesozoic metamorphic basement rocks. These continental sediments were deposited on a broad floodplain that existed prior to the mid-Tertiary uplift of the North Cascade Range. Isolated exposures extend along fault zones to connect the main outcrop belt on the west side of the Cascade Range with the Swauk Formation in central Washington. Correlative strata also extend north into British Columbia where they are called the Huntingdon Formation (Mustard and Rouse, 1994). Mustoe and Gannaway (1997) suggested that this map pattern is evidence of a large depositional basin that was dissected by strike-slip faulting. Johnson (1984a, b, 1985) believed these outcrops represent sediments deposited in a series of adjacent fault-bounded basins.

Johnson (1984a) used petrologic criteria to divide the Chuckanut Formation into seven partially interfingering stratigraphic members with an overall thickness of ›6,000 m. Discontinuous outcrops and the lack of distinctive marker beds hinder detailed stratigraphic interpretation. Fission-track ages of detrital zircons indicate that the Bellingham Bay Member, the oldest component of the Chuckanut Formation, is no older than late Paleocene. A tuff bed from the upper Bellingham Bay Member was fission-track dated at 49.9 ± 1.2 Ma (Johnson, 1984a). The ichnofossils described herein were collected from the Slide Stratigraphic Member, a 2,000-m-thick unit that lies between the Bellingham Bay Member and the Padden Member. The latter unit is estimated to be late Eocene or early Oligocene based on palynology (Reiswig, 1982; Mustard and Rouse, 1994). The Padden Member consists primarily of braided-stream deposits that originated during an episode of regional uplift (Johnson, 1984a, b). The Slide Member and Bellingham Bay Members both preserve abundant plant fossils, including palms, tree ferns, taxodiaceous conifers, and angiosperms indicative of a subtropical climate (Pabst, 1968; Mustoe and Gannaway, 1995). Paleoclimate analysis of angiosperm leaf fossils using the Computerized Leaf Analysis Multivariate Program (Wolfe, 1993, 1995) indicates the Bellingham Bay and Slide Members accumulated under sub-tropical conditions, with a mean annual temperature of approximately 16°C. Temperatures remained well above freezing even during the coldest months, and annual precipitation was in the range of 150–250 cm (Mustoe and Gannaway, 1997).

The geographic distribution of track sites within the Chuckanut Formation appears to reflect outcrop geometry rather than stratigraphy. No tracks have been found in the nearly continuous 3,000-m-thick Bellingham Bay Member stratigraphic section exposed along Chuckanut Drive south of Bellingham, or in 3,000 m of Padden Member strata bordering nearby Interstate 5, even though ar-

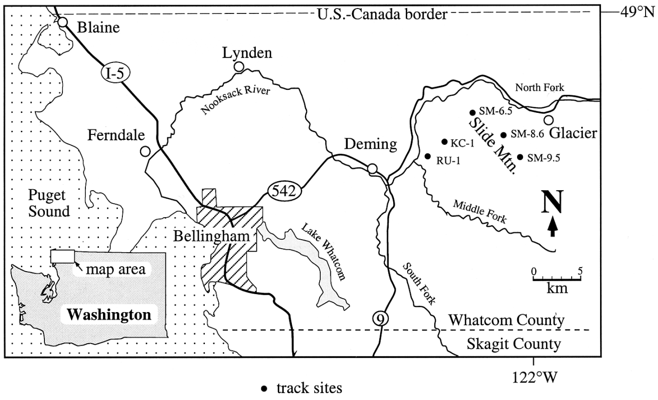

FIGURE 1—Track sites in the Chuckanut Formation of northwest Washington State.

kosic beds are common in both units. The apparent absence of tracks in these rocks probably is related to outcrop architecture. Most Bellingham Bay and Padden Member outcrops occur at roadcuts that expose the edges of steeply-dipping beds, reducing the probability of finding ichnofossils. In the Cascade Foothills, Slide Member strata are folded gently, and tracks were relatively abundant at four sites where road construction revealed large bedding planes (Fig. 1).

DESCRIPTIONS OF ICHNOFOSSILS

The Chuckanut Formation preserves ichnofossils from four types of birds, a turtle, and two varieties of mammals. Three of the four sites (Fig. 1) preserve footprints of at least two types of animals. In the following descriptions, the avian tracks are assigned to morphofamilies and ichnogenera using the definitions of Sarjeant and Langston (1994). The identities of the makers of the two types of mammal tracks are uncertain, but possible candidates are suggested.

Heron-like tracks

Morphofamily Gruipedidae: Ichnogenus Ardeipeda

The first vertebrate ichnofossils to be discovered from the Chuckanut Formation were revealed during logging road construction near Kenney Creek (WWU Site KC-1). The trackway extends 2 m and contains nine tracks clustered into two groups separated by a gap of 0.5m (Figs. 2, 3). Four tracks show imprints left by a long straight hallux (rear toe) lying in the same horizontal plane as the three front digits.

The digit pattern is typical of large wading birds in the order Ciconiiformes. The trackway probably was made by an early member of the Ardeidae, which presently contains approximately 64 species of herons, bitterns, and egrets. The footprints average 11.0 cm in both width and length, similar in size and shape to tracks of extant *Ardea herodius* (Great Blue Heron). Two other explanations are possible. The first is that the tracks might represent an extinct avian family. Members of three modern Ciconiiform families (Balaencipitiidae, Scopidae, and Coclearidae) produce heron-like footprints. Each of these archaic families contains only a single species, none of them inhabiting North America, but they raise the possibility that other families of heron-like birds lived during the early Tertiary. Alternatively, the Kenney Creek tracks may have been made by a non-Ciconiiform wading bird whose descendants later became adapted to terrestrial habitats, accompanied by a corresponding evolution in foot architecture.

Sarjeant and Langston (1994) modified earlier work by Panin and Avram (1962) and Vialov (1965) to provide an ichnotaxonomic scheme that divides the Class Aves into four Morphofamilies: Gruipedidae, Charadriipedidae, Avipedidae, and Anatipedidae. According to this classification, the Chuckanut tracks belong to the ichnogenus *Ardeipeda*, Morphofamily Gruipedidae, erected to contain four-digit avian footprints that have a large and backward-directed hallux.

The trackway likely represents a feeding strategy used by modern herons. These birds rely on three techniques for capturing small fish, crustaceans, amphibians, insects, and other aquatic prey: (1) standing still, waiting for edible organisms to approach within range; (2) slowly strolling through shallow water in search of a meal; and (3) using quick wing or foot motions to startle small creatures (Kushlan, 1985). The Chuckanut trackway appears to represent the third technique, indicating that the bird used a short aerial hop to interrupt its gait. This interpretation is based on several features (Fig. 3). The even spacing of tracks R1-R2 indicate the rhythmic stride of a bird wading with a slight forward lean, as evidenced by the absence of hallux impressions. This locomotion style is used commonly by extant herons as they scrutinize the water while foraging. The incomplete tracks L2 and L3 represent takeoff and landing marks, and the irregular spacing and rear-weighted position of tracks R3-R4 were produced as the bird regained balance. Track L5 shows the return to a more normal stride.

Webbed Bird Track

Morphofamily Charadriipedae: Ichnogenus Charadriipeda

A single webbed bird track (Fig. 4) discovered at site KC-1 has a length of 11.5 cm and width of 8.2 cm. The fossil is attributable to the ichnogenus *Charadriipeda* (Morphofamily Charadriipedae). Sarjeant and Langston (1994) erected this ichnotaxon to describe tracks that have three forward-directed digits of unequal length, separated by interdigital angles of less than 70° and connected by webbing that fills most of the interdigital space.

Small Shorebird Tracks

Morphofamily Avipedidae

Shorebird tracks (Fig. 4) were found at two other sites. In 1998, highway workers briefly uncovered a bedding plane that contained bird and mammal trackways (WWU Site RU-1), but the outcrop was destroyed before the fossils could be studied. The few fragments that were recovered later include a rock slab containing three small bird tracks and five mammal tracks. The tridactyl bird tracks consist of slender straight digits that each terminate in a small claw. The two most complete tracks exhibit interdig-

TABLE 1—Occurrences of Cenozoic tracks

AGE	LOCATION	M = mammal, B = bird, T = turtle, A = amphibian TRACT TYPE	REFERENCE
Pleistocene	Alberta, Canada	M	McNeil and others, 1999
Pleistocene	New Mexico	M	Lozinsky and Tedford, 1991
Pleistocene	Arizona	M	Nininger, 1941; Brady and Seff, 1959
Pleistocene	Oregon	M	Packard and Allison, 1980
Pleistocene	South Dakota	M	Laury, 19890; Agenbroad, 1984
Pleistocene	Nevada	M, B	Blake, 1884; Marche, 1986
Pleistocene	Argentina	M	Aramayo and de Bianco, 1987
Pliocene	Iran	B	Lambrecht, 1983; Vialov, 1989
Pliocene	Nevada	M, B	Lockley and Hunt, 1995
Pliocene	Arizona	M, B	Nations and others, 1981; Lockley and Hunt, 1995
Pliocene	California	A	Peabody, 1959
Pliocene	Japan	B	Yoshida, 1967; Ono, 1984
Pliocene	Tanzania	M	Leaky and Harris, 1987
Miocene	California	M, B	Curry 1941, 1957; Alf, 1966; Scrivner and Bottjer, 1986
Miocene	Ukraine	M, B	Vialov, 1965
Miocene	Romania	M, B	Panin and Avram, 1962; Panin, 1965
Miocene	Louisiana	B	Wetmore, 1956
Miocene	New Mexico	M, B	Lockley and Hunt, 1995
Miocene	Washington	M, B	Kaler, 1998
Miocene	Kansas	M	Robertson and Sternberg, 1942
Miocene	Hungary	B	Kordos, 1983
Miocene	Peru	B	Lockley and others, 1999
Miocene or Oligocene	West Antarctica	B	Covacevich and Rich, 1977
Miocene or Oligocene	Utah	M	Lockley and Hunt, 1995
Oligocene	Switzerland	B	Bräm, 1954; Clercq and Holst, 1971
Oligocene	Spain	M, B	Raaf and others, 1965; Santamaria and others, 1989; Casanovas-Cladellas and Santafé-Llopis, 1982
Oligocene	New Mexico	M	Lockley and Hunt, 1995
Oligocene	Arizona	M	Lockley and Hunt, 1995
Oligocene	Nebraska	M, B	Nixon and LaGarry-Guyon, 1993
Oligocene	South Dakota	M	Chaffee, 1943; Bjork, 1976
?Eocene to Oligocene	China	M	Lockley and others, 1999
Paleogene	Nepal	M	West and others, 9183
Eocene	France	M, B	Ellenberger, 1980
Eocene	Texas	M, B, T	Sarjeant and Wilson, 1988; Sarjeant and Langston, 1994
Eocene	Utah, Colorado	M, B	Erickson, 1967; Moussa, 1968; Lockley and others, 1999; Greben and Lockley, 1992
Eocene	Oregon	M	Lockley and Hunt, 1995
Eocene	New Mexico	M	Lockley and Hunt, 1995
Eocene	Washington	M, B, T	Mustoe, 1993; Lockley and Hunt, 1995; Mustoe and Gannaway, 1997; Anonymous, 1997
Paleocene	Wyoming	M	Lockley and Hunt, 1995
Paleocene	Colorado	B	Lockley and Hunt, 1995
Paleocene	Montana	B, A	Gilmore, 1928; Peabody, 1954; Johnson, 1986
Paleocene	Alberta, Canada	M	Russell, 1930

ital angles of 46–51°, much narrower than the foot pattern of most birds. Averaging 1.5 cm in length and width, the size and close spacing of the footprints suggest they were made by a small bird with short legs. These tracks belong to the ichnogenus *Avipeda* (Morphofamily Avipedidae), characterized by three forward-directed digits of similar length with a total interdigital spacing of less than 95° (Sarjeant and Langston, 1994)

Larger tridactyl tracks (Fig. 4) found at WWU Site SM-9.5 also belong to the Avipedidae. These footprints average 2.5 cm in length and 3.0 cm in width. Their 95–105° interdigital angles slightly exceed values for ichnogenus *Avipeda*, but the tracks are quite different from *Fuscinapeda*, the only other established Avipedidae ichnogenus. *Avipeda* was proposed originally by Vialov (1965) to include all fossil bird tracks. The emendation of this ichnogenus (Sarjeant and Langston, 1994) is still so broad that it contains footprints from a great variety of birds. Erecting a new ichnogenus for the Slide Mountain tracks based on the slight discrepancy over interdigital angles is unjustified. Also, amending the definition of *Avipeda* to include these specimens is best delayed until better descriptions are available for tridactyl bird tracks from other Tertiary localities.

Figure 5 compares all of the Chuckanut Formation bird tracks to avian ichnofossils from other Paleocene and Eocene sites in North America. The only locality that contains tracks that resemble the Chuckanut specimens is the middle Eocene Green River Formation at Soldier's Summit, Utah, which contains tridactyl bird tracks that

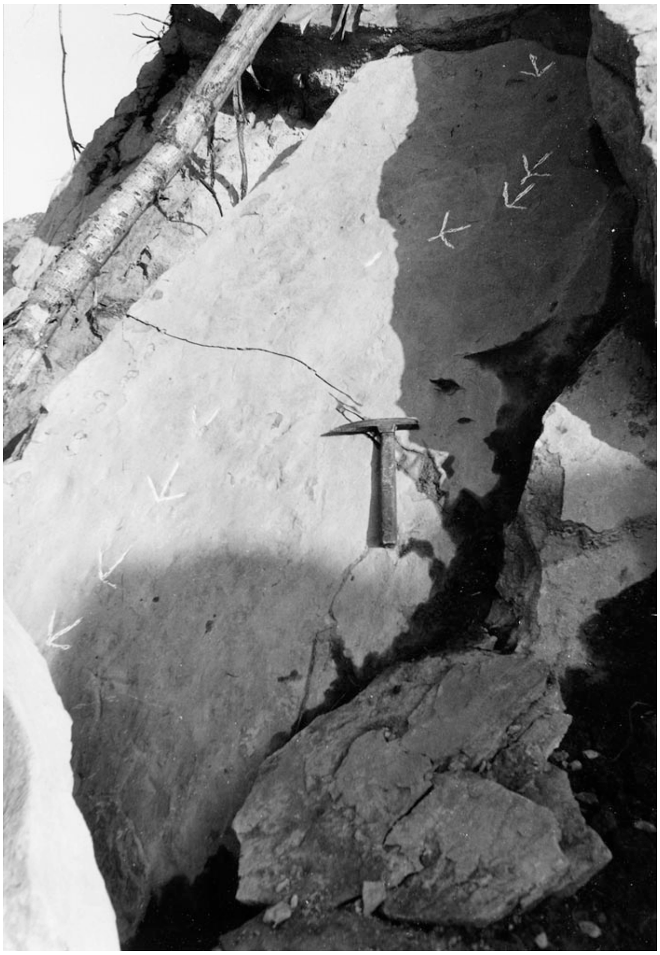

FIGURE 2—Sandstone bedding plane at site KC-1 with a trackway from a large heron-like bird. Tracks are highlighted with chalk.

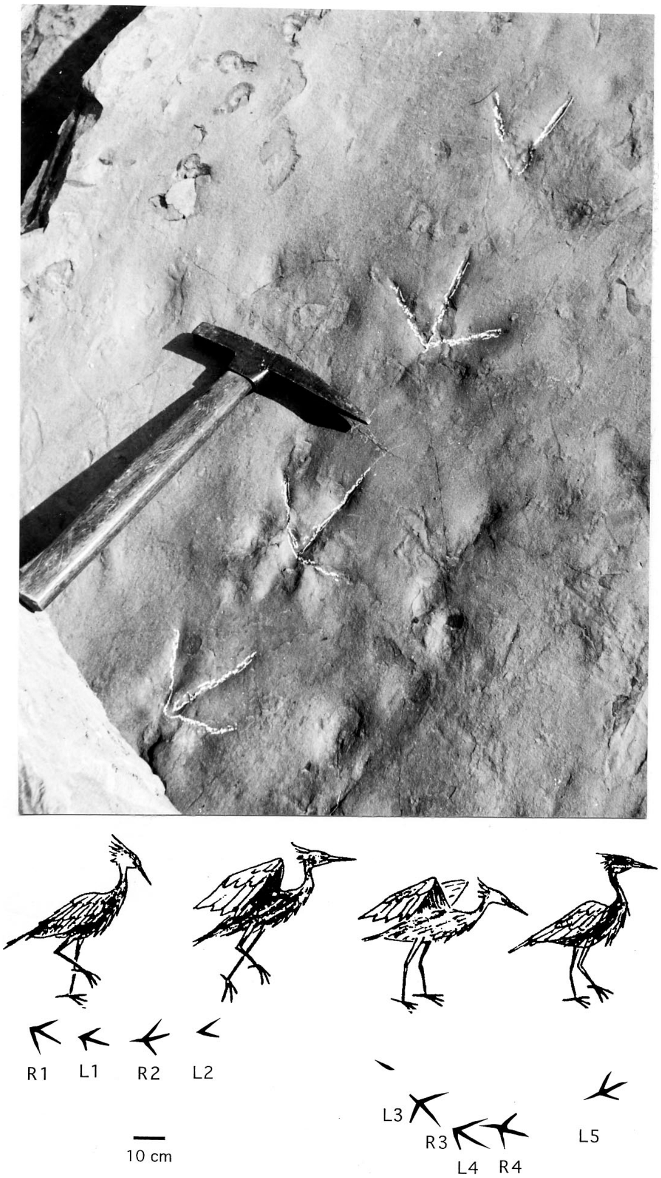

FIGURE 3—The site KC-1 avian trackway shows a gap between footprints L2 and L3. This interruption in gate is interpreted as evidence of foraging behavior (see text for details).

resemble fossils from Slide Mountain site SM-9.5 (Moussa, 1968). The absence of hallux impressions and the presence of the tracks in fluvial sediments suggest the likelihood that tracks of this type were left by early members of the Order Charadriiformes, whose extant members include plovers and sandpipers. However, footprints left by many modern shorebirds are so similar to each other that the Green River and Chuckanut specimens may have been produced by members of different families who shared a common body size.

Turtle Tracks

Morphofamily Chelonipedidae

In July, 1993, the Kenney Creek avian trackway was quarried by a team led by University of Washington paleontologist John Rensberger, and the slab is now on display at the Burke Museum of History and Culture in Seattle. The excavation revealed 13 shallow depressions interpreted as a turtle trackway (Fig. 6). The asymmetric ovoid tracks are approximately 3 x 4 cm, averaging 1 cm in depth. The 13 cm trackway width is evidence of a creature that was larger than the turtle whose carapace was preserved in Padden Member strata near Bellingham (Mustoe and Pevear, 1983; Mustoe and Girouard, 2001). The absence of plastron drag marks and the indistinct nature of the tracks suggest that they were made by a turtle that was wading in shallow water. The tracks lack claw marks, but their digitigrade orientation indicates the direction of travel.

Sarjeant and Langston (1994) proposed the Morphofamily Chelonipedidae to include turtle tracks. They defined only one ichnogenus, *Chelonipus*, which includes Triassic tracks from Germany and Eocene footprints from Texas. Lack of preservational features prevents assignment of the Chuckanut Formation turtle to this ichnogenus.

Plantigrade Mammal Tracks

In the spring of 1996, an outcrop on Slide Mountain (WWU Site SM 6.5) was found that contains approximate-

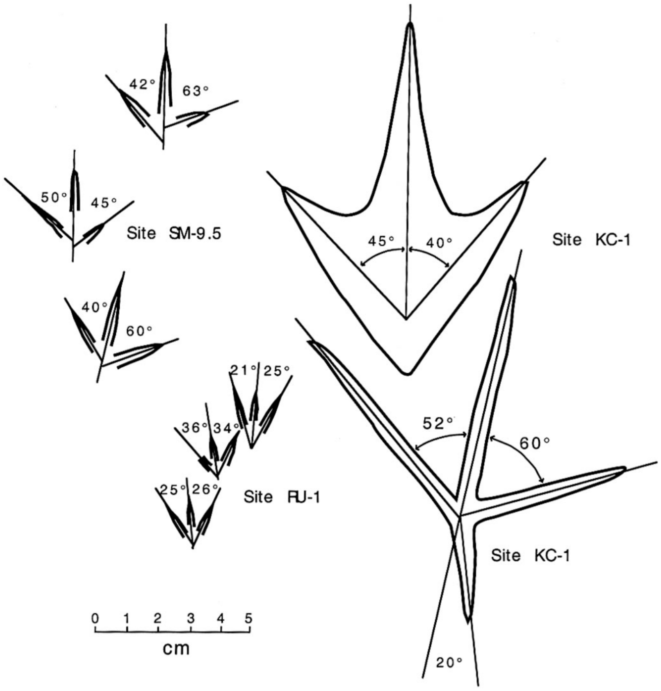

FIGURE 4—Interdigital geometry of Chuckanut Formation bird tracks from localities KC-1, RU-1, and SM-9.5.

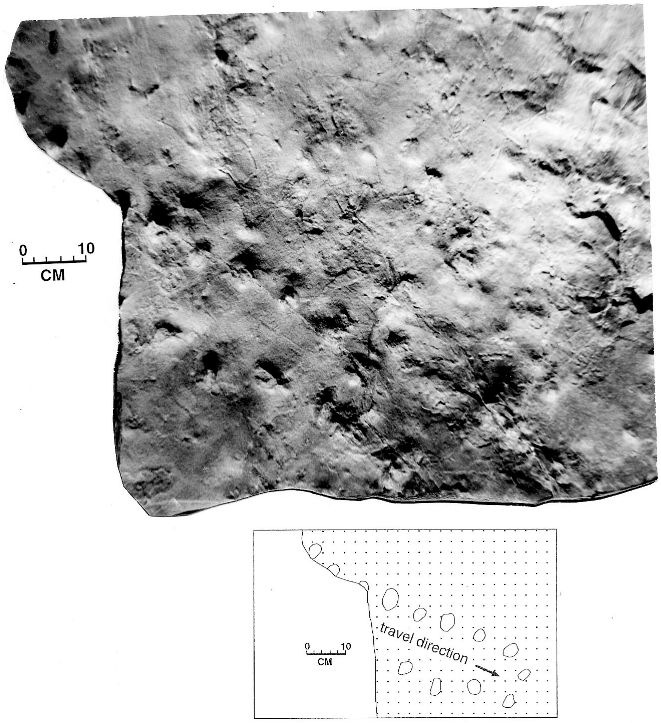

FIGURE 6—Turtle trackway from site KC-1.

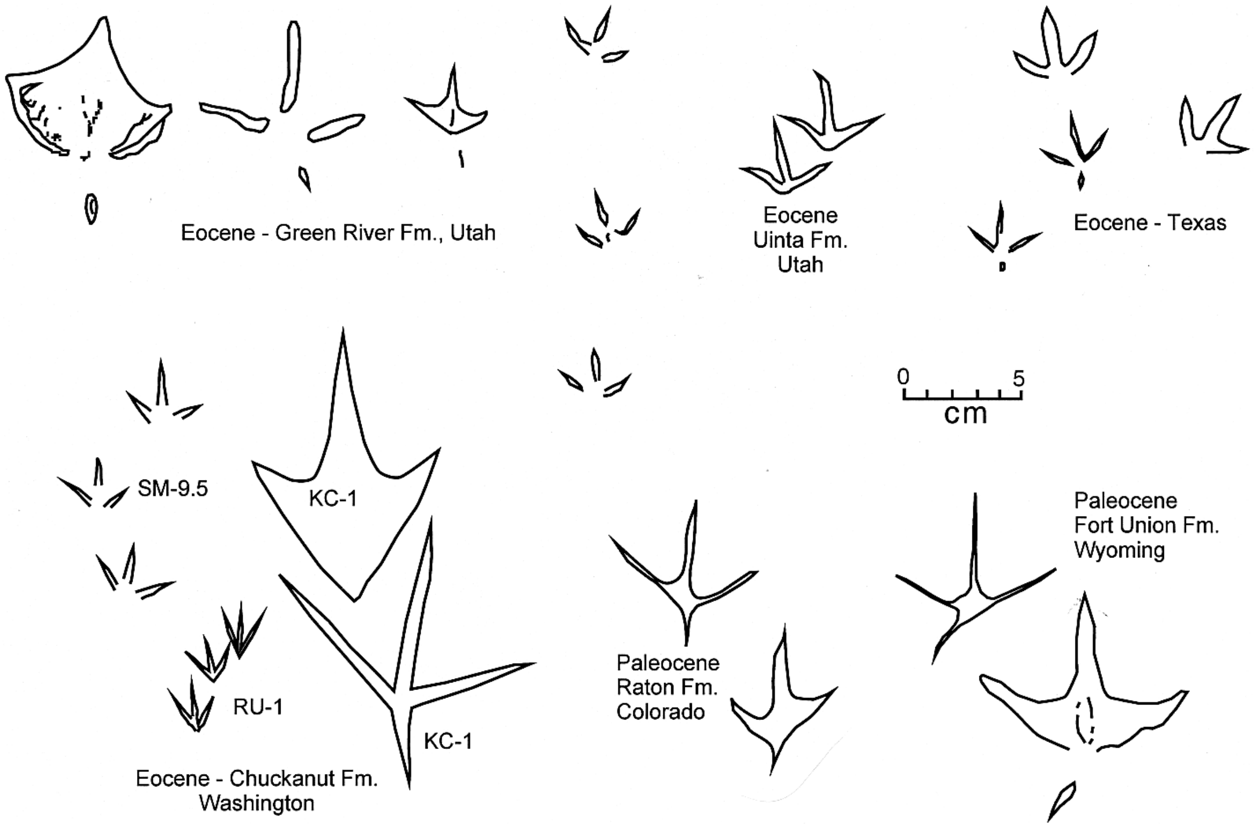

FIGURE 5—Comparison of Chuckanut Formation bird tracks with other North American Paleogene trace fossils. Footprints from Slide Mountain site SM-9.5 resemble tridactyl tracks from the Eocene Green River and Uinta Formations of Utah. Sketches adapted from Sarjeant and Langston (1994) and Lockley and Hunt (1995).

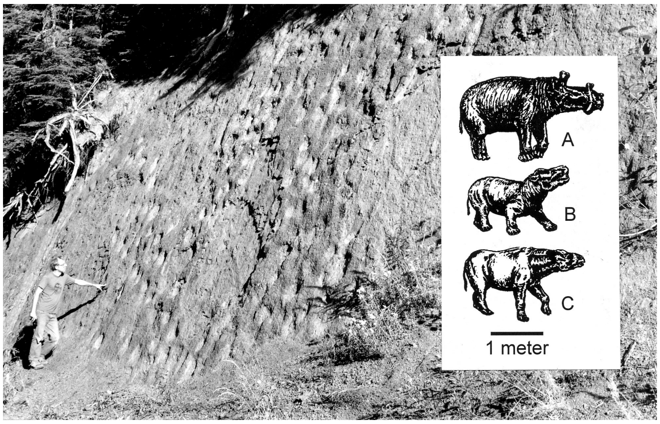

FIGURE 7—Slide Mountain site SM-6.5 reveals more than 200 shallow sub-circular depressions. The indistinct outlines suggest that the features originated as squelch tracks when a herd of animals walked in shallow water. Possible track-makers known from skeletal remains at other Eocene site in western North America include (A), *Eobasileus* (Dinocerata, middle and late Eocene); (B), *Coryphodon* (Pantodonta, early Eocene), and (C), *Palaeosyops* (Dinocerata, middle Eocene). Drawings adapted from Rich et al. (1996).

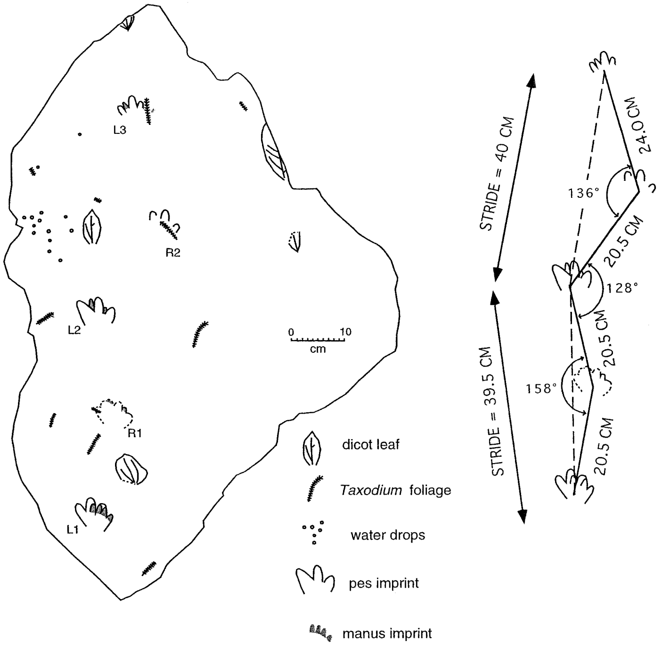

FIGURE 9—Perissodactyl trackway from KC-1 site showing footprint geometry.

ly 200 large mammal tracks, composed of roughly circular depressions 12–18 cm in diameter and 4–6 cm deep. The tracks are dispersed over a single weathered bedding plane of sandy siltstone (Fig. 7). This bed also preserves abundant fragments of a small variety of *Equisetum* (horsetail), indicative of a shallow-water environment. The general form of the tracks suggest that they are "squelch tracks" left by a group of animals traveling in saturated sediment. In a few places the tracks show the path of a single individual (Fig. 8).

Animals that might have produced the large round tracks include members of the Pantodonta or Dinocerata, two extinct orders of herbivores. The best known pantodont is *Coryphodon*, one of the most common early Eocene land mammals of Europe and North America (Cailleux, 1945). The discovery of a cluster of skeletons in New Mexico suggests that these swamp-dwelling animals traveled in herds (Lucas, 1984). The Dinocerata include titanotheres (brontotheres) and uintatheres, both of which were abundant in North America and Asia during the middle and late Eocene. Titanothere fossils from the Clarno Formation of central Oregon (Retallack et al., 1996) and Quesnel, British Columbia (McAnally, 1996) establish their presence in the Northwest approximately when the Chuckanut sediments were deposited.

FIGURE 8—Section of bedding plane at site SM-6.5 showing trackway from a single animal.

Perissodactyl Mammal Tracks

The University of Washington 1993 field party that excavated the Kenney Creek avian trackway also recovered a sandstone slab that contains perissodactyl footprints. At first glance, the trackway appears to consist of five tracks that have anywhere from three to five toes. Close examination reveals that the tracks are composites formed when pes imprints were superimposed upon manus impressions (Fig. 9).

Similar tracks were discovered at an outcrop at Rutsatz Road in 1998 (WWU Site RU-1). Specimens recovered include a slab that contains 5 perissodactyl footprints, as well as the three small avian tracks described earlier in this paper. Smaller specimens preserve individual manus and pes impressions, and three partially overlapping manus tracks (Fig. 10). Plant fossils recovered from the site include palm fronds and a variety of dicot leaves. *Platanus* (Sycamore) and *Sassafras* leaves are among the most com-

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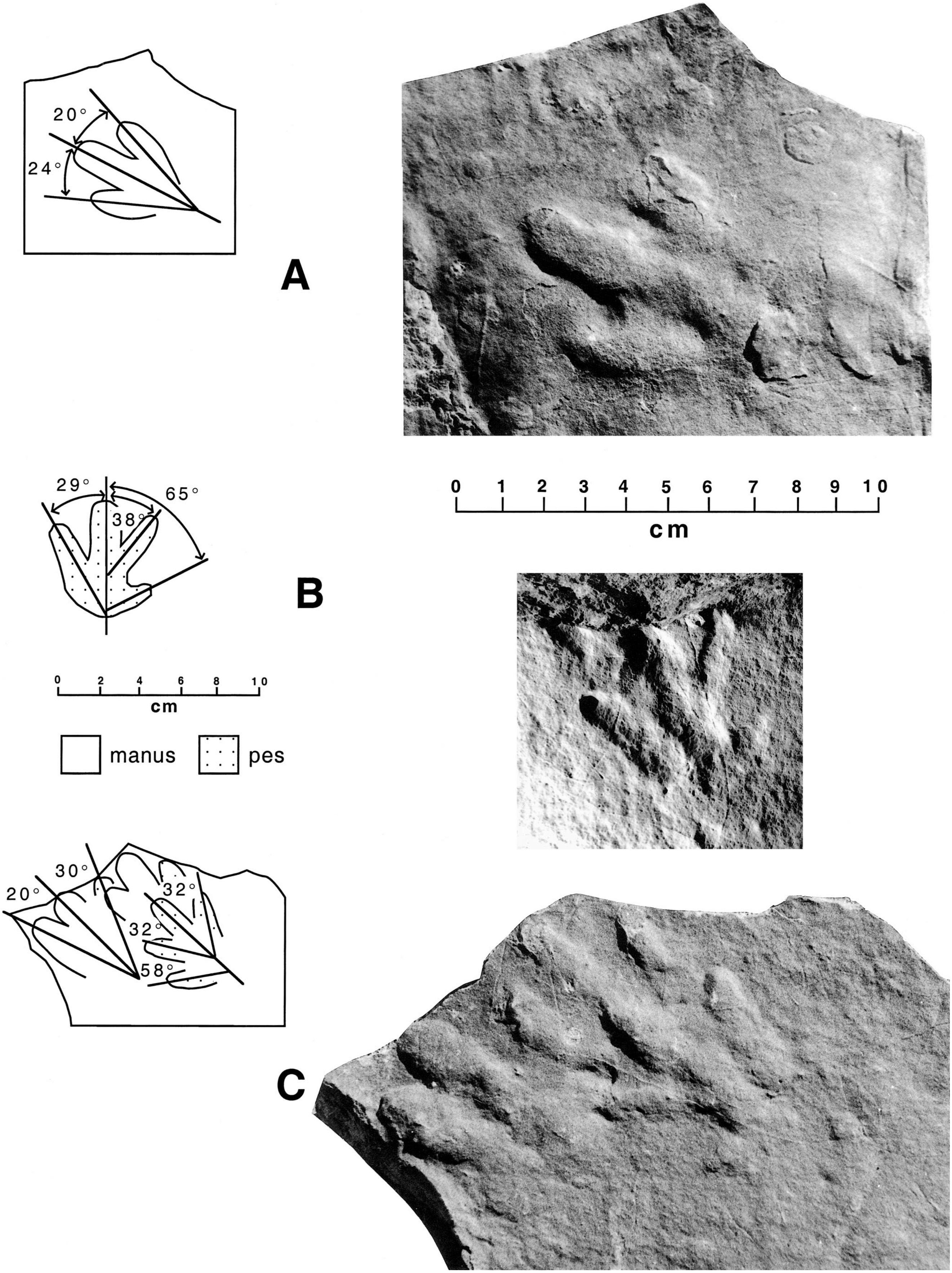
FIGURE 10—Three specimens from site RU-1 showing manus and pes impressions: (A) left pes; (B) left manus; (C) right manus and two partially overlapped pes imprints.



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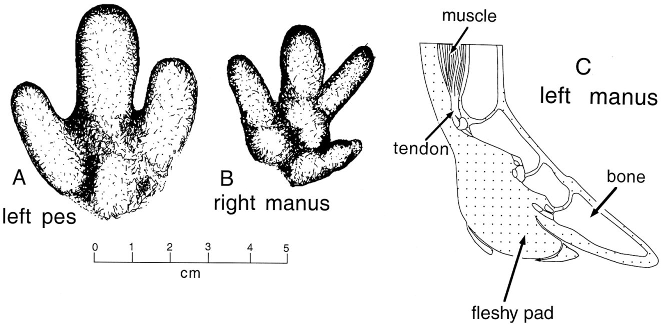

FIGURE 11—Site RU-1 tracks show impressions of fleshy pads (A, B), consistent with earlier interpretations of digitigrade architecture of *Hyracotherium* and other early perissodactyls (C; from Camp and Smith, 1942).

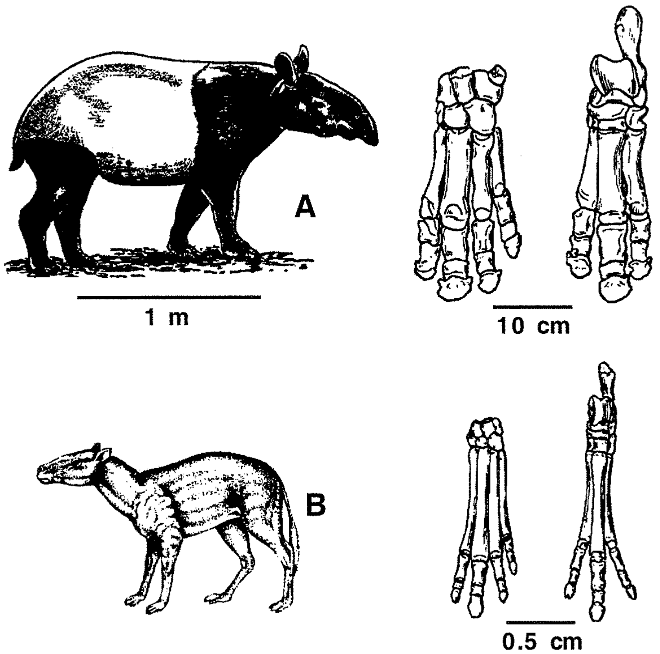

FIGURE 12—Skeletal reconstructions of (A) *Hyracotherium*, and (B) extant *Tapirus indicus* (Malay Tapir) show the tetradactyl manus/tridactyl pes morphology and digitigrade gait characteristic of Chuckanut Formation perissodactyl tracks. Sketches adapted from Tate (1947), Colbert (1955), and McFadden (1992).

mon taxa. *Equisetum* stems buried in growth position are abundant, and nearby sandstone beds enclose *in situ* roots of a large tree. The tracks are preserved in a very thin layer of siltstone interbedded in fine-grained arkose, providing excellent preservation. Several manus and pes tracks show impressions left by fleshy pads, consistent with earlier hypotheses (Camp and Smith, 1942) regarding the foot structure of the first perissodactyls (Fig. 11).

The tetradactyl manus/tridactyl pes pattern is a characteristic of *Phenacodus*, a Paleocene condylarth. However, the middle Eocene age inferred for the Chuckanut Fm. suggests that the tracks were more likely made by an early horse or a tapiroid, two types of animals that also had this foot architecture (Fig. 11).

Hyracotherium was the earliest known member of the Equidae, first appearing during the late Paleocene (Morris, 1968; Jepson and Woodburne, 1969) and flourishing in Europe and North America during the Eocene. The taxonomic status of *Hyracotherium* is uncertain, the genus being a "wastebasket" category that includes several different types of early horses (Hooker, 1989; Prothero and Schoch, 1989; McFadden, 1992). Skeletal remains of hundreds of *Hyracotherium* have been collected from sites in the American West, but no fossil tracks have been found. The Chuckanut tracks are consistent with the architecture of *Hyracotherium* foot bones (Fig. 12). These early horses commonly are described as having a body mass of approximately 10 kg (Radinsky, 1978). McFadden (1987) studied three *Hyracotherium* species and concluded that their weight ranged from 25 to 35 kg, and Gingerich (1989) described a 3–5 kg cat-sized variety. The distance between the manus and pes imprints of the Kenney Creek trackway indicates that the animal had a hip-to-shoulder girdle (glenoacetabular) distance of 37.5 cm, which is within the range of body size estimates for *Hyracotherium*.

An alternate interpretation is that the tracks represent a tapiroid, a group of early ungulates prevalent in North America during the Eocene. The first Tapiroidea in North America was the early Eocene *Homogalax*, a small perissodactyl that had a body mass of approximately 10 kg (Radinsky, 1963). A slightly larger tapiroid, *Heptadon*, became abundant during the middle Eocene (Radinsky, 1965), and by the close of the epoch at least ten tapiroid genera had evolved (Prothero and Schoch, 1989; Schoch, 1989). As with *Hyracotherium*, the size range of tapiroids is great enough to include track-makers of the size required for the Chuckanut tracks. Remains of tapiroids are very rare in post-Eocene deposits, but four species belonging to a single genus still live in Asia and South and Central America.

Indirect evidence suggests that the Chuckanut perissodactyl tracks more likely represent a tapiroid than an equid. The low-crowned teeth of *Hyracotherium* indicate that these animals were browsers rather than grazers. Gingerich (1981) suggested that their appearance in the Rocky Mountain Region during the early Eocene occurred during a time of transition from heavily forested lowlands to a mosaic of open park woodlands and savannas separated by forested zones. These habitats were quite unlike the dense subtropical rain forests of the Chuckanut Formation, a paleoenvironment that resembles locations where tapirs are found today. All extant tapirs have a short, flexible proboscis (Fig. 12A) that aids the in foraging for leaves, tender shoots, and fruit (Janis, 1984). Lowland-dwelling species consume aquatic vegetation; tapirs are good swimmers and fond of splashing in water, wallowing in mud, and seeking refuge in water when threatened (Nowak and Paradiso, 1983). These behaviors would be well-suited for an ungulate inhabiting northwest Washington during the Eocene.

The Chuckanut perissodactyl tracks cannot be described using present categories of ichnotaxonomy. Sarjeant and Langston (1994) proposed the ichnogenus *Apoxypus* for Texas tracks that they thought represented a late Eocene tapiroid, but these footprints are not at all similar to the Chuckanut footprints. Eocene perissodactyl tracks from France were named *Paleotherupus*, implying that they were made by a paleothere, an animal that did not reach North America (Ellenberger, 1980). Other tridactyl tracks from the same locality were placed in the ichnogenus *Lophiopus*, believed by Ellenberger to represent a tapir-

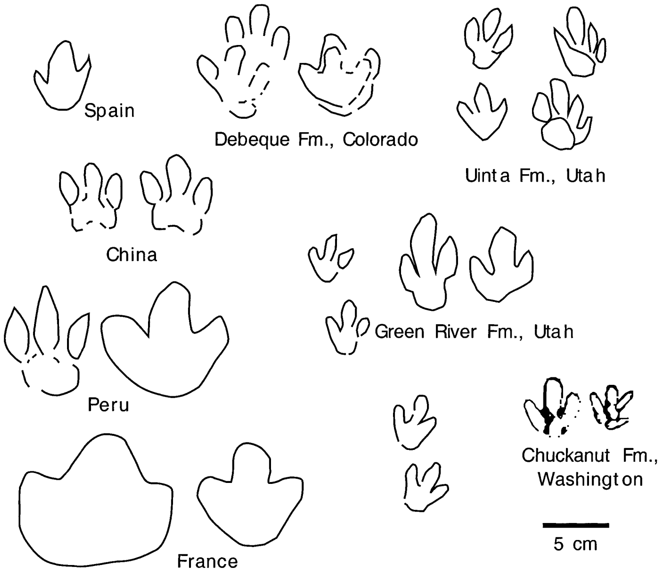

FIGURE 13—Comparison of Chuckanut RU-1 tracks with other Paleogene perissodactyl tracks. Tridactyl pes imprints from the middle Eocene Green River and Uinta Formations resemble the Chuckanut specimens, but the Utah fossils have not been studied in detail. sketches adapted from Lockley and Hunt (1995) and Lockley et al. (1999).

like lophiodontid. Oligocene tridactyl mammal tracks from Spain were named *Plagiolophustipes*, creating a second ichnogenus presumed to represent tracks from a paleothere (Santamaria et al., 1989). None of these perissodactyl ichnogenera are adequate to describe the tetradactyl manus/tridactyl pes tracks from the Chuckanut Formation. Although it is tempting to propose a new ichnogenus to describe these well-preserved tracks, ichnotaxonomy probably is served best by waiting until detailed descriptions are published for similar tracks from other locations (Fig. 13). In particular, tridactyl pes imprints from the Eocene Green River and Uinta Formations of Utah include a form that appears to be very similar to Chuckanut fossils (Moussa, 1968; Greben and Lockley, 1992; Lockley and Hunt, 1995; Lockley et al., 1999).

CONCLUSIONS

Track fossils provide an intriguing snapshot of Eocene vertebrate life in northwest Washington that is not documented by body fossils, but these ichnofossils probably represent only a portion of the vertebrate community. Vertebrates no doubt inhabited other environments, but preservation of the footprints required a combination of circumstances found along the river margin. One requirement was moist, plastic sediment capable of retaining well-defined impressions. Fossilization also required partial drying of the surface to preserve these marks and create an incipient bedding plane, and a subsequent rise in water level that allowed deposition of a protective overlying stratum. Track-makers occupied several quite different ecological niches in the alluvial ecosystem. Turtles and shorebirds both depended on aquatic invertebrates for food, but otherwise led dissimilar lifestyles. Large plantigrade footprints may have been made by bank-dwelling mammals that foraged for aquatic vegetation or consumed streamside plants. Perissodactyl tracks are suggestive of agile forest-dwellers who ventured to the riverbank to graze or frolic. Shorebirds would have provided a food source for raptors, and large carnivores probably preyed on the mammalian track-makers. Perching birds and forest-dwelling herbivores are examples of other creatures whose presence in the Eocene ecosystem were not likely to be documented in the fossil record. Although track fossils in the Chuckanut Formation do not provide a panoramic view of life in the Eocene subtropics, these discoveries are important because they provide evidence of biodiversity within a regional ecosystem that previously has been shrouded in mystery. A student recently brought in a small slab from the Eocene Chumstick Formation in central Washington that preserves a shorebird track much like specimens from Chuckanut Formation site SM-9.5 (Fig. 4), and a perissodactyl pes impression that is similar in geometry to tracks from sites KC-1 and RU-1 (Figs. 9 and 10). This discovery is evidence that the search for vertebrate ichnofossils should be extended to include other Paleogene formations in the Pacific Northwest.

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REFERENCES

AGENBROAD, L.D., 1984, Hot Springs, South Dakota: Entrapment and taphonomy of Columbian Mammoth: *in* Martin, P.S., and Klein, R., eds., Quaternary extinctions: A prehistoric revolution: University of Arizona Press, Tucson, p. 113–127.

ALF, R.M., 1966, Mammal trackways from the Barstow Formation, California: California Academy of Sciences, v. 65, p. 258–264.

ANONYMOUS, 1997, Eocene footprints discovered: Washington Geology, v. 25,4, p. 29.

ARAMAYO, S.A., and DE BIANCO, T.M., 1987, Hallazgo de una ichnofauna continental (Pleistoceno tardío) en la localidad de Pehuenen-Co (partido de Coronel Rosales), Provincia de Buenos Aires, Argentina, Pt. 1, Edentata, Litopterna, Proboscidi. Pt. 2, Carnivora, Artiodactyla y Aves: IV Congress of Latinoamerican Paleontology (Bolivia), v. 1, p. 516–531, p. 532–547.

BJORK, P.R., 1976, Mammalian tracks from the Brule Formation of South Dakota: Proceedings of the South Dakota Academy of Science, v. 55, p. 154–158.

BLAKE, W.P., 1884, The Carson City ichnolites: Science, v. 4, p. 273–276.

BRADY, L.F., and SEFF, P., 1959, "Elephant Hill": Plateau, v. 31, p. 80–82.

BRÄM, H., 1954, Fährten von Wirbeltieren aus der subalpinen Molasse des Bergsturzgebietes von Goldau: Eclogae Geologicae Helvetiae, v. 47, p. 406–417.

Cailleux, A., 1945, *Coryphodon* Europaeus et Americans: Mammalia, v. 9, p. 33–46.
Camp, C.L., and Smith, N., 1942, Phylogeny And functions of the digital ligament of the horse: University of California Memoir 13, p. 69–124.
Casanovas-Cladellas, L., and Santafë-llopis, J.V., 1982, Ichnofauna oligocena de Agramunt (Lérida, Espanä): Acta Geologica Hispanica, v. 17, p. 113–119.
Chaffee, R.G., 1943, Mammal footprints from the White River Oligocene: Notulae Naturae, Academy Natural Sciences of Philadelphia, v. 116, p. 1–13.
Clercq, S.W.G., and Holst, H.K.H., 1971, Footprints of birds and sedimentary structures from the subalpine molasse near Flühli (Canton of Luzern): Eclogae Geologicae Helvetia, Basel, v. 64, p. 63–69.
Colbert, E.H., 1955, Evolution of the Vertebrates: John Wiley, New York, 479 p.
Covacevich, V., and Rich, P.A., 1977, New bird ichnites from Fildes Peninsula, King George Island, West Antarctica: Antarctic Geoscience, 3rd Symposium, Antarctic Geology and Geophysics, p. 245–254.
Curry, H.D., 1941, Mammalian and avian ichnites in Death Valley: Geological Society of America Bulletin, v. 52, p. 1979.
Curry, H.D., 1957, Fossil tracks of Eocene vertebrates, southwestern Uinta Basin, Utah: Intermountain Association of Petroleum Geologists, 8th Annual Field Conference, Guidebook to the Geology of the Uinta Basin, p. 42–47.
Ellenberger, P., 1980, Sur les empreintes des pas des gros mammifers de L'Eocene Superieur de Garrigues-Ste-Eulalie (Gard): Paleovertebrata, Mémoire Jubilé R. Lavocat, Montpellier, p. 37–78.
Erickson, B.R., 1967, Fossil bird tracks from Utah: Museum Observer (St. Paul, MN), v. 5,1, p. 6–12.
Gilmore, C.W., 1928, Fossil footprints from the Fort Union (Paleocene) of Montana: U.S. National Museum Proceedings, v. 74, no. 5, 3 p.
Gingerich, P.D., 1981, Variation, sexual dimorphism, and social structure in the early Eocene horse *Hyracotherium* (Mammalia, Perissodactyla): Paleobiology, v. 7, p. 443–455.
Gingerich, P.D., 1989, Newest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: Composition and diversity in a rarely-sampled high-floodplain assemblage: University of Michigan Papers in Paleontology, v. 28, p. 1–97.
Greben, R., and Lockley, M.G., 1992, Vertebrate tracks from the Green River Formation, eastern Utah: Geological Society of America, Abstracts with Programs, v. 24, p. 16.
Hooker, J.J., 1989, Character polarities in early perissodactyls and their significance for *Hyracotherium* and infraordinal relationships: *in* Prothero, D.R., and Schoch, R.M., eds., The Evolution of Perissodactyls: Oxford University Press, New York, p. 79–101.
Janis, C., 1984, Tapirs as living fossils: *in* Eldridge, N., and Stanley, S.M., eds., Living Fossils: Springer-Verlag, New York, 241 p.
Jepson, G.L., and Woodburne, M.O., 1969, Paleocene hyracothere from Polecat Bench Formation, Wyoming: Science, v. 164, p. 543–547.
Johnson, K.R., 1986, Paleocene bird and amphibian tracks from the lower Fort Union Formation, Bighorn Basin, Wyoming: Contributions to Geology, University of Wyoming, v. 24, p. 1–10.
Johnson, S.Y., 1984a, Stratigraphy, age, and paleogeography of the Eocene Chuckanut Formation, northwest Washington: Canadian Journal of Earth Sciences, v. 21, p. 92–106.
Johnson, S.Y., 1984b, Cyclic fluvial sedimentation in a rapidly-subsiding basin, northwest Washington: Sedimentary Geology, v. 38, p. 361–391.
Johnson, S.Y., 1985, Eocene strike-slip faulting and nonmarine basin formation Washington: *in* Biddle, K.T., and Christie-Blick, N., eds., Strike-slip Deformation, Basin Formation, and Sedimentation: Society of Economic Paleontologists and Mineralogists Special Publication No. 37, p. 283–302.
Kaler, K.L., 1998, Early Miocene trace fossils from southwest Washington: Washington Geology, v. 26,2/3, p. 48–58.
Kordos, L., 1983, Lábynomok az Ipolytarnóci alsó-Miocén koró homokköben: Geologica Hungarica, v. 44–46, 368 p.
Kushlan, J.A., 1985, Herons: *in* Campbell, B., and Lack, E., eds., A Dictionary of Birds: Buteo Books, Shipman, p. 282–284.
Lambrecht, K., 1983, *Urmiornis abeli* n. sp., eine Pliozäne Vogelføärtt aus Persien: Paleobiologica, v. 6, p. 424–425.
Laury, R.L., 1980, Paleoenvironment of a late Quaternary mammoth-bearing sinkhole deposit, Hot Springs, South Dakota: Bulletin of the Biological Sciences of America, v. 91, p. 465–475.
Leaky, M.D., and Harris, J.M., 1987, Laetoili, a Pliocene Site in Northern Tanzania: Clarendon Press, Oxford, 561 p.
Leonardi, G., 1994, Annotated Atlas of South American Tetrapod Footprints (Devonian to Holocene): Publication of the Companhia de Perquisa de Recursos Minerais, Brasilia, 248 p.
Lockley, M., and Hunt, A.P., 1995, Dinosaur Tracks and Other Fossil Footprints of the Western United States: Columbia University Press, New York, 338 p.
Lockley, M.G., Ritts, B.D., and Leonardi, G., 1999, Mammal track assemblages from the early Tertiary of China, Peru, Europe and North America: PALAIOS, v. 14, p. 398–404.
Lozinsky, R.L., and Tedford, R.H., 1991, Geology and paleontology of the Santa Fe Group, southwestern Albuquerque basin, Valencia County, New Mexico: New Mexico Bureau of Mines and Mineral Resources Bulletin, v. 132, p. 1–30.
Lucas, S.G., 1984, Systematics, biostratigraphy, and evolution of Cenozoic *Coryphodon* (Mammalia, Pantodonta): Unpublished PhD Dissertation, Yale University, New Haven, 673 p.
Marche, J.D., Jr., 1986, Extraordinary petrifactions: Footprints at Nevada State Prison: Terra, v. 24,5, p. 12–18.
McAnally, L.M., 1996, Paleogene mammals on land and sea: *in* Ludvigsen, R., ed., Life in Stone, a Natural History of British Columbia's Fossils: University of British Columbia Press, Vancouver, p. 202–211.
McFadden, B.J., 1987, Fossil horses from "Eohippus" (*Hyracotherium*) to *Equus*: scaling, Cope's law, and the evolution of body size: Paleobiology, v. 12, p. 355–369.
McFadden, B.J., 1992, Fossil Horses. Systematics, Paleobiology, and Evolution of the Family Equidae: Cambridge University Press, New York, 369 p.
McNeil, P., Hills, L., Kooyman, B., and Tolman, S., 1999, First reported Canadian proboscidean trackway, probably mammoth, from the St. Mary Reservoir, Alberta, Canada (abstract): 3rd British Columbia Paleontological Symposium, Victoria, p. 51.
Morris, W.J., 1968, A new early Tertiary perissodactyl *Hyracotherium seekinsi*, from Baja, California: Los Angeles County Museum Contributions in Science, v. 151, p. 1–11.
Moussa, M.T., 1968, Fossil tracks from the Green River Formation (Eocene) near Soldier Summit, Utah: Journal of Paleontology, v. 42, p. 1433–1438.
Mustard, P.S., and Rouse, G.E., 1994, Stratigraphy and evolution of Tertiary Georgia Basin and subadjacent Upper Cretaceous sedimentary rocks, southwestern British Columbia and northwestern Washington: *in* Monger, J.W.H., ed., Geology and Geological Hazards of the Vancouver Region, Southwestern British Columbia: Geological Society of Canada Bulletin No. 481, p. 97–169.
Mustoe, G.E., 1993, Eocene bird tracks from the Chuckanut Formation, northwest Washington: Canadian Journal of Earth Sciences, v. 30, p. 987–990.
Mustoe, G.E., and Gannaway, W.L., 1997, Paleogeography and paleontology of the early Tertiary Chuckanut Formation, northwest Washington: Washington Geology, v. 25,3, p. 1–18.
Mustoe, G.E., and Girouard, S.P., Jr., 2001, A fossil trionychid turtle from the early Tertiary Chuckanut Formation of northwestern Washington: Northwest Science, v. 75, p. 211–218.
Mustoe, G.E., and Pevear, D.R., 1983, Vertebrate fossils from the Chuckanut Formation of northwest Washington: Northwest Science, v. 57, p. 119–124.
Nations, J.D., Hevly, D.W., Blinn, D.W. and Landye, J.J., 1981, Paleontology, paleoecology, and depositional history of the Miocene-Pliocene Verde Formation, Yavapai County, Arizona: Arizona Geological Society Digest, v. 13, p. 133–149.
Nininger, H.H., 1941, Hunting prehistoric lion tracks in Arizona: Plateau, v. 14, p. 21–27.
Nixon, D.A., and LaGarry-Guyon, H.E., 1993, New trackway site in the White River Group type section at Toadstool Park, Nebraska:

Paleoecology of an Oligocene braided stream, riparian woodland, and adjacent grassland: Journal of Vertebrate Paleontology, v. 13(supplement to no. 3), p. 50A.

NOWAK, R.M., and PARADISO, J.L., 1983, Walker's mammals of the world, 4th ed.: Johns Hopkins University Press, Baltimore, p. 1163–1165.

ONO, K., 1984, Fossil wading birds from northeast Honshu, Japan: Memoirs of the Natural Science Museum (Tokyo), v. 17, p. 39–46.

PABST, M.B., 1968, The flora of the Chuckanut Formation—the Equisitales, Filicales, and Coniferales: University of California Publications in Geological Sciences, v. 76, 85 p.

PACKARD, E.L., and ALLISON, I.S., 1980, Fossil bear tracks in Lake County, Oregon: Oregon Geology, v. 42, p. 1–2.

PANIN, N., 1965, Coexistence de traces de pas de vertébrés et de mécanoglyphes dans le Molasse Miocèn des Carpates orientales: Revue Roumaine de Géologie, Géophysique, et Géographie, v. 7, p. 141–163.

PANIN, N., and AVRAM, E., 1962, Noe urme de vertebrate in Miocenul Subcarpatilor Ruminestya: Studii si Cercetari de Géologie, Géophyzica, si Géografie, Serie de Géologie, v. 7, p. 455–484.

PEABODY, F.E., 1954, Trackways of an amnystomoid salamander from the Paleocene of Montana: Journal of Paleontology, v. 28, p. 79–83.

PEABODY, F.E., 1959, Trackways of living and fossil salamanders: University of California Publications in Geological Sciences, v. 63, p. 1–72.

PROTHERO, D.R., and SCHOCH, R.M., 1989, Origin and evolution of the perissodactyla: Summary and synthesis: *in* Prothero, D.R., and Schoch, R.M., eds., The Evolution of Perissodactyls: Oxford University Press, New York, p. 504–529.

RADINSKY, L.B., 1963, Origin and early evolution of North American Tapiroidea: Bulletin of the Peabody Museum of Natural History, v. 17, p. 1–106.

RADINSKY, L.B., 1965, Evolution of the tapiroid skeleton from *Heptadon* to *Tapirus*: Bulletin of the Museum of Comparative Zoology, v. 134, p. 308–328.

RADINSKY, L.B., 1978, Evolution of brain size in carnivores and ungulates: American Naturalist, v. 112, p. 815–831.

RAAF, J.F.M., DE BEETS, C., and KORTENBOUT VAN DER SLUIJS, G., 1965, Lower Oligocene bird-tracks from northern Spain: Nature, v. 207, p. 146–148.

REISWIG, K.N., 1982, Palynological differences between the Chuckanut and Huntingdon Formations, northwest Washington: Unpublished M.S. Thesis, Western Washington University, Bellingham, 61 p.

RETALLACK, G.J., BESTLUND, E.A., and FREMDT, T.J., 1996, Reconstruction of Eocene and Oligocene plants and animals of central Oregon: Oregon Geology, v. 58, p. 51–69.

RICH, P.V., RICH, T.H., FENTON, M.A., and FENTON, C.L., 1996, The Fossil Book, A Record of Prehistoric Life: Dover Publications, Garden City, 760 p.

ROBERTSON, G.M., and STERNBERG, G.F., 1942, Fossil mammal tracks in Graham County, Kansas: Transactions of the Kansas Academy of Science, v. 45, p. 258–261.

RUSSELL, L.S., 1930, Early Tertiary mammal tracks from Alberta: Transactions of the Royal Canadian Institute, v. 17, p. 217–221.

SANTAMARIA, R., LOPEZ, G., and CASANOVAS-CLADALLAS, M.L., 1989, Nuevos yacimentos con ichnitas de mamíferos del Oligoceno de los alredoredos de Agramunt (Leida, España). Paleontologia i Evolució: Instituto Paleontològic Dr. M. Crusafont, Dispautació de Barcelona, No. 23, p. 141–152.

SARJEANT, W.A.S., and LANGSTON, W., JR., 1994, Vertebrate footprints and invertebrate traces from the Chadronian (late Eocene) of Trans Pecos, Texas: Texas Memorial Museum Bulletin, v. 36, p. 1–86.

SARJEANT, W.A.S., and WILSON, J.A., 1988, Late Eocene (Duchesnean) mammal footprints from the Skyline Channels of Trans-Pecos, Texas: Texas Journal of Science, v. 40, p. 439–446.

SCRIVNER, P.J., and BOTTTJER, D., 1986, Neogene avian and mammalian tracks from Death Valley National Monument, California; Their context, classification, and preservation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 57, p. 285–331.

SCHOCH, R.M., 1989, A review of the tapiroids: *in* Prothero, D.R., and Schoch, R.M., eds., The Evolution of Perissodactyls: Oxford University Press, New York, p. 298–320.

TATE, G.H.H., 1947, Mammals of Eastern Asia: Macmillan, New York, p. 349–351.

VIALOV, O.S., 1965, Stratigrafiya neogenovix molass Predcarpatskogo probiga: Naukova Dumka (Kiev), Part K, 191 p.

VIALOV, O.S., 1989, Pliocene bird tracks from Iran assigned to the genus *Urmiornis*: Paleontological Journal, v. 23,3, p. 119–121.

WEST, R.M., PANT, T.R., HUTCHINSON, J.R., and CONROY, G.C., 1983, Fossil mammal footprints from the Siwaliks of south-central Asia: Current Science, v. 52, p. 12–16.

WETMORE, A., 1956, Footprint of a bird from the Miocene of Louisiana: Condor, v. 58, p. 389–390.

WOLFE, J.A., 1993, A method of obtaining climatic parameters from leaf assemblages: United States Geological Survey Bulletin 2040, 71 p.

WOLFE, J.A., 1995, Paleoclimatic estimates from Tertiary leaf assemblages: Annual Reviews of Earth and Planetary Sciences, v. 23, p. 119–142.

YOSHIDA, S., 1967, Fossil footprints of birds from the Pliocene Formation in the Mogami Coal Field, Yagama Prefecture: Bulletin of Yamagata University (Natural Science), v. 6, p. 495–500.

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