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GIANT EOCENE BIRD FOOTPRINTS FROM NORTHWEST WASHINGTON, USA

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Abstract. Tridactyl bird footprints preserved in Lower Eocene sandstone of the Chuckanut Formation in Whatcom County, Washington, USA, were made by a species of giant ground bird that walked along the subtropical lowland riverbank. The morphology and age of the tracks suggest the track maker was *Diatryma* (? = *Gastornis*). Although these birds have long been considered to be predators or scavengers, the absence of raptor-like claws supports earlier suggestions that they were herbivores. The Chuckanut tracks are herein named as *Rivavipes giganteus* ichnogenus and ichnospecies nov., inferred to belong to the extinct family Gastornithidae.

Key words: Chuckanut Formation, *Diatryma*, *Gastornis*, ichnofossils.

In 1896, Edward Drinker Cope discovered fossil bones from a giant bird in Lower Eocene rocks in New Mexico, USA, named by him as *Diatryma* (Cope 1896). Twenty-one years later, a nearly complete skeleton was found in Wyoming, USA (Matthew and Granger 1917). Fossil bones from giant ground birds had previously been found at several localities in Europe. The genus name *Gastornis* was established by Prevost (1855) to honour Gaston Planté, the discoverer of the first specimen. North American *Diatryma* is perhaps congeneric with European *Gastornis*, but a careful comparison of type specimens has not yet been done, and as discussed later, we have chosen to retain *Diatryma* as the genus name.

The excitement generated by the discovery of *Gastornis/Diatryma* was amplified by reports of giant bird bones from Argentina (Ameghino 1895; Andrews 1899). Popularly known as 'terror birds', Phorusracids evolved in relative geographic isolation after South America became separated during the late Cretaceous breakup of Gondwana. These birds are divided into three families comprising approximately 25 species (Marshall 2004). By the early Eocene, the southern range of Phorusracids extended as far south as West Antarctica (Case *et al.* 1987). Late Pliocene emergence of the Isthmus of Panama allowed terror birds to migrate to North America (for an evolutionary summary, see Feducca 1999).

Common attributes of both gastornithids and phorusracids include huge bodies, large heads and enormous beaks. Evidence that these anatomical attributes are indicators of carnivore is weaker for the heavy-bodied gastornithids than for the more agile phorusracids, which were top predators in grasslands and open forests of the Cenozoic Era. The common belief that *Diatryma* (? = *Gastornis*) was likewise a carnivore is more a result of guilt by association than actual anatomical evidence. As discussed below, the limb anatomy and beak morphology are very different from phorusracids. The presence of skeletal fossils of small mammal remains in Lower Eocene formations in North America that contain *Diatryma* bones does not necessarily demonstrate predator–prey relationships, only that the various creatures lived together in the same environment. The recent discovery of giant bird tracks in Lower Eocene strata in northwest Washington, USA, sheds new light on this mystery and supports the hypothesis that *Diatryma* was a herbivore whose ecological niche was very different from that of carnivorous terror birds.

GEOLOGY

Early Eocene track fossils have previously been found in Chuckanut Formation strata in the Mount Baker foothills in western Whatcom County, Washington, at sites where large bedding plane surfaces are exposed (Fig. 1). The Chuckanut Formation consists of beds of conglomerate, arkosic sandstone, siltstone and coal that unconformably overlie Palaeozoic and Mesozoic metamorphic basement rocks. These fluvial sediments were deposited on a broad floodplain that existed prior to the mid-tertiary uplift of

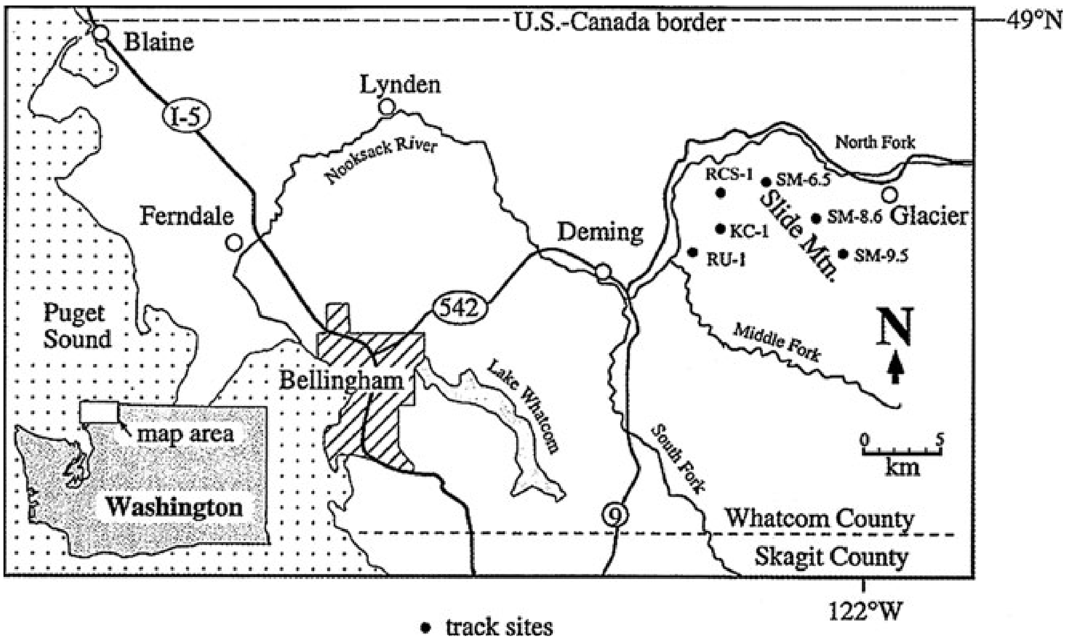

FIG. 1. Chuckanut Formation sites where track fossils have been found. Racehorse Creek landslide = RCS − 1. Adapted from Mustoe (2002).

the North Cascade Range (Johnson 1984*a*, *b*). 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 (Mustoe and Gannaway 1997). Correlative strata also extend north into British Columbia where they are called the Huntingdon Formation (Mustard and Rouse 1994). Estimates of the total thickness of the formation in the main outcrop belt in north-west Washington range from 3000 m (Haugerud 1998) to 8300 m (Mustoe *et al.* 2007).

Evidence for the age of the Chuckanut Formation has come from palaeobotany (Pabst 1968), palynology (Hopkins 1966; Griggs 1970; Reiswig 1982; Breedlovestrout 2011), fission track ages for detrital zircons (Johnson 1984*a*, *b*) and U-Pb ages for interbedded tephra (Breedlovestrout 2011). These data support a Late Palaeocene – Late Eocene age range. The track fossils described in this paper are from a stratigraphic sequence that overlays a tephra horizon with a U-Pb age of 53.676 ± 0.023 Ma (Breedlovestrout 2011). This date is consistent with known occurrences of *Diatryma* skeletal fossils in North America, which have so far been found only in rocks referred to the Wasatchian North American Stage (Eocene; Fig. 2).

SITE DESCRIPTION

The 2009 landslide (Fig. 3) extends over 1 km in length, with an estimated 5×10^5 m^3 of displaced rock distributed over an elevation range of 800 m (Crider *et al.* 2009). Shorebird and mammal tracks in talus blocks scattered over a large part of the slide area include several types of bird and perissodactyl mammal footprints that have been previously described from the Chuckanut Formation (Mustoe 1993, 2002; Mustoe and Gannaway 1997; Mustoe *et al.* 2007). New discoveries that will be described in a later report include tracks from a creodont, a small carnivore, and several types of shore and wading birds. The most spectacular trace fossils are numerous large tridactyl footprints. In rocks of Mesozoic age, tracks of this size and shape would likely be interpreted as having been made by a small dinosaur, but during the Cenozoic Era, the track maker could only have been a giant ground-dwelling bird; we infer the tracks to have been made by *Diatryma* (? = *Gastornis*).

Giant bird tracks have only been found in sandstone slabs scattered along the upper margin of the slide, but the exact bedrock source can not be established. Individual track-bearing blocks are as large as several cubic meters. Tracks are preserved in a thin silty stratum underlain by a massive layer of well-sorted sandstone. Identical characteristics of the matrix for most of the tracks suggest that they were imprinted on a single bedding plane, but lithologic variations on a few slabs suggest that more than one track-bearing surface may have been present. On the basis of general similarities in size and shape, all tracks appear to represent adult birds.

To date, 18 giant bird tracks have been discovered at the site, preserved on 15 landslide blocks. Seven well-preserved tracks are at Western Washington University,

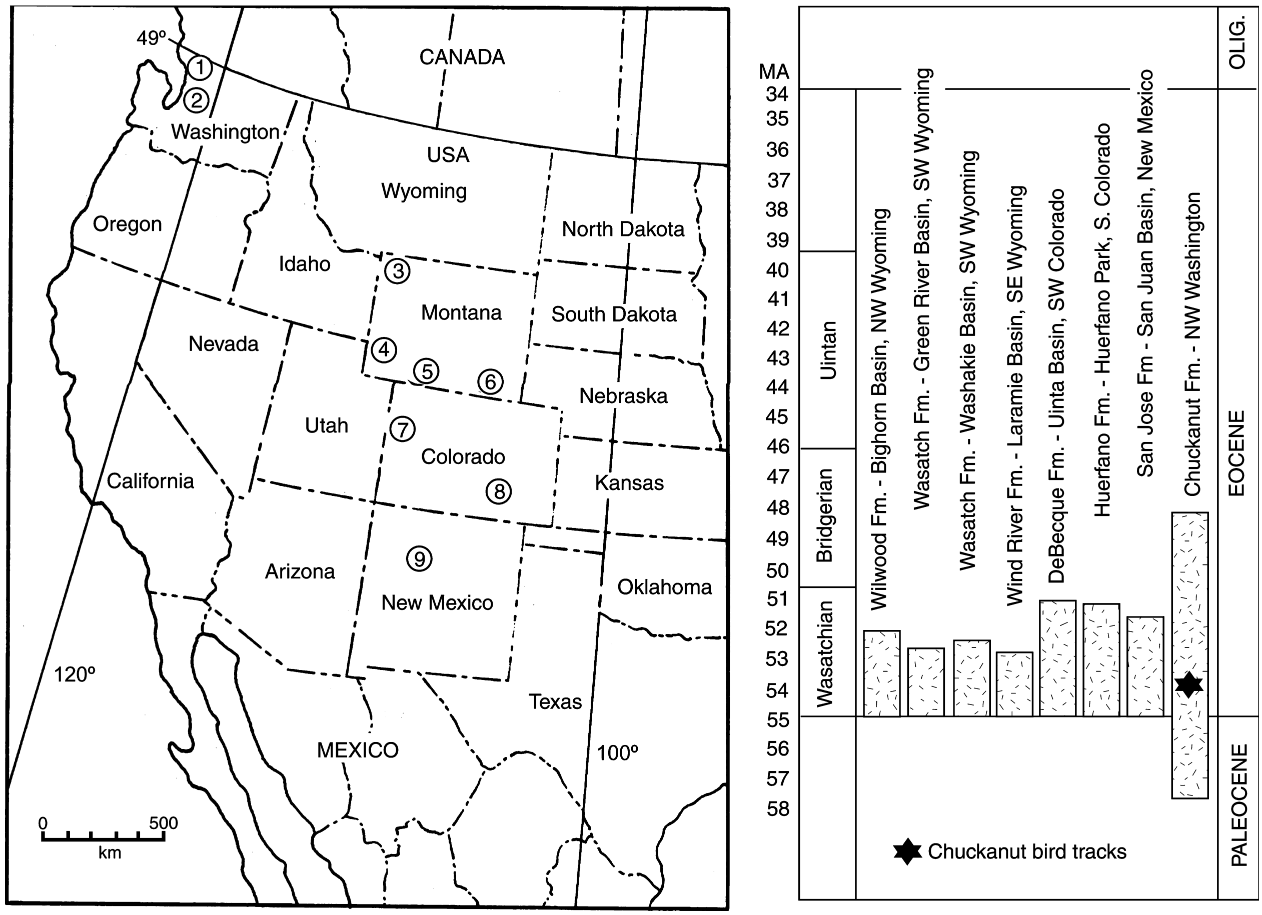

FIG. 2. *Diatryma* occurrences in western North America. Adapted from Andors (1992), using age ranges from Smith *et al.* (2008). 1, Chuckanut Formation, Racehorse landslide; 2, Puget Group, Green River (alleged track); 3, Willwood Formation Bighorn and Clark's Fork Basins; 4, Wasatch Formation, Green River Basin; 5, Wasatch Formation, Washakie Basin; 6, Wind River Formation, Laramie Basin; 7, DeBeque Formation, Uinta or Picea Creek Basin; 8, Huerefano Formation, Huerefano Park; and 9, San Jose Formation, San Juan Basin.

including three that are on public exhibit. Three incomplete specimens are known to be in local private collections; others remain at the site. Silicone moulds have been made from four individual tracks (WWU-TR-059, 067, 068, 072) that were preserved on sandstone blocks too large to transport. Tracks are preserved as either positive or negative footprints, including both single tracks and multiples. When two or more tracks are preserved on the same rock surface, the imprints are typically close together and do not provide an indication of body width or stride length (Figs 4 and 5).

TAXONOMIC CONSIDERATIONS

Chuckanut Formation giant ground bird tracks were probably made by a gastornithid, but because the makers of ancient tracks can seldom be established with certainty, ichnological taxonomy is based on morphotypes. This strategy is particularly an advantage in this case because the taxonomic classification of *Diatryma/Gastornis* remains uncertain.

Andors (1988, 1992) recognized two North American *Diatryma* species, *D. gigantea* Cope 1876 (= *D. steinii* Matthew and Granger 1917) and *D. regens* Marsh 1894 (= *D. ajax* Shufeldt 1913). *Omorhampus storchii* Sinclair (1928) is considered by Andors to be a juvenile stage of *D. gigantea*. As discussed below, *Gastornis*, a giant Eocene ground bird from Europe, has been considered congeneric with *Diatryma*. Over the years, *Diatryma* has been hypothesized to belong to six avian families: Palaeognathae (Cope 1876), Psittaciformes (Andrews 1917), Gruiformes (Matthew and Granger 1917), Anseriformes (Shufeldt 1913) and Ciconiiformes (Troxell 1931). Using cladistic analysis, Andors (1988, 1992) placed *Diatryma* within the order Gastornithiformes, a sister group to the Anseriformes. Mayr (2009) synonymized *Diatryma* with *Gastornis*, but this taxonomic declaration was made without comparative examination of type specimens. Buffetaut (1997*a*, *b*, 2008) had previously suggested that

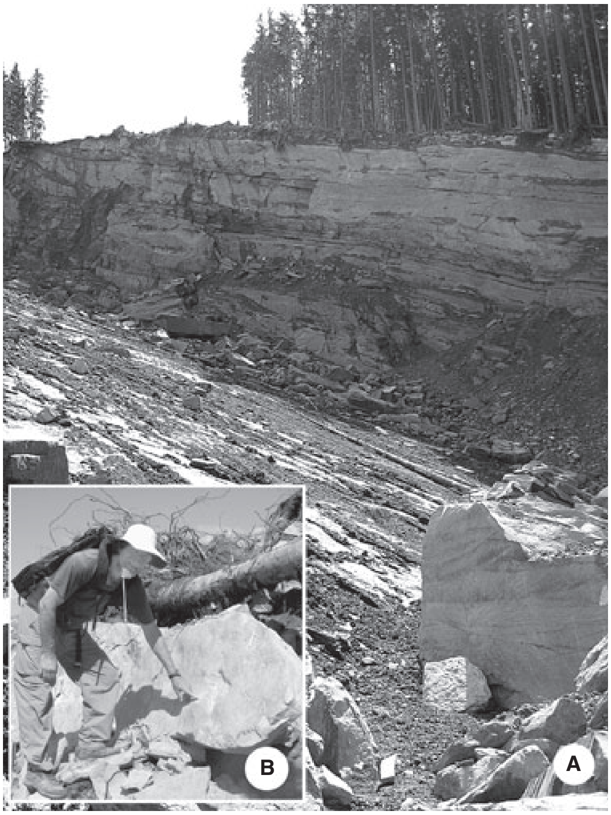

FIG. 3. A, Racehorse Creek landslide. B, K. Kemplin with *Rivavipes giganteus* type specimen, WWU-TR-066, on discovery day, 27 May 2009.

Gastornis and *Diatryma* were congeneric. The Chuckanut tracks offer no new evidence for resolving this taxonomic issue.

SYSTEMATIC PALAEONTOLOGY

Class AVES Linnaeus, 1758
Order GASTORNITHIFORMES Stejneger, 1885
Family GASTORNITHIDAE Fürbringer, 1888 (= DIATRYMIDAE Shufeldt, 1913)

Genus RIVAVIPES ichnogen. nov.

Type species. *Rivavipes giganteus* ichnosp. nov.

Derivation of name. Latin *ripa*, river; avis, bird; *pes*, foot; in reference to footprints from a riverbank-dwelling bird.

Rivavipes giganteus ichnosp. nov.
Figure 6

Holotype. Specimen WWU-TR-066 (Fig. 6).

Paratypes. Specimens WWU-TR-057, WWU-TR-058, supplemented by silicone moulds and plaster replicas for uncollected specimens WWU-TR-059, WWU-TR-067, WWU-TR-068, WWU-TR-072. These type materials are archived at Western Washington University Geology Department, Bellingham, Washington, USA.

Derivation of name. *Giganteus* refers to the large size of the tracks.

Remarks. This terminology shares the etymology of the species name for the North American diatrymid, *D. gigantea* Cope, but there is no certainty that members of this taxon were the track makers.

Type locality. Racehorse Creek landslide, Mount Baker foothills, Whatcom County, Washington. N48°5′, W122°0′, elevation 600 m.

Type horizon. Slide Stratigraphic Member, Chuckanut Formation.

Diagnosis. Large plantigrade tridactyl bird tracks showing robust oval heel pad and three elongate digits. Hallux impression is not present. Phalanges in the shape of elongate triangles, rather than parallel sided. Digit III is elongate relative to digits II and IV, which are approximately equal in length. Heel pad deeper proximally than distally.

Description. Digit I (hallux) impressions are not present. Phalanges are broad, with most footprints showing merging of impressions for the heel pad and digits II–IV. Ungual impressions show the presence of a small triangular claw, but tracks commonly have indistinct digit terminations, as either an acute or a rounded apex. Tridactyl shape typically fairly symmetric. Interdigital angles for digits II–IV are less than 90 degrees.

Track widths measured from apices of digits II and IV are 10–15 cm. Interdigital angles for digits II–III and III–1V are variable, typically between from 32 to 45 degrees. Interdigital angles for digits II–IV range from 60 to 85 degrees. Digits II and IV are approximately equal in length, and approximately 0.8 the length of digit III. For footprints that preserve distinct ungual impressions, digits II–IV each terminate in a small equilaterally triangular toenail.

Dimensions. Measured for nine tracks (Table 1).

Remarks. For extant ground-dwelling birds, the outward digit of each foot may be slightly longer and at a broader angle than the inward digit. Accordingly, as an example, the holotype specimen WWU-TR-066 (Fig. 6) may be a right footprint. In contrast, the three tracks in trackway WWU-TR-058 (Fig. 5) are relatively symmetric. Symmetrical shapes of many tracks make reliable recognition of left and right footprints impossible. Because of

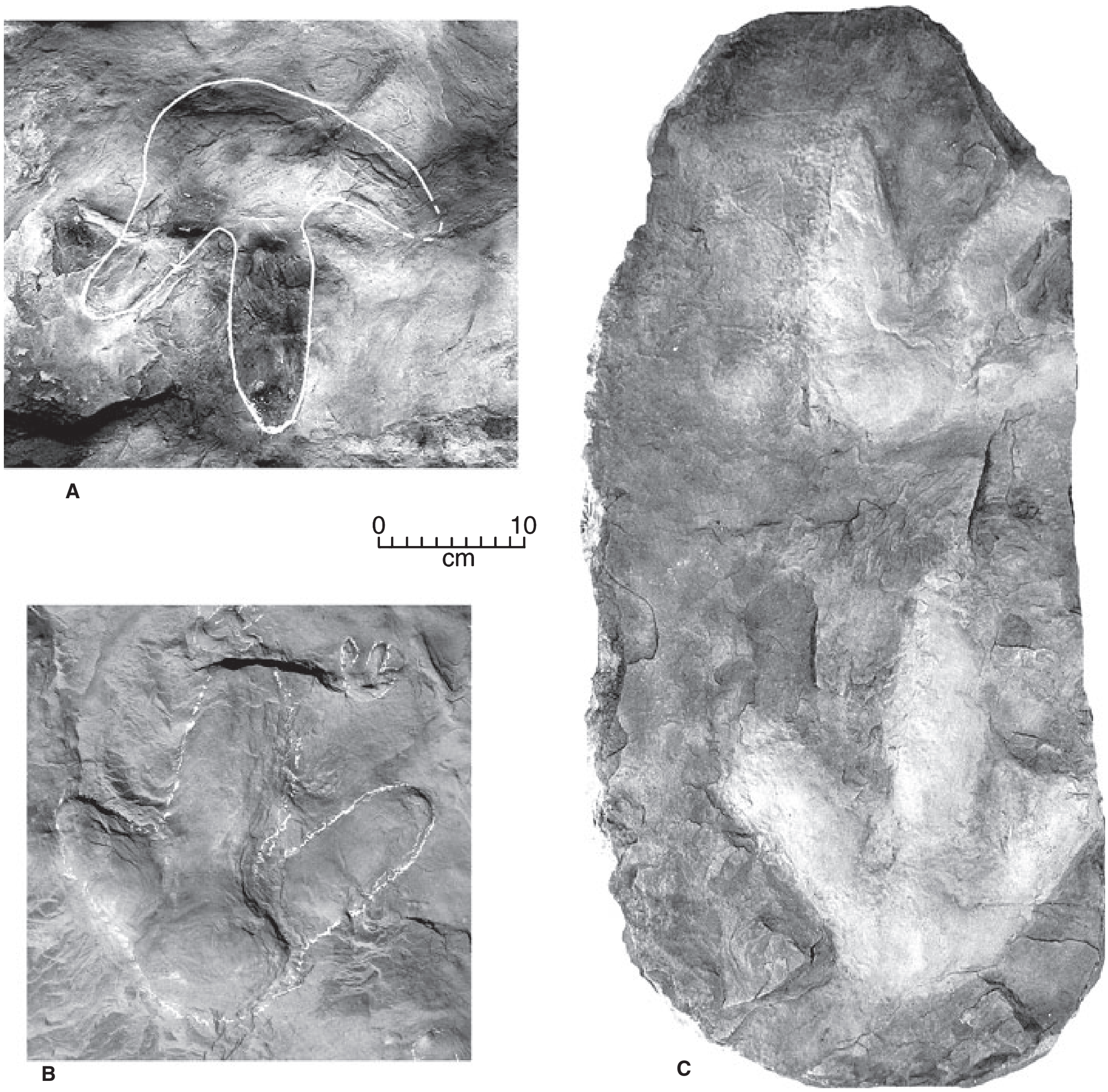

FIG. 4. Three of the best-preserved gastornithid tracks from Racehorse Slide showing plantigrade form and absence of claw impressions and hallux imprints. A, WWU-TR-067; B, WWU-TR-059b; C, WWU-TR-057.

this uncertainty in discriminating between digits II and IV, Table 1 lists interdigital angles as measured for digits left and right relative to the central digit III. Variations in interdigital angles among different specimens suggest that the digits were rather flexible, and footprint shapes may have varied depending on the substrate and the body posture of the track maker; angles measured for an individual track are therefore not a dependable taxonomic characteristic. In the field, deep imprints of the heel pad are the most useful visual characteristic for recognizing these tracks. A small dimple-textured portion of the distal margin of the heel pad imprint of specimen WWU-TR-066 preserves the skin texture (Fig. 6).

DISCUSSION

The Chuckanut Formation giant bird tracks are a noteworthy discovery. Previously described tracks of giant ground birds are limited to early Cenozoic ratite or phorusracid tracks from West Antarctica (Case *et al.* 1987; Covacevich and Rich 1977), Quaternary ratite tracks from New Zealand (Aramayo and Manera de Bianco 1987, 1996) and Holocene moa tracks from New Zealand (Gillies 1872; Williams 1872; Hill 1895). As discussed later, *Ornithiformipes controversus* Patterson and Lockley (2004), a purported *Diatryma* track from Washington, may be either a footprint of some other giant bird or a pseudofossil. Giant tridactyl footprints found in 1859 from Upper

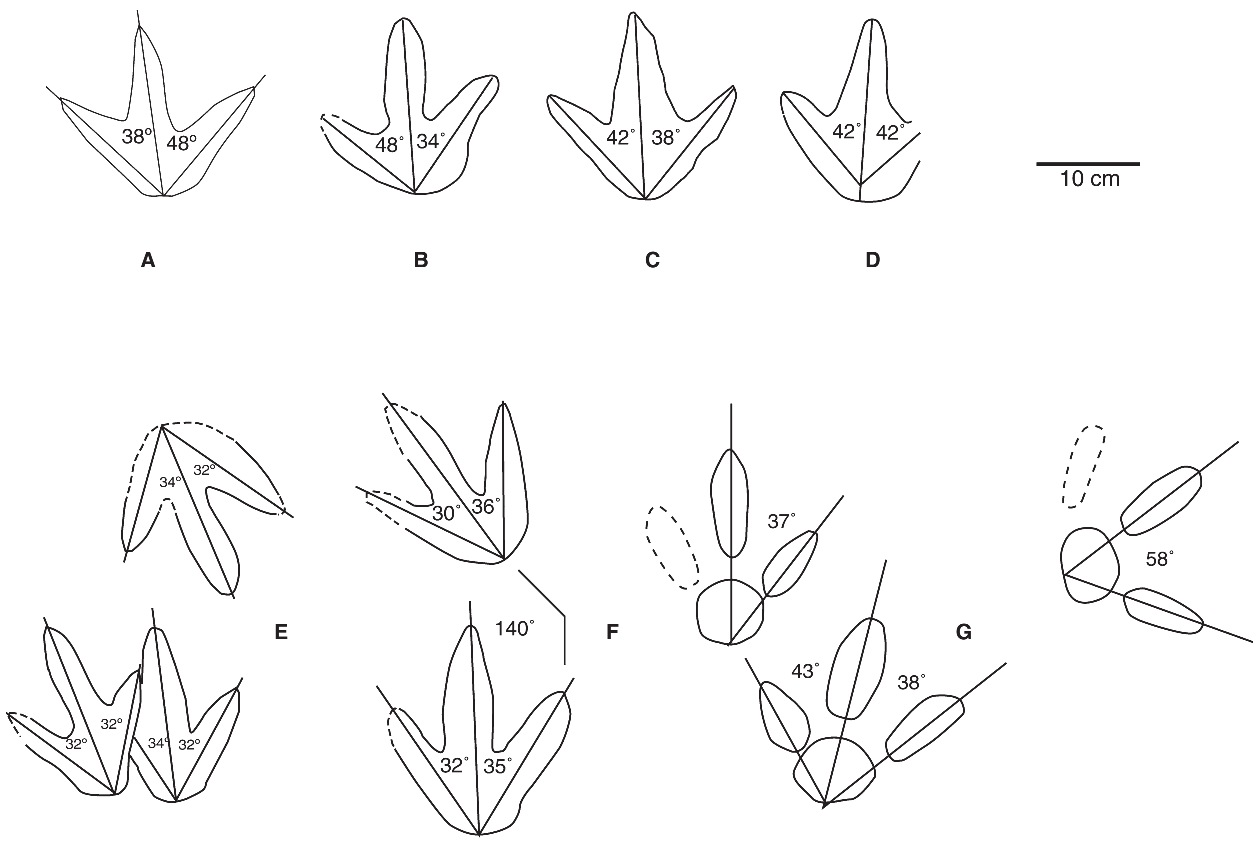

FIG. 5. Outlines and geometric data for single and multiple gastornithid tracks from Racehorse Slide. A, WWU-TR-066; B, WWU-TR-067; C, WWU-TR-068; D, WWU-TR-072; E, WWU-TR-058; F, WWU-TR-057 and G, WWU-TR-059. Multiple track specimens WWU-TR-057, 058 and 059 show closely-spaced footprints that were not made during normal walking, and thus provide no information for determining stride or gait.

Eocene gypsum deposits in the Paris Basin may be evidence of *Gastornis* (? = *Diatryma*), but these specimens were only briefly described (Desnoyers 1859*a*, *b*), and their present location is unknown (Buffetaut 2004).

Habitat: Palaeoenvironment and palaeoclimate

The presence of *Diatryma*-like tracks in Slide Member strata is consistent with known occurrences of skeletal remains, in terms of the early Eocene age, the subtropical rainforest palaeoenvironment and the fluvial depositional setting. Depositional environments for fossil bones from North America (reviewed by Andors 1988, 1995) indicate that *Diatryma* lived in habitats that varied from riparian woodlands, coastal marshes, forested lake margins, coal swamps and relatively open savannas in climates that range from subtropical to warm temperate.

At the Racehorse Slide locality (Fig. 3), trackways are preserved on bedding planes in sandstone that originated as point bar deposits bordering the ancient river. Nearby fine-grained facies originated as overbank deposits; these beds contain abundant subtropical rain forest plant fossils. Three of the most common fossils are *Sabalites* palm fronds, fronds of a tree fern, *Cyathea pinnata* Pabst, and foliage of *Glyptstrobus*, a conifer. More than 30 species of angiosperms are represented by leaf and seed fossils. Mustoe and Gannaway (1997) used the CLAMP multivariate analysis method of Wolfe (1993) to calculate a mean annual temperature (MAT) of 16 degrees and an estimated annual precipitation of 150–250 cm for Slide Member strata. Breedlovestrout (2011) employed the leaf margin analysis method (Wilf 1997) to calculate a MAT of 19.8 degrees for the same fossil assemblage and 21.9 degrees for specimens from a nearby site. The presence of tracks from several species of wading birds and perissodactyl mammals on the same bedding surfaces as the gastornithid tracks is an indication that the giant birds were part of a diverse ecosystem.

Carnivore or herbivore?

The Chuckanut tracks provide evidence of the ecological role of these ground birds. *Diatryma* was initially assumed to be a carnivore because of its large size and prominent

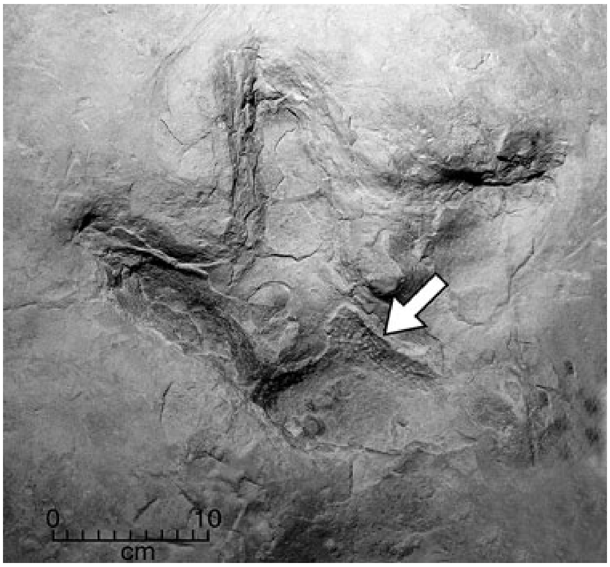

FIG. 6. *Rivavipes giganteus* ichnosp. nov., holotype WWU-TR-066, with arrow showing preservation of heel pad skin imprint.

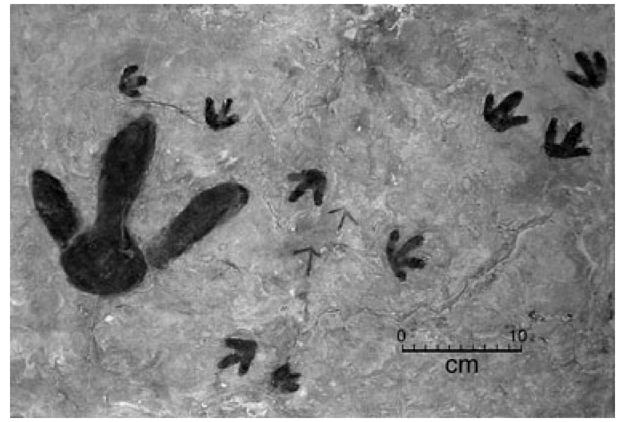

FIG. 7. Track WWU-TR-070 (plaster replica) with perissodactyl mammal and small shorebird tracks. The mammal tracks probably represent an equid (e.g. *Hyracotherium*) or a tapiroid, two groups characterized by three-toed manus and four-toed pes anatomy. Two footprints from a small wading bird are visible near the centre.

beak. The presence of *Hyracotherium* bones in Willwood Formation strata has been suggested as evidence that these small horses were a dietary preference (Witmer and Rose 1991). Several of the Chuckanut Formation giant bird tracks are on slabs that also preserve perissodactyl mammal footprints having a three-toed pes and four-toed manus (Fig. 7). These tracks may have been made by *Hyracotherium* or a small tapiroid (Mustoe 2002). However, the association of footprints is not proof of a predator–prey relationship and may instead simply demonstrate shared habitat preferences.

Witmer and Rose (1991) suggested Diatryma was probably a carnivore or at least a scavenger, with a sturdy skull and mandible that would have been well suited for crushing bones. These authors noted 'Diatryma could have been a gigantic nutcracker, using its immense bill to open gigantic seeds' (Witmer and Rose 1991, p. 109), but they concluded that the large skull appeared to be much larger than necessary for this dietary mode. Watson (1976) asserted that *Diatryma* was primarily a folivore, an interpretation that was presented in much greater detail by Andors (1988, 1991, 1992, 1995). Evidence for herbivory includes a beak that lacks the rostral hook typical of raptors, and hind limb proportions that suggest *Diatryma* was a slow walker rather than a fast runner. These characteristics include the massive, elongate femur, short

TABLE 1. Dimensions and angles for nine tracks.

	WWU-TR-057A	WWU-TR-O57B	WWU-TR-58B	WWU-TR-058C	WWU-TR-059B	WWU-TR-066	WWU-TR-067	WWU-TR-068	WWU-TR-072
Width*, mm	245	225	*c.* 230	*c.* 230	265	280	230	225	Incomplete
Length†, mm	285	262	280	285	245	250	260	285	285
Digit II–IV angle, degrees	66	67	64	66	84	86	82	80	84
Digit III maximum width, mm	48	52	50	48	58	47	50	55	55
Interdigital angles‡, degrees	30, 36	32, 35	32, 32	32, 34	43, 38	48, 38	45, 37	42, 38	42, 42
Length left digit‡, mm	239	210	200	220	190	192	190	200	200
Length right digit‡, mm	*c.* 205	*c.* 200	*c.* 200	Incomplete	222	210	195	228	Incomplete
Heel pad imprint maximum depth, mm	18	18	16	16	15	32	30	22	12

*Width measured as distance between apices of digits II and IV.

†Length measured from proximal margin of heel pad to apex of digit III.

‡Digits II and IV can not be reliably identified based on length or interdigital angle relative to digit III. Measured angles refer to left and right position of digits, as shown in Figure 8.

tarsometatarsus, and short, broad toes. Because leaves are a low-energy food source, they must be eaten in large quantity and require long digestion time. Herbivory is therefore poorly suited for birds that fly, but for ground-dwellers, long retention time, slow energy release and large body size become feasible options.

Andors believed that *Diatryma* possessed a hind toe (hallux) that reached the ground and was fully functional, in contrast to the tracks of extant large ground birds. However, none of the Chuckanut Formation tracks record a hallux impression. The elongate hallux visible in the Wyoming *Diatryma gigantea* skeleton (Fig. 8) appears to have been non-functional for walking, with Chuckanut Formation tracks showing that the robust heel pad prevented this digit from touching the ground.

On the basis of skeletal architecture, Andors (1995, p. 386) concluded that '*Diatryma* seldom ran, but moved typically at a slow stately gait'. The plantigrade Chuckanut Formation footprints suggest slow walking, rather than digitigrade impressions typical of a running biped. In slabs that contain two or more tracks (Fig. 6), the impressions are close together, suggesting leisurely locomotion. *Diatryma* illustrations have commonly shown the bird to have sharp claws, even though evidence from skeletal fossils has not supported this interpretation. The terminal phalanges are short, pointed, slightly curved and lack prominent flexor tubercles. These characteristics suggest that the toes did not terminate in sharp claws suited for capturing prey. Andors (1988) speculated that digits II–IV were broad and hoof-like. Interpretation of foot anatomy has been hindered by the fact that although many toe bones have been collected, none were found in articulation. The sizes and shapes of the Chuckanut Formation tracks resemble the pedal anatomy known for *Diatryma gigantea* (Fig. 8), but the tracks indicate that digits were splayed at broader angles than indicated by the mounted skeleton.

The Chuckanut Formation tracks show a prominent depression left by the fleshy heel pad, which appears to have supported much of the bird's weight. (Figs 5 and 6). The plantigrade form of the tracks suggests that had elongate claws been present, they would have left imprints. Instead, tracks (including type specimen WWU-TR-066) clearly show that digits terminate as short triangular toenails.

Figure 9 shows a reconstruction of *Diatryma* as a gentle herbivore, in a palaeoenvironment that is depicted based on evidence from the sedimentology and palaeobotany of the track-bearing strata.

Relationship of Diatryma *to* Gastornis

We have conservatively chosen to describe the hypothetical track maker as *Diatryma*, the name traditionally used to describe giant bird fossils from North America. *Diatryma* is increasingly being considered to be a junior synonym of *Gastornis*, a name established to describe similar fossils from Europe (Buffetaut 1997*a*, *b*, 2000). Our use of *Diatryma* does not imply that we reject the possibility that *Diatryma* and *Gastornis* are congeneric, only that we await a consensus among palaeoornithologists as to the correct terminology. The close anatomical similarities suggest that European and North American fossils likely belonged to the same family, with Gastornithidae having precedence.

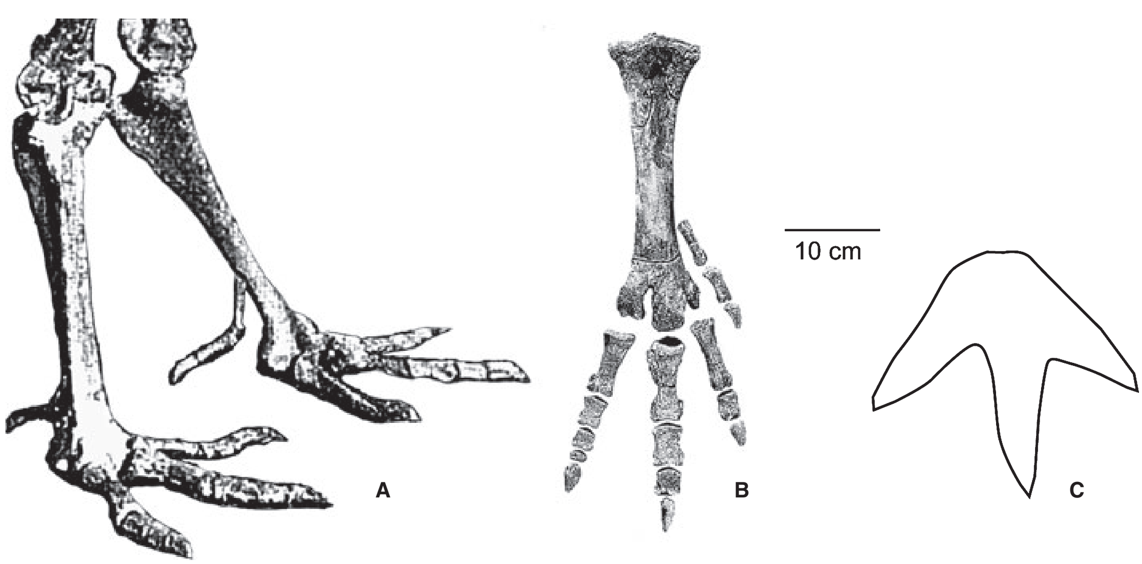

FIG. 8. Foot bones of *Diatryma gigantea* (American Museum of Natural History 6169, adapted from Matthew and Granger (1917): A, assembled skeleton; B, bones prior to mounting; and C, outline of Chuckanut Formation track WWU-TR-066.

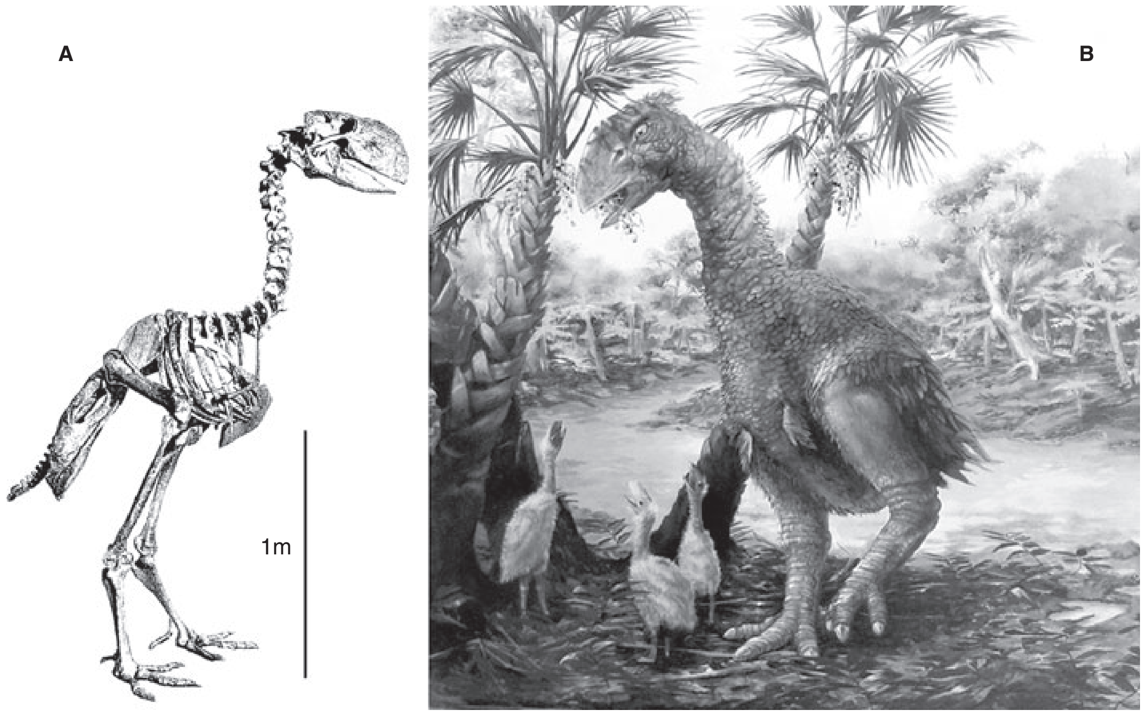

FIG. 9. A, Skeleton of *Diatryma gigantea* (American Museum of Natural History 6169, adapted from Matthew and Granger (1917). B, reconstruction of *Diatryma* in an ancient landscape based on Chuckanut Formation plant fossils and sedimentary rock types, by Marlin Peterson, 2011.

Temporal range of *Gastornis* skeletal remains in Europe is upper middle Palaeocene to Lower Eocene. *Diatryma* fossils from North America are known only from Lower Eocene deposits. Taxonomic uncertainty is evidenced by the past use of both genus names to describe European specimens. Giant ground bird fossils from Europe classified as *Diatryma* include *D. sarasini* Schaub (1928), *D.? cotei* Gaillard (1936), *D.* cf. *steini* Berg (1965) and *D. geiselensis* Fischer (1962, 1978). Other giant bird fossils from Europe have been described as *Gastornis*: *G. parisiensis* Hébert (1855*a*, *b*), *G. edwardsii* Lemoine (1878, 1881) and *G. klaasseni* Newton (1886). *Zhongyuanus xichuanensis* Hou (1980) from China may be a gastornithid. Shell fragments from large eggs from early tertiary sediments in southern France have been suggested as representing *Gastornis/Diatryma* (Mikhailov 1997; Bousquet and Varney-Liaud 2001; Buffetaut 2008).

Andors (1988, 1992) asserted that *Diatryma* and *Gastornis* were closely related, but he believed that detailed taxonomic review of *Gastornis* was needed before possible synonymy could be established. Andors (1988) placed the two ground birds in separate families, Diatrymidae and Gastornithidae. Martin (1983) claimed that *Diatryma* and *Gastornis* could be divided by unspecified tarsometatarsal characteristics. Buffetaut (2008) concluded that small differences in the tibiotarsi were insufficient to justify a separation between the two genera.

Relationship of Chuckanut Formation tracks to Green River ‘Diatryma *track*’

Patterson and Lockley (2004) recount the story of the discovery of a large tridactyl-like impression in late Eocene Puget Group sandstone along the Green River in King County, Washington (Fig. 10). Much controversy has surrounded the issue of whether or not the impression is a footprint or a pseudofossil. Patterson and Lockley attributed the imprint to *Diatryma* or a *Diatryma*-like bird, and named it O*rnithoformipes controversus*. The original specimen was not available to Patterson and Lockley during their investigation, and their taxonomic description was based on a resin cast. The Green River slab (Washington State Parks # 32.19921.1) is presently on display at Western Washington University. Patterson and Lockley (2004) asserted that the impression matched the geometry of *Diatryma* foot bones, but biometric measurements compiled from North American *Diatryma* specimens (Andors 1988, pl. 18, table 13) do not show a close correspondence with the Green River impression. In particular, the length of digits II, III and IV is approximately equal in the purported Green River track, in contrast to the elongate digit III evidenced in *Diatryma* foot bones. The Green River impression is also significantly larger in overall size. Finally, the late Eocene age lies outside the known temporal range of *Diatryma*. These differences can

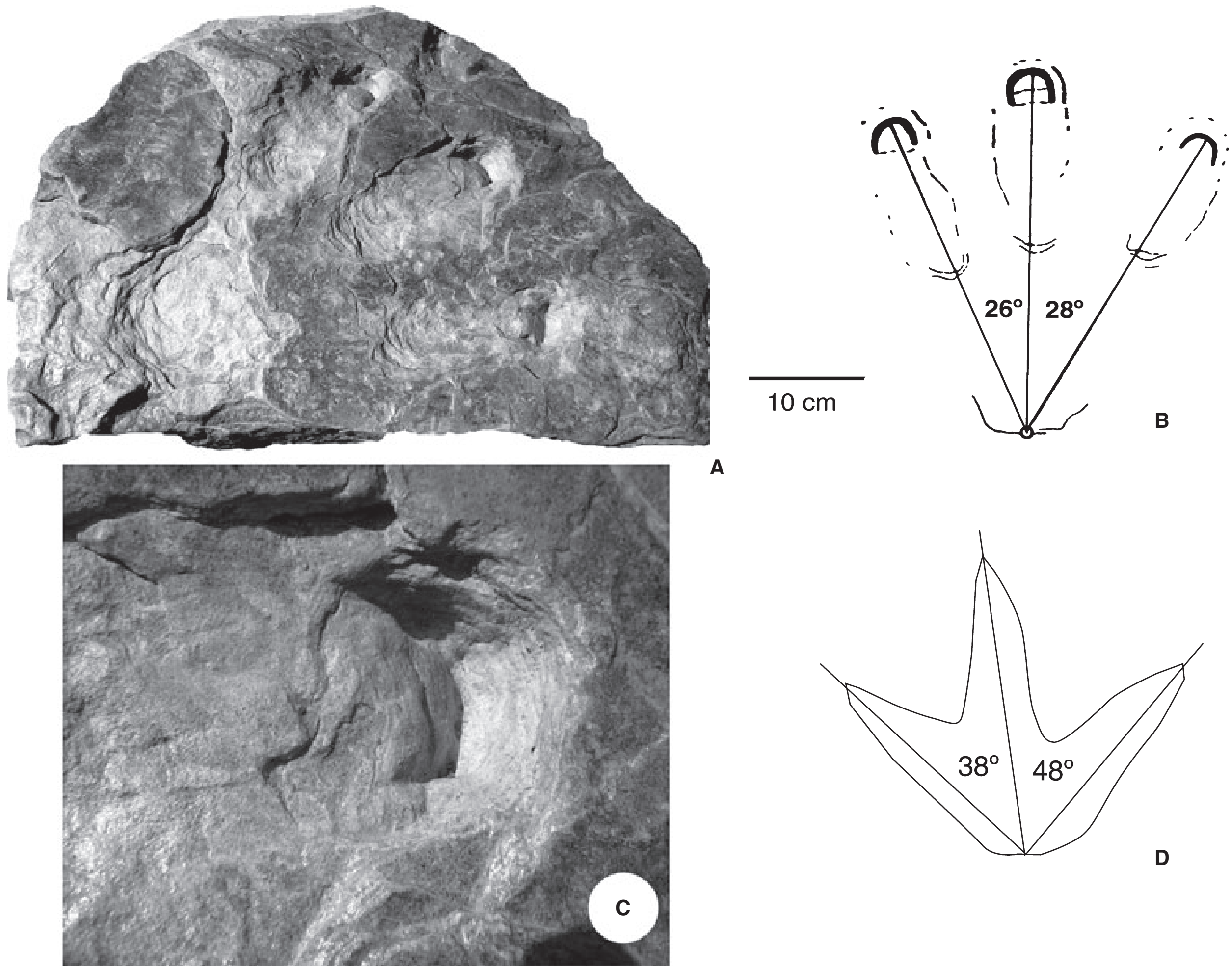

FIG. 10. A, Purported *Diatryma* track from Green River, Washington. B, Sketch adapted from Patterson and Lockley (2004). C, close-up of broad, rounded alleged ungual impression from digit III. D, outline of Chuckanut *Rivavipes giganteus* holotype track WWU-TR-066.

be explained if the impression represents the footprint of some other giant ground bird, one that has not been recognized from skeletal remains. However, the replica used to prepare the taxonomic description did not preserve petrologic characteristics of the matrix. The tridactyl depression lies parallel to bedding, but it is not located on the surface of a bedding plane. Possibly, the shape represents a compressional undertrack produced when a giant bird walked on damp sand. However, depressed areas do not appear to have caused plastic deformation. Instead, the alleged toe and heel pad impressions crosscut thin sedimentary laminae. These characteristics suggest the possibility that the impression is a pseudofossil. Our intention is not to present a detailed analysis of the enigmatic Green River specimen, but instead to assert that if the impression is indeed a footprint, it was not made by *Diatryma*, and that it is not from the same ichnogenus of giant ground bird that produced the Chuckanut Formation tracks. Key differences include overall size, interdigital angles and the shape of the ungual impressions. We have chosen not to use or redefine the *Ornithoformipes* ichnogenus name established by Patterson and Lockley (2004) to describe the Chuckanut tracks because their diagnostic description refers to tridactyl tracks where digits II–IV are subequal in length and the authenticity of the holotype remains controversial.

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